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# The Holism/Reductionism Debate in Ecology: Toward a Middleway Approach

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## Abstract

In this thesis, I first illustrate the nature of the Holism-Reductionism debate in ecology, presenting the historically opposing classical positions. Then, in order to articulate a moderate approach in ecology, I critically analyze the reductionist mechanistic approaches and the modern holistic ecosystem approaches, disclosing their most relevant elements and addressing their virtues and limits. Hence, I concentrate on analyzing the principles and assumptions underlying the moderate approach in ecology, i.e., modern ecosystems ecology, particularly highlighting its reductionist and holistic elements from the perspective of a relational emergentist ontology. I then scrutinize its explanatory prospects in light of the endorsement of two recently developed ecosystems concepts: ascendency and eco-exergy. Finally, I present an empirical example that uses these concepts in order to explain a complex phenomenon of eutrophication. This example substantiates the moderate framework that I articulate and defend, implicating a systemic view of life and showing how systemic interactions, interpreted from the perspective of a relational emergentist ontology, lead to the complex organization and dynamics of ecosystems.

Keywords: Holism, Reductionism, Mechanisms, Emergence, Relationalism

#### <u>Resumo</u>

Na presente tese, começa-se por introduzir alguns problemas associados à ecologia teórica, como o recorrente uso de metáforas e analogias em modelos ecológicos e a questão da possível existência de leis em ecologia, tema que tem suscitado grande discussão sobre as limitações da ecologia enquanto ciência, e até em relação à sua maturidade enquanto disciplina científica, dentro das ciências da vida. Referem-se então as duas grandes perspectivas possíveis na explicação dos fenómenos ecológicos e na resposta às questões levantadas à essência da própria ecologia: a perspectiva mereológica e a perspectiva holológica, perspectivas que dominaram o desenvolvimento teórico da ecologia durante todo o século XX.

No seguimento desta introdução é então descrito, de uma forma mais detalhada, o debate que envolve Holismo e Reducionismo em ecologia, apresentando as respectivas posições clássicas que são historicamente opostas, que tomam a forma de uma oposição entre organicismo e individualismo, respectivamente. São de seguida descritas as assumpções ontológicas, metodológicas e epistemológicas das duas posições, cuja confrontação estruturou o pensamento ecológico moderno, no intuito de preparar a formulação de uma abordagem moderada, putativamente situada entre as duas posições, que seja robusta na explicação dos fenómenos ecológicos. É assim destacado o que opõe as duas posições clássicas, o que, numa primeira análise, as poderia tornar incomensuráveis, mas também o que elas têm de similar e partilham, num modo preparatório para a referida abordagem moderada. É referida a questão das propriedades emergentes dos sistemas ecológicos, propriedades que os sistemas adquirem à medida que a sua complexidade organizacional em níveis aumenta, uma questão que é determinante para o desenvolvimento da tese.

Na posição reducionista, são apresentadas as visões dos ecologistas mais proeminentes, em particular Gleason, cujo trabalho de campo e posterior desenvolvimento teórico tiveram grande impacto numa abordagem reducionista em ecologia. É apresentada uma resenha histórica da evolução da posição reducionista e individualista, que levou ao desenvolvimento de uma abordagem reducionista mecanicista em ecologia, nas últimas décadas, que descreve os fenómenos ecológicos em termos de processos organizados entre partes de um todo que realizam operações específicas e bem definidas, dando então origem ao fenómeno ecológico em estudo. São então descritas e analisadas diferentes abordagens mecanicistas. Em primeiro lugar, é referida a agregação de parâmetros ecológicos, na qual se discute a possibilidade de redução da ecologia de comunidades à ecologia individual através da ecologia de populações. Em segundo lugar, descreve-se, de forma sucinta, a Teoria Metabólica da Ecologia, que propõe uma explicação mecanística para relações alométricas conhecidas entre biomassas e taxas metabólicas. A formulação é baseada na hipótese teórica de que a estrutura e dinâmica das comunidades ecológicas estão inextricavelmente ligadas ao metabolismo individual, no sentido em que as interacções entre os organismos e o ecossistema estão constrangidas por taxas metabólicas, que, por sua vez, dependem de factores como dimensão corporal, temperatura corporal e disponibilidade de recursos - como consequência é expectável que estas interacções expliquem algumas características de níveis ecológicos superiores. Finalmente é analisada a possível contribuição da Nova Filosofia Mecanicista para uma explicação mecanística em ecologia. Tendo em conta a descrição mecanística subjacente, é verificada se esta filosofia consegue capturar o mecanismo que produz um dado fenómeno ecológico, mostrar os componentes biológicos que formam as partes do mecanismo, identificar as relações causais constituintes do mecanismo e estabelecer a sua organização espacial e temporal.

Este estudo e análise destas diferentes abordagens têm como objectivo revelar os elementos mais importantes, quais as unidades ecológicas respectivas e enfatizar as virtudes e os limites de cada abordagem, que possam contribuir para a formulação de uma abordagem moderada em ecologia.

Após o estudo da abordagem reducionista, é analisada, de forma crítica, a posição holística clássica, fazendo-se um pequeno resumo histórico dos trabalhos de Clements e Philips, que posteriormente levaram à ideia do conceito de ecossistema, formulado por Tansley. De seguida, é apresentado o desenvolvimento da abordagem holística moderna em ecologia, com o trabalho pioneiro de Odum e dos primeiros ecologistas de sistemas, com a sua leitura energética e termodinâmica dos ecossistemas, a partir do trabalho de Lindeman e das suas noções de níveis tróficos, e muito influenciada pelo conceito de níveis integrativos, desenvolvido por Feibleman. É também referido o contributo da Teoria de Sistemas e das noções de *feedback* para o estudo do possível carácter cibernético dos ecossistemas. Posteriormente são escrutinadas as hipóteses explanatórias da ecologia moderna de ecossistemas, uma abordagem que é feita à luz de dois conceitos da ecologia de ecossistemas pósclássica, recentemente desenvolvidos por Ulanowicz e Jørgensen, respectivamente: ascendência e ecoexergia. O conceito de eco-exergia surge da aplicação da análise de sistemas em engenharia a partir de uma termodinâmica não conservativa, que estuda sistemas que trabalham longe de um equilíbrio termodinâmico, e que assume que os ecossistemas são estruturas dissipativas com processos irreversíveis, que dependem de um fluxo de energia constante para contrariar a produção de entropia no seu interior. O conceito de ascendência é desenvolvido a partir da aplicação da Teoria da Informação ao estudo dos ecossistemas, que permite analisar os constrangimentos e os graus de liberdade subjacentes ao estado organizacional da rede de interacções que ocorrem num ecossistema. Ambos os conceitos possibilitam um entendimento mais completo sobre o crescimento e o desenvolvimento de um ecossistema, num processo de sucessão ecológica, no qual um ecossistema tem quatro possibilidades para crescer e desenvolver-se: aumentando as suas fronteiras, aumentando a sua biomassa, complexificando a sua rede de interacções e intensificando o seu fluxo de informação. São então destacados os elementos de relevo, desta perspectiva pós-clássica da ecologia de ecossistemas, que contribuem para uma abordagem moderada em ecologia.

A partir deste ponto, em que foram escrutinadas as posições clássicas do Holismo e do Reducionismo em ecologia, e os seus respectivos desenvolvimentos mais recentes, são analisados os princípios e assumpções subjacentes a uma abordagem moderada em ecologia, ou seja, a ecologia de ecossistemas moderna, sendo enfatizados, em particular, os seus elementos reducionísticos e holísticos a partir da perspectiva de uma ontologia emergentista relacional desenvolvida por Santos. É então enfatizada uma perspectiva sobre os ecossistemas na qual estes não podem ser explicados ou determinados pelas propriedades dos componentes que os constituem, no sentido que não pode haver uma redução unilateral ou assimétrica de um sistema ecológico às suas partes, mas em que há inequivocamente uma determinação recíproca entre os níveis ecológicos inferiores e superiores. Explica-se então como é que o todo não pode ser apenas a soma das partes, não sendo assim completamente explicável pelas propriedades intrínsecas das suas partes componentes, e analisa-se como é que os vários níveis de organização ecológica são caracterizados por propriedades novas e específicas de cada nível, as propriedades emergentes, que aumentam o grau de complexidade de um dado nível, em comparação com os níveis que o compõem.

Finalmente é apresentado um exemplo empírico que usa os conceitos de eco-exergia e ascendência com o objectivo de explicar um fenómeno complexo de eutrofização no estuário do rio Mondego, em Portugal. Observa-se, neste exemplo, a aplicação destes conceitos como indicadores ecológicos, que indicam a condição do ecossistema do referido estuário, sendo também propriedades emergentes do ecossistema em causa. Este exemplo substancia a abordagem moderada articulada e defendida na

presente tese, que implica uma visão sistémica da vida e que evidencia como é que interacções sistémicas, interpretadas na perspectiva de uma ontologia emergentista relacional, conduzem à organização complexa e à dinâmica que são inerentes a todos os ecossistemas.

Palavras-chave: Holismo, Reducionismo, Mecanismos, Emergência, Relacionalismo

## **Contents**

Acknowledgments		ii
Abstract		.iii
Resumo		.iv
List of tables and figures		. ix
Abbreviations		x
1. Introduction		1
1.1. Theoretical Ecology and its problems		1
1.2. The Holism Reductionism Debate in Ecology		6
2. The Reductionist Approach in Ecology		9
2.1. The Classical Individualistic-Reductionist Position		9
2.2 The Reductionist Mechanistic Approach in Ecology		16
2.2.1. Aggregation and Reductionism	21	
2.2.2. The Metabolic Theory of Ecology	25	
2.2.3. The New Mechanicist Philosophy and Mechanistic Explanation in Ecology	35	
3. The Holistic Approach in Ecology		39
3.1. The Classical Holistic-Organicist Position		39
3.2. The Modern Holistic Ecosystems Approach in Ecology		46
3.2.1. The Ecosystem Concept in Classical Ecosystems Ecology	46	
3.2.2. The Post-Classical Ecosystems Ecology: Eco-exergy and Ascendency	54	
4. The Moderate Approach in Ecology		71
4.1. An empirical example in modern ecosystems ecology		76
5. Conclusion		79
References		81
Glossary		88
Annex 1 – Mathematical structure of Metabolic Theory of Ecology		97
Annex 2 – Ecosystems as Cybernetic Systems	1	00
Annex 3 – Laws of Thermodynamics and Ecology	1	.05
Annex 4 – Autocatalysis	1	18
Annex 5 – Ascendency	1	.23
Annex 6 – Application of ecological indicators to the Mondego Estuary	1	26

## List of tables and figures

Figure A. 1 Analysis of basic input-output systems and feedback controlled systems104
Figure A. 2 Calculation of exergy of an ecosystem, relative to a reference environment of the same
ecosystem at thermodynamic equilibrium110
Figure A. 3 Hypothetical three-component autocatalytic cycle118
Figure A. 4 Scheme for the Utricularia plant system and its cycle of rewards119
Figure A. 5 Autocatalytic cycle exhibiting centripetality120
Figure A. 6 Successive replacement of components in an autocatalytic loop
Figure A. 7 The emergence of non-mechanical behavior as the scope of observation is enlarged121
Figure A. 8 Schematic representation of the major effects that autocatalysis exerts upon a system 122
Figure A. 9 The different types of exchanges to quantify ecosystem flows network
Figure A. 10 Representation of The Mondego estuary
Figure A. 11 Density and exergy relative of the taxonomic groups for the different simulations in the
Mondego estuary
Figure A. 12 Variation of exergy and specific exergy in comparison with heterogeneity and species
richness along the gradient of eutrophication gradient in the Mondego estuary

Table A. 1 Exergy and plant biomass peak results for the different simulations in Mondego estu	ary 129
Table A. 2 Major contributors to the exergy in the Mondego estuary benthic communities al	long the
gradient of eutrophication	131
Table A. 3 Network analysis ecosystems indices for the three different areas of eutrophicatio	n in the
Mondego estuary	135

## **Abbreviations**

- AMC Average mutual constraint
- AMI Average mutual information
- ELT Ecological Law of Thermodynamics
- $IBM-Individual \ based \ model$
- MI Methodological Individualism
- MTE Metabolic Theory of Ecology
- NMP New Mechanicist Philosophy
- TST Total System Throughput

#### **1. Introduction**

#### 1.1. Theoretical Ecology and its problems

Ecology deals with complex, multilevel, heterogeneous systems that are the products of evolution. Problems arise in defining entities, such as populations, communities, and ecosystems, in testing hypotheses, in operating or clarifying concepts, and in agreeing on standards of explanatory sufficiency (Loehle, 1988). The existence of hierarchies, holism vs. reductionism, and the role of mathematics are strongly debated. I shall argue that philosophy can help to contribute to the solution of these problems using tools such as historical analysis, formal and foundational analysis of theory structure, and conceptual analysis. Thus philosophical analysis can prove beneficial.

Ecology has been criticized for being richer in metaphors than in true general theories, in disanalogy with the physical sciences. However, as I shall show, it is the elaboration of these metaphors that has provided inspiration to guiding research in ecology, especially that of balance-ofnature and the analogy between the development of an organism to maturity and community changes during "succession". In my opinion, the use of analogies – pointing to a resemblance between two different domains –, and metaphors – whereby a linguistic expression is transferred from one domain of application (source domain), where it is common, to another (target domain) in which it is unusual– can enrich one scientific domain (Bailer-Jones, 1992). This transfer serves the purpose of creating a specifically suitable description of aspects of the target domain, where there was no description before or none was judged suitable. Metaphoric expressions are used for descriptive purposes, an epistemic need arising when the two domains between which the transfer occurs can be viewed as related: by similarity of object attributes or by similarity of relationships.

The claim that ecological models are metaphors is tied to the fact that often an analogy is exploited to construct an ecological model, a model being an interpretative description of a phenomenon facilitating access to it. Thus, if ecological models are metaphors, then analogy is an important factor in their construction, as is the case with expressions such as the *balance-of-nature*, *cybernetic ecosystems* and *homeostasis in ecosystems*, concepts that I shall develop in the context of the holistic approach. Metaphors are often construed to be "as-if" devices and hence tend to have no place in a proper scientific description of the world, which pretends to tell things as they are (Bradie, 1999). Metaphors are based on analogies and similarities but, unlike mere comparisons, the metaphors create or induce similarities and analogies (Bailer-Jones, 1992). I believe that metaphors makes us aware of what we were not aware of before, and I tend to agree with Bradie (1992) when he claims that metaphors play a central role in the articulation and development of scientific theories; particularly, Bradie takes the application of a theoretical structure to a set of experiential or experimental data to involve such metaphorical re-descriptions. In brief, metaphors play a crucial mediating role in bringing formal structures to bear on the real world systems we are trying to describe and explain.

However, when one metaphor creates similarity, metaphorical meaning can no longer be viewed as a sheer function of the literal meaning of linguistic expressions belonging to a different domain (Bailer-Jones,1992). Instead, the meanings of the linguistic expressions associated with either domain shift. The meanings of the expressions are extended due to new ideas that are generated when the meanings associated with primary and secondary domain interact. The interaction takes place on account of the metaphor which forces one to consider the old and the new meaning together.

Correspondingly, a shift in meaning can involve change in associated ideas, change in reference and/or change in use. On these grounds, one gets close to dissolving the literal/metaphorical distinction and the two domains become more like each other; they seem to interact and adapt to one another, even to the point of invalidating their original literal descriptions if these are understood in the new, post metaphoric sense (Bailer-Jones, 1992). At this point, the effect of this metaphorical identification between two domains can involve distortions (Bradie, 1999). I suspect that the criticisms advanced against the fact that ecology is excessively metaphorical are related to this latter possibility. My aim is to show that a correct philosophical analysis of the reductionist and holistic approaches to ecology, and their possible metaphor can generate new knowledge by changing relationships between the things designated in different domains.

The discipline of ecology has been described as the new Natural History (McIntosh, 1980) and its intellectual roots are clearly in the broad span of biological insights, most significantly the origins of environmental studies traceable to the beginnings of 19<sup>th</sup> century, which addressed the issue of a "designed" Earth, of environmental influences on humans, and of humans' influence on biosphere. At this time a notion of "designed completeness" ruled environmental studies. The providential order in nature had been expressed under the metaphorical phrase economy-of-nature or balance-of-nature since Antiquity (Egerton, 1973), and during the 20<sup>th</sup> century it was transformed from a divinely ordered nature to an order generated by Nature itself via evolution.<sup>1</sup> Balance-of-Nature concepts apparently have receded in importance with the rise of ecological specialization, probably because ecologists have developed more precise concepts of productivity, ecosystem, or energy flow, which can serve about the same explanatory functions. Nonetheless, I shall argue that the balance-of-nature concept never provided the foundation of ecological approaches, even though it influenced a few of them to some extent. Indeed, as I will relate in section 3.1, organismic ecology was influenced by this concept. This approach is still alive and well, having been transformed into ecosystems ecology, showing that the balance-of-nature concept still provides a powerful metaphor in this discipline, in some cases in merely heuristic terms, while in other cases it is not altogether clear whether the usage is only metaphorical (Simberloff, 1980). Even after the Second World War, ecological organicism still exerted a profound influence on the discipline and "Balance-of-Nature" was an excellent catch phrase, with strong metaphorical content, even though it turned out difficult to transform it into a genuine theoretical asset in ecology. As a matter of fact, many strands of the theoretical debate in current ecology centers on the nature of ecosystem, a concept that could be considered as a lineal descendant of the concept of Balance-of-Nature. Counterparts of the latter concept, such as climax, stability, equilibrium or homeostasis, are very much features of the discussion in current ecology, as well as being used extensively in mathematical models and experimental approaches.

Thus, I believe that it would be important to reassess the value of the concept of Balance-of Nature, even if it has been superseded by contemporary concepts. The reason is that some ecologists still think, often implicitly, in terms of the balance of nature, probably for purely poetic or propagandistic reasons. A better approach might be for ecologists to define the limits of validity of the concept within the context of contemporary ecology. Simberloff (1980) has argued that the reason for the ecosystem paradigm to persist is the resilience of Greek Metaphysics (Egerton, 1973). Simberloff (1980) seems to believe that the main features of ecosystems, such as ecological homeostasis, are conceptualized by systemic ecological approaches as being co-determined by the "interests" of a

<sup>&</sup>lt;sup>1</sup> Egerton (1973) provides a detailed analysis of the concept of the Balance of Nature throughout history, which, he argues, has been a background assumption in Natural History since Antiquity. Egerton also contends that some naturalists and ecologists have postulated somewhat mystical supra-organismic concepts along the same lines.

higher-level ideal entity, in which all parts affect the whole and the whole affects the parts. According to Simberloff, this amounts to appeal to the metaphysics of the Platonic idealists or Aristotelian essentialists. I shall instead argue that we can pursue a completely materialistic approach to ecology, without appeal to idealism, and use the concept of Balance-of- Nature as an important heuristic device in order to do so.

In fact, the first papers on ecology were a statement in favor of the concept of Balance-of-Nature, simultaneously reflecting the influence of Darwinism and the then forming concept of *community*. Darwinism provided the conceptual means to transfer the causes of the balance-of-nature from Divine Providence to natural selection. For instance, Forbes, a founder of aquatic ecosystem science and a dominant figure in the rise of American ecology in the 19<sup>th</sup> century, deduced from evolutionary principles that ecological phenomena promote an ideal balance of nature in the form of the highest good for all species (Forbes, 1887). For Forbes, the balance of nature maintains each species' population size within the limits of a uniform average number, as a consequence tending to maintain life at the highest limit of production.<sup>2</sup>

Perhaps the earliest and most significant general phenomenon observed by plant ecologists, interpreted from the vantage point of the balance-of-nature, was the organization of plants into vegetation entities known as *formations*. Analogously, animal ecologists also came to recognize the importance of ecological *communities*. Thus, ecologists started to study the process of change in communities, trying to comprehend how the balance was achieved. There was an effort to study laws which govern change and dynamics. As a consequence, the concept of succession – which will be explained in section 3.1 – became the standard descriptive tool for explaining change in ecology.

Despite relative success, some ecologists complained about the intellectual immaturity of their discipline at this time (Hagen, 1989). Many interesting questions about ecology were posed, trying to understand what made it different from emerging disciplines like genetics or biochemistry. It was in trying to tackle these questions that two basic alternative approaches arose in ecological research (Hagen, 1989): the *mereological perspective*, which focuses upon populations of independent organisms and is based on the assumption that individual and population phenomena determine the properties of higher levels of ecological organization; the *holological perspective*, which focuses upon the flow of materials and energy through ecosystems without considering the individual organisms that are constituents of the system. The crucial debate between these two approaches concerns the nature of the unit of ecological analysis, by reference to which the most accurate explanations and predictions result. This is an issue on which the reductionist and holistic approaches thoroughly disagree, as I shall articulate in the following sections.

Hagen (1989) argues that these two approaches actually reflect two broad intellectual perspectives and that it is their very existence that is largely responsible for the apparent intellectual immaturity of ecology. However, I shall argue, following Hagen, that they are not incommensurable worldviews and that they can complement and enrich each other. This is the issue that I shall explore more deeply in the next section, trying to give a detailed overview concerning the classical holism-reductionism debate in ecology.

Another standing problem in ecology concerns the nature of valid scientific explanation. Because of the complexity of ecological systems, the nature of adequate explanation becomes a pivotal issue in the debate, within which an important element is whether there are *ecological laws* 

 $<sup>^{2}</sup>$  Forbes (1887, pp. 549) argues that there is a *community of interest* whose common interest is promoted by the process of natural selection.

(McIntosh 1980; Loehle, 1988). Some authors argue that there are not and that useful research should focus on making predictions, others argue that ecology explains particulars rather than deriving universal laws. According to some ecologists, even if there were some laws in ecology, they would not be precise, and this lack of precision has prompted many ecologists to deny the existence of laws and call those statements *generalizations*.<sup>3</sup> Calling such statements generalizations rather than laws implies that they are not universally true or constraining but that they merely represent *trends*. Concerning explanation in ecology, it is also important to identify the level at which explanation is sought; this is because a certain phenomenon might be explained in terms of controlling or driving forces at a higher level, while another phenomenon might be explained in terms of components at a lower level. As I shall relate below, it is also useful to distinguish between phenomenological and mechanistic explanations. And, as will become conspicuous in section 3.1, on the issue of "Succession", it is also important to distinguish between phenomenological explanations is a common historical explanation in ecology.

Ecology, like biology more generally, has been often criticized, by mathematicians and physicists, for its lack of a sound theoretical approach (McIntosh, 1980). These critics have thus urged ecologists to develop ecology as a theoretical and mathematical science. According to these critics, when a theory is sufficiently precise, logical or formal analysis of theory structure can be very informative. Given a theory, the process of deriving predictions from the model is often a cause for concern. Explicit mathematical formulations are less problematic, but typical theories in ecology are verbal or semi-quantitative. Thus, a common complaint about inadequate explanation in ecology involves the inaccuracy of mathematical models. Within such models, predictions that are not logically implied by the theory are easily derived, often exceeding the theory's scope, as well as predictions that involve unstated auxiliary assumptions or boundary conditions. Therefore, a careful formal analysis of the predictive apparatus can be helpful.

A broad debate on whether ecology is a law–governed science at all has unsurprisingly ensued. Although this ecological debate is not the main topic of this thesis, the debate is nevertheless relevant. The reason is that Hempel's covering law account (Hempel, 1948, 1965) suggests an influential and relevant epistemological solution to this debate, namely that it is the function of laws to furnish us with scientific explanations. According to the covering-law account, a phenomenon is explained and predicted by subsuming it under general laws, thereby showing that the phenomenon occurred in accordance with or followed from the operation of those laws. Without this justification, it is difficult to understand why ecologists are engaged in the laws debate, given that there do not appear to be many ecological laws. Thus, I believe that the laws debate is understandable within the context set by the covering law account, according to which laws are necessary or indispensable for scientific explanations. Some of the candidate laws include allometries, scaling and some equations in population dynamics, which will be relevant for the discussion of the reductionist mechanistic approach in ecology, in section 2.2. In my opinion, the case against the existence of laws in ecology is based on some common misconceptions about what laws of nature are and about the role they play in the physical sciences.

Some authors have tried to clear up these misconceptions about laws in ecology (Lawton, 1999; Colyvan, 2003; Lange, 2005). According to Colyvan (2003), the first misconception about laws

<sup>&</sup>lt;sup>3</sup> Loehle (1988, pp. 101) gives examples of truly ecological laws, which, for some ecologists, are not precise in the sense of a physical law, even if he considers that they are always and universally true in the sense of forbidding certain phenomena from happening.

is that they must be *exceptionless*.<sup>4</sup> According to this author, something like an idealization is needed, in the sense that laws of nature describe the dispositions physical systems have to behave in certain ways in these idealized setups, and that idealizations are important for the articulation and understanding of putatively exceptionless laws of nature. Even in physics one can find exceptions to laws: for example, Galileo's law that all massive bodies must fall with constant acceleration irrespective of their mass has to accept the exceptions of hailstones or snowflakes, which fall with different accelerations; or, in another classical example, a collision of two billiard balls, in which the kinetic energy of the system, after the collision, is slightly less than before the collision, an outcome at odds with the law of conservation of kinetic energy in a closed system. We have here good examples of idealized situations in physics: frictionless collisions, perfect elastic collisions and a two body system. In fact, idealizations are essential for our understanding of laws of nature.

Another misconception is that laws *should make precise predictions*, or that laws should be falsifiable, in the Popperian sense (Colyvan, 2003); the point is that a single law typically does not make specific predictions on its own, because a great deal of extra theory and information about initial conditions are required to make predictions. Thus, for instance, while Newtonian gravitational theory makes some really precise predictions, for example about Halley's comet trajectory, it makes much poorer predictions about the trajectories of asteroids in a belt, because we need a huge amount of information in case numerous objects interact. I do not deny that predictive power is an epistemic virtue in the case of a law; however, we can think about other virtues, such as simplicity or elegance.

The final misconception is that laws *cannot be mere regularities*. According to this line of thought, laws must distinguish cause and effect, or determine whether both events are the result of a common cause (Colyvan, 2003). However, it is not clear, for example, if there is any role for causation in our most fundamental physics: quantum mechanics. The author also thinks that the suggestion that laws, and not mere regularities, are explanatory is difficult to sustain, because explanation must end somewhere, and typically it ends with reference to the laws of nature. But, according to Colyvan, in a very important sense, such laws do not explain anything as they merely state the fundamental assumptions of the theory. Thus, it seems that fundamental laws need not to be explanatory but, rather, that they are an appropriate place for explanation to stop, making them, ultimately, not explanatory. Following Colyvan, I would argue that one should not expect laws to be exceptionless, to be always predictive, and to be explanatory: these cannot be necessary conditions to be a law.

The case for laws in ecology is thought to be weaker, compared to other parts of biology, since ecology lacks an embracing and widely-accepted explanatory theory such as Darwinism. It seems that the great deal of the dissatisfaction with the candidate laws in ecology is that they are not exceptionless (Lawton, 1999; Colyvan, 2003, Lange, 2005). Most laws in ecology are inaccurate in the sense that they have many exceptions or that they only hold approximately, as I shall show when discussing the cases of allometry and scaling in section 2.2.2. However, even in physics, as showed above, approximations and simplifications are used, with the implication that laws need not to completely explain the relationships they describe. Therefore, I believe that both ecology and physics have laws that typically have exceptions, that are not necessarily explanatory, that may not be predictive, and that often invoke idealized situations.

According to Robert McIntosh (1980), ecologists never worried about their own theories (meant as well-defined sets of explanatory propositions), generally abstracted from aspects concerning

<sup>&</sup>lt;sup>4</sup> Colyvan (2003, pp. 650) claims that the exceptionlessness requirement is too strong, and that if we require laws to be exceptionless, there are no, or very few, laws, even in physics. He refers to the work of some philosophers of science, such as van Fraassen and Nancy Cartwright, who have been somewhat deflationary about the role of laws in physics.

their historical development, and had never developed a hypothetico-deductive philosophy according to the tenet of logical positivism. This would have been a step towards recognizing the legitimacy of epistemological issues concerning internal theory structure within a hypothetico-deductive frame, and the use of a variety of modeling assumptions and definitions from which deductions might be derived. In fact, positivism was supplanted in the 1970s by the "historicist turn", which includes the development of a theory in its appraisal. However, few ecologists are adept of the task of historians of their own discipline and many are substantially ignorant about the history of ecology; accordingly, they are not able to incorporate a historical overview of ecology in their research (McIntosh, 1980).

Nevertheless, even if ecologists are not worried about constructing a robust explanatory body about their domain, according to the standards of logical positivism such as that of physics, they assume *general* laws, recognizing that ecology has rather few *universal* laws (Lawton, 1999; Colyvan, 2003). Ecologists seek regular patterns in nature; however, they do not try to subsume these patterns, linking them to a body of theoretical explanations (Lawton, 1996). However, I think that, although ecology has not universal laws, it captures widely *observable tendencies*, that is, lawful generalizations that cannot simply be derived from first principles. Arguably, there are some lawful generalizations underpinning all ecological systems, in the form of a set of general physical principles (Lawton, 1999): the first and the second law of thermodynamics; the rules of stoichiometry, which refers to the quantities, proportions or ratios of chemical elements composing different entities, such as organisms or their environments; Darwin's law of natural selection as an explanation for evolution; the set of general physical principles that govern all the physiology of organisms, as well as the diffusion and transport of chemical elements; and the trivial observation that organisms interact with one another and with their environment.

These lawful generalizations and the ecological general laws will become prominent in the following sections, for articulating the discussion concerning the nature of explanation and prediction of ecological phenomena, the dialectic relation between wholes and parts and the relevant unit of ecological analysis according to, respectively, the reductionist or holistic approach.

#### 1.2. The Holism Reductionism Debate in Ecology

The philosophical debates that have accompanied the development of science have often been expressed in terms of dichotomous choices between opposing viewpoints about the structure of nature, the explanation of natural processes and the appropriate methods for research.

We can ask if the different levels of organization<sup>5</sup> such as the atomic, the molecular, the cellular, the organismal, the species, and community level are only the epiphenomena of underlying physical processes or whether the levels are ontologically separated by real discontinuities. Or, put differently, if the objects at one level are fundamentally similar despite apparent differences, or whether there is only one basic ontological level despite the seeming similarities between objects at different levels.

The holism-reductionism controversy in ecology is about the relationship between wholes and their parts (Lewontin *et al*, 1980; Bergandi, 2011; Trepl *et al*, 2011). The contrast between reductionism and holism in ecology tends to take the form of an opposition between *individualism* and

 $<sup>^{5}</sup>$  I shall refer to the different levels of organization in ecology henceforth respectively as: population as a collection of individual organisms of the same species; community as a collection of species' populations; ecosystem as a collection of communities and their physical environment, thus, as a unit of biological organization made up of all of the organisms in a given area interacting with the physical environment.

*organicism*. Community, according to individualism, is merely a name for a certain collection of individual organisms, gathered together more or less at random, who are considered to be autonomous and who alone are seen to be real. In organicism, by contrast, community is conceived as an organic entity or as a *superorganism*. In other words, the relationship between the part and the whole is conceptualized in analogy to the relationship between cell/tissue/organ and organism. The idea entailed by organicism is that a biotic community is of the same character as an individual organism.

It might be argued that what links together all the variants of the holistic thesis is not much more than the principle that "the whole has priority over the parts"- whatever "priority" might mean exactly – and a set of reservations about any form of reductionism. On the reductionist side, what is common between different variants of this thesis is arguably above all the commitment to derive statements about phenomena of a complex nature from statements about phenomena of a simpler nature, and that science essentially consists in this kind of reduction.

To encompass the whole classical holism-reductionism debate in ecology it is useful to map out a clear conceptual, logical and epistemological framework (Bergandi, 2011).<sup>6</sup> By revealing the basic assumptions of each theoretical approach, we should be better able to understand the points that are similar and shared, as well as the incommensurable ones. It is however important to note that in ecology, as in all other natural sciences, the ontological and epistemological foundations are essentially naturalistic and materialistic. Thus, it is thought that we can understand all objects, processes and events without references to vitalistic, supernatural, teleological or theological entities and causes. The order and laws structuring reality are in principle intelligible, and the way to seek knowledge is through a scientific and naturalistic epistemology. This naturalistic standpoint should be remembered every time we use the key terms of "holism" and "reductionism".

In ecology, the classical confrontation between holism and reductionism plays a structuring role, and we must be aware that their basic assumptions involve different and generally antinomian ontologies (worldviews), methodologies (research strategies) and epistemologies (Trepl *et al.*, 2011).

The theories and methods that are called holistic differ greatly according to which aspect of the concept of *wholeness* they highlight (Trepl *et al.*, 2011). It is the organic interaction of the parts that constitutes the holistic element in life. According to this view, for biological holism the key element of life is not seen to lie in an inner force inaccessible to scientific methods. Biological holism consists, instead, in the view that the characteristic of being alive can only be attributed to objects that are a whole, and that this whole exists in a special relationship to its parts that is not found in non-living objects. Understanding these wholes requires an epistemic approach that is different from that of physics. To the extent that holistic theories divide reality into different levels or autonomous wholes they can be called ontologically pluralistic.

Conversely, the reductionist ontology has its antecedents in the mechanistic worldview, originating with the Greek Atomists, in which reality has been defined from an atomistic perspective: reality consists of distinct, discrete, invisible atoms with fixed spatial-temporal amplitude. Unlike reductionism, the ontological perspective of holism is continuistic and relational: reality consists of a continuum of events and processes that are intrinsically interconnected and interdependent.

<sup>&</sup>lt;sup>6</sup> Bergandi (2011, pp 31-32) argues that the issue is easier to grasp if we keep in mind that holism generally represents the ontological background of emergentism but does necessarily coincide with it. Thus we can speak, in very loose terms, of the holism-reductionism debate, although it would be better characterized in terms of emergentism and reductionism. However, in definitional terms, there is not just one kind of emergentism and reductionism, but various kinds of it. There is a point of contact between holism and emergentism, but holism demands something more: the character of wholeness as an active cause.

At first sight, both reductionism and holism share a common scientific philosophy, namely, that all biological phenomena are fundamentally physico-chemical and that the laws of physics and chemistry are applicable to biological phenomena. Nevertheless, holism holds that the various levels of organization are characterized by new and specific properties (Lovejoy, 1927; Philips, 1935; Ablowitz, 1939; Emmeche *et al.*, 1997; Kim, 1999; Humphreys, 2006; MacLaurin and Sterelny, 2008; Bergandi, 2011; Santos, 2015; O'Connor, 2020; Santos, 2020). These *emergent properties* increase the degree of complexity of a given level compared with the various levels of which it is composed.<sup>7</sup> For this reason, even if physics and chemistry are normally applicable to ecological phenomena, each level of organization acquires appropriate laws and can be explained by theories that allow for an understanding of the specific properties of that particular level. By contrast, reductionism denies the existence of emergent properties or else considers them an epiphenomenon strictly dependent on the state of our knowledge, in the sense that these properties will eventually be explained, by the identification of the components and mechanisms from which they supposedly emerge.

These ontological assumptions have significant consequences in the methodological and epistemological domains (Bergandi, 2011): reductionism considers that at a given level of organization, the analytical study of constituent parts and their relations is necessary and sufficient to predict, or at least explain, all the properties of that level. Fundamentally, reductionism is a "bottom-up" strategy (Bergandi, 2011), which takes into account the level at which the events to be explained occur, e.g., the ecological level, as well as the lower levels that contribute to the explanation, e.g., the chemical and physical, for example. An analytical and additive method, therefore, dissects the entity, or decomposes the process into its component parts and attempts to take into consideration the relations among them. A successive summation of the individual component intrinsic properties or interactional properties should allow the extrapolation of the global properties of the entity as a whole.

Methodologically, the holistic approach, while recognizing the need for analytic decomposition, considers its explanatory power limited. In fact, from the holistic perspective, the feedback interactions that link different levels of organization play a role of the utmost importance in the determination and causation of emergent properties. This approach does not limit the analysis to the constitutive parts of –or their relations in – a specific level of organization. For this approach, both the higher levels ("downward causation") and the lower ones ("upward causation") participate in determining the properties of specific levels. It is a multilevel triadic approach, which constitutes a methodological necessity in holism.<sup>8</sup>

After this brief introduction to the Holism-Reductionism debate in ecology, I will now describe and scrutinize, in more detail, the classical positions on these controversies, and their more recent developments, which have shaped the development of ecology in the 20<sup>th</sup> century. My objective

<sup>&</sup>lt;sup>7</sup> According to Kim (1999, pp. 3-4), at the core of the ideas associated with emergentism is the thought that as systems acquire increasingly higher degrees of organizational complexity they begin to exhibit novel properties that in some sense transcend the properties of their constituent parts, thus behaving in ways that cannot be predicted on the basis of the laws governing simpler systems.

<sup>&</sup>lt;sup>8</sup> According to Kim (1999, pp. 22-23), when we analyze an ecological situation from the perspective of the layered model, with differentiated levels, we see that the following three types of inter- or intra-level causation must be recognized: (i) *same-level causation*, (ii) *downward causation*, and (iii) *upward causation*. Same-level causation, as the expression suggests, involves causal relations between two properties at the same level – including cases in which the instantiation of one property causes another property to be instantiated. Downward causation occurs when a higher-level property, which may be emergent, causes the instantiation of a lower-level property; similarly, upward causation involves the causation of a higher-level property by a lower-level one. Kim believes that, for the emergentist, there is good reason to believe that downward causation is fundamental and of crucial importance. For it can be shown that both upward and same-level causation (except same-level causation at the ultimate bottom level, if there is such a level and if there are causal relations at this level) presupposes the possibility of downward causation. I agree with this position, which I will develop below in the section on holistic systems approach.

will be, at the end of the analysis, to characterize a moderate approach, with elements from both positions, which should become important to explain ecological phenomena, within my perspective.

#### 2. The Reductionist Approach in Ecology

In this section I will start with the foundations of the reductionist position in ecology and, afterwards, describe how this position has driven the construction of modern reductionist mechanistic approaches in ecology. The objective is to identify the reductionist elements that I consider more relevant to elaborate a moderate approach to ecology.

#### 2.1. The Classical Individualistic-Reductionist Position

Individualistic reductionism was introduced in ecology as a critique of Clements's superorganism theory by Gleason in 1917 (McIntosh, 1980; Simberloff, 1980; Loijeen, 2000; Bergandi, 2011; Trepl 2011). Gleason (1917) formulated an "individualistic concept" of the (plant) community. It is "individualistic" in the sense that it results from individual organisms' adaptations to local environmental conditions:

"Vegetation, in its broader aspects, is composed of a number of plant individuals. The development and maintenance of vegetation is therefore merely the resultant of the development and maintenance of the component individuals, and is favored, modified, retarded, or inhibited by all causes which influence the component plants. According to this view, the phenomena of vegetation depend completely upon the phenomena of the individual. It is in sharp contrast with the view of Clements that the unit of vegetation is an organism (...)" (Gleason, 1917, pp. 464-465; bold is added)

The specific stimulus for Gleason's earliest formal exposition of his views on the nature of the plant association was, in fact, Clements' description of vegetation as an organism. It was a response to Clements' crystallization of ecological phenomena into fixed and inviolable laws (McIntosh, 1975). Gleason (1926) thus argued that the distribution and abundance of species populations is first of all determined by the factors of migration and by the environmental conditions, both of which are characterized by an element of *randomness*. Then Gleason stressed that no two areas of vegetation are exactly similar, either in species composition, the relative number of individual organisms of each or their spatial arrangement. Environmental conditions are rarely, if ever, discretely distributed but vary continuously, both in space and time. Since the environmental tolerances of different individuals and populations are not the same, moreover, one cannot expect different species to occupy exactly the same area. Therefore, according to Gleason, communities are rarely, if ever, clearly delineated entities but rather aggregations of species that gradually flow into one another. And since environmental conditions vary continuously in time too, neither can there be a deterministic succession towards one stable end phase. Thus, succession<sup>9</sup> is not, within this perspective, an orderly and predictable process and can be explained only through the dynamics of individual species' interaction.

<sup>&</sup>lt;sup>9</sup> Ecological succession is the process of change in the species structure of an ecological community over time. It is a phenomenon or process by which an ecological community undergoes more or less orderly and predictable changes following a disturbance or the initial colonization of a new habitat. There are eventually different stages in succession that will to reach a state of maturity: the climax.

Hence views concerning the way in which "communities" change through time differ fundamentally in several ways within the individualistic-reductionist approach compared to the organicist holistic approach, whereby changes are seen as developments (Trepl *et al.*, 2011). For Gleason (1926), changes in the environment are not primarily an outcome of the activity of organisms but rather occur, above all, by chance: the succession of different species combinations is determined by the randomness of migration and by the randomness of changing environmental conditions for the individual species. Thus, succession does not proceed towards a particular end state; rather it is random, *it involves change but not development*. In this context, the phenomenon of climax might merely refer to a phase in which no changes take place for a certain period of time. The further off in the future it lies, the less the state of a community can be predicted, because one cannot know enough in advance about the environmental changes and migration events determining it. This contrasts with the organicist-holistic view, in which the random and unpredictable nature of the initial conditions is emphasized, while at the same time the end state is always the same: if we look further into the future, we can predict which state will become established, namely, the climax state (see section 3.1).

In the context of the reductionist perspective, the adaptiveness of the individual organism is the starting point for the creation of a community. In every phase of succession, those organisms that are adapted to the condition existing in that location become more commonly established. *It makes no sense to speak of a community adapting*. The role accorded to adaptation is distinct from the one it plays in the holistic approach, where adaptiveness is ascribed to the community and explained as the outcome of a developmental process that leads to the climax community, because the community is increasingly constituted of those species that are useful to its development in analogy to the homeostatic maintenance of the individual organism.

For individualistic ecologists, the individual organism, or the intraspecific population, are the fundamental units granted the status of *being real*, because they ignore the relevance of interactions between populations (and between these and the abiotic environment). The theories endorsed by them embody a form of *biological mechanicism*, even though the "fundamental units" are living organisms or populations, rather than mechanical components (Levins *et al.*, 1980; McIntosh, 1980; Simberloff, 1980; Looijen, 2000; Bergandi, 2011; Trepl *et al.*, 2011).

The starting point of the individualistic position is that the existence and the expansion of each species depend only on the realization and quality of its own environment – every species is left to fend for itself within that environment. A community does not exist for the organisms, and the "(...) individual shows no physiological response to geographical location or to surrounding vegetation *per se*, but is limited to a particular complex of environmental conditions, which may be correlated with location, or controlled, modified, or supplied by vegetation" (Gleason, 1926, pp. 17). This individualistic position sees the units called by ecologists as communities and ecosystems as products of human imagination. Thus, they cannot be the object of scientific enquiry, adding that communities and ecosystems do not exist as discrete, structurally or spatially distinct entities (Looijen, 2000). According to this position, following the tradition initiated by Gleason, what are called communities and ecosystems are essentially nothing but *accidental* collections of species (populations), which can be fully explained in terms of properties of populations, or individual organisms, on the one hand, and local environmental conditions on the other. The general idea behind this is that, in searching for explanations of community structure, one should first assume that this is purely the result of chance processes before looking at deterministic explanations.

However, the logic of the individualistic approach grants a certain heuristic usefulness to the concept of community. On the one hand, communities must not be viewed as real entities, as they are

in the organicist-holistic view: not only are they not superorganisms, but they are also not "natural" units, for instance containing individual organisms occurring only in quite specific combinations and that may be discovered and described, as individuals species are, by rigorous research. While it is true to say that individual organisms form groups with other organisms in a given area, the composition of these groups will change depending on environmental factors and the random nature of migration patterns. On the other hand, it can be useful to give some of these groups a name, in order to establish some point of reference amid the many different combinations occurring.

According to the reductionist approach, one has to be aware that quite different species combinations can also came about, and that the frequency of the species groupings identified as associations is only due to the coincidental fact that the external circumstances required by these associations occur frequently (Trepl *et al.*, 2011). But they occur not because of any internal rule of development, which, even given very different initial conditions, gives rise time and again to specific combinations, as proposed by the holistic approach (Trepl *et al.*, 2011).

When ecologically-relevant communities are isolated out by the ecologist from among the multitude of possible species combinations, other boundaries and therefore other units might emerge, depending on the focus of inquiry. A network of relationships will come to an end at different points, depending on whether mutualistic, competitive or predatory relationships are selected for study, so that the outcome is a different community. In a sense, the ecologist is *constructing* communities.

In summary, Gleason argued, against Clements' theories, that nothing special makes a community or ecosystems cohesive and, moreover, that the assemblage of species in an ecological grouping does not reflect any kind of organicity. Gleason opposed the rigid conceptions of community and succession, which are characteristic in the holistic approach, holding that the association was a product of the largely chancy arrival of individual organisms selected by a continuously varying environment and that the results of succession need not to follow in any orderly predictable way. The resulting association was just a fortuitous juxtaposition of living beings, and "(...) it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements" (Gleason, 1926, pp. 26).

Gleason's challenge to Clements's organicist view was largely ignored until 1950, when it was resurrected and subsequently widely adopted as the forerunner of a *population-centered view of ecology*, an approach which most ecologists today tend to favor (McIntosh, 1980; Simberloff, 1980; Trepl, 1994; Looijen, 2000; Bergandi, 2011). Theoretical population ecology, considered a predecessor of the population-centered view in ecology, emerged in the 1920s and the 1930s, with the contributions of biologists and mathematicians associated with the works of Lotka and Volterra (McIntosh, 1980). Mainstream population ecology defined the object of ecology as simply the distribution and abundance of animals and plants. Thus, it was a simplistic view of ecology, which takes into account only the numbers of populations, nonetheless engendering an extensive debate about density-dependent and density-independent theories of population control in the 1930s and thereafter. For these reductionist ecologists, the most important theoretical development in general ecology has been the application of the famous logistic equations of Lotka-Volterra, also known as the predator–prey equations, a pair of first-order nonlinear differential equations frequently used to describe the dynamics of biological systems in which two species interact, one as a predator and the other as prey.

However, already in the 1930s some criticisms arose concerning the general applicability of Lokta-Volterra type models, which were showed inadequate even for laboratory populations

(Simberloff, 1980). Aside from the inappropriateness of the logistic equations for modeling the dynamics of even a laboratory population in a controlled environment, Lokta-Volterra type models did not take into account climatic, edaphic (relative to soil characteristics), biotic, and evolutionary influences. The development of mechanistic models ensued, which attempted partially to account for these more idiosyncratic factors, sacrificing generality for realism and achieving an impressive match to population data in certain instances, as in the work of Gause with microorganisms in 1934 (Simberloff, 1980). The primary emphasis of these post Lokta-Volterra studies was not on modeling ideal population trajectories, but rather on examining how physical environmental factors affect the outcome of competition between two populations and on identifying the physical mechanisms by which the outcome is achieved. The most relevant aspect of these works, however, was the discovery that, under certain environmental conditions, a specific outcome could not be predicted: the process was thus stochastic, and the best prediction one could possibly make was probabilistic. This was one of the first inroads of statistics into population ecology, constituting an explicit recognition that processes at the population level are not deterministic. The success of these population models aided the shift from superorganismic communities to populations as an object of study in the 1930's (Simberloff, 1980). This did not imply that the new interest in single species populations should be at the exclusion of community properties (McIntosh, 1980; Simberloff, 1980). Rather, the growing conception of the community as a collection of species populations, rather than as a superorganism, led in some quarters to an *analytic* mode of community research: community properties were approached through the analysis of assemblies of populations and the dynamics of populations' interactions, which were ostensibly well studied first, as if they were components.

In fact, in the steady development of mathematical population ecology in the 1940's, one can perceive an extensive clash between ecologists who endorsed deterministic mathematical models, based on logistic equations, and ecologists who advocated stochastic approaches. Progressively, the Lokta-Volterra mathematical models were rejected, seen as extreme oversimplifications (McIntosh, 1980), as it became also evident that even a simple deterministic model of a simple population can lead to dynamic trajectories which are indistinguishable from a random process, an observation that creates problems for data analysis and long term population forecasting.

After the Second World War, ecology saw the rise of new perspectives: quantitative, functional, trophic, theoretical and systemic (McIntosh, 1980; Simberloff, 1980). Much of this revolution in the 1950s and 1960s, took the form of an increasing reliance on quantitative methodology and the introduction of diverse external bodies of theory into ecology, particularly efforts to merge ecology with other biological disciplines, especially genetics and evolution. During these decades, the Clementsian climax and superorganism theory was progressively abandoned, although some traces of it were perpetuated in systems ecology's analysis, while the long submerged individualistic approach inaugurated by Gleason gradually became a robust population-oriented ecology, widely replacing the Clementsian community concept and subsequently leading to a *population-based view of ecosystems*, using the new available and powerful quantitative tools.

Thus, as advocated in the reductionist approach, if communities and ecosystems do not exist as discrete, structurally and/or spatially distinct entities, one must be focused upon individual organisms and populations, assuming that organismal and population phenomena *determine* the properties of higher levels of ecological ones. Therefore, the very possibility of endorsing *methodological individualism* in ecology comes to the fore, with the ensuing need to compare the strength of this approach with the population-based view in ecology, comparing also the different types of properties that populations and individual organisms manifest.

Methodological individualism (henceforth, MI) was introduced in ecology as a methodological precept from the social sciences (Heath, 2020), where it amounts to the claim that social phenomena must be explained by showing how they result from individual actions, which in turn must be explained through reference to the intentional states motivating individuals. According to this methodological stance, privileging individual action, for instance in sociological explanation, is the only way to make an action understandable by comprehending the agent's underlying motive. This permits the social scientist to accomplish something that is never attainable in the natural sciences, *namely the subjective understanding of the action of the component individuals* (Heath, 2020). Thus, most generally, MI commonly means privileging individuals in explanations, representations, and theories of higher-level phenomena.

In ecology, MI finds clear expression in the *individual-based-modeling* strategy (Grimm, 1999; Justus, 2014). Just as expected, utility calculations and individual agents' actions constitute the preferred level of analysis according to MI in the social sciences. In ecology, the behavior and physiology of individual organisms function similarly to individual agents' actions in social sciences for individual-based-models (henceforth, IBMs). Justus argues that, when properly construed, MI does not need to commit to population-level or community-level properties, ontologically reducing them to individual organism-level properties. According to Justus (2014), classical ecological models based on population and community variables (e.g. rates of birth, death, and reproduction; migration rates) also called state variable models - are typically highly idealized and unrealistic. More sophisticated models avoid conspicuously unrealistic assumptions, even though ignoring individual organisms means sacrificing maximal realism. This does not necessarily detract from the insights the models provide. Besides the tractability that simplifying assumptions provide, they also help devising representations of complex systems. Indeed, aggregating or abstracting from organismal details also seems reasonable since organisms of a single species share most genetic properties. As a result, some authors contend that the population should be the appropriate central concept for ecology. For instance, Berryman (2002), starting from the recognition that ecological landscapes are made up by individual organisms affecting each other in multiple ways, argues that, although an individual approach may seem logical, it is impractical. The alternative is to work at a higher level of abstraction (Berryman, 2002). The most proximate level of ecological abstraction above the individual is the population, where one deals not with individual organisms but, rather, with the average properties of a group of similar organisms belonging to the same species. Although variability from this average may be described statistically (e.g. by the variance around the mean), the identity and uniqueness of the individual organism is lost in the abstraction because, naturally, some information is sacrificed. Following the same reasoning, a population approach to ecology would be less tractable than a community or ecosystem approach because the latter entities, being at higher levels of abstraction, would allow capturing even more general statistical correlations, despite losing information concerning the uniqueness of individual populations.

Nevertheless, and I have to agree with Justus in this respect, the classical models in population ecology overlook two significant drivers of ecosystem dynamics, namely the *variability between organisms* and the *locality interactions*, both spatially and temporally (Lomnicki, 1978). IBMs are not blind to these features, and I think that this point is a great advantage of this kind of reductionist approach. The fundamental point remains that, biologically speaking, individual organisms are not equal, and IBMs aim to capture this important fact. In a sense, the main difference between classical state variable models and IBMs may lie in the different notions of theory and generality. Classical theoretical population ecology, following Lokta-Volterra mathematical models, has tried to formulate general questions and general answers, whereas IBMs seem to acknowledge that the answers of

ecology may not be very general, *i.e.*, each population and community may have its own peculiarities, which are essential to understand their dynamics.

Individual organisms, rather than populations, are the basic units of IBMs, and organismal behavior, development, reproduction and interactions are represented explicitly at the level at which they occur (Justus, 2014). A set of variables represents each individual organism, and a set of equations represents the relation between them and the abiotic factors. These variables are intended to reflect the detailed physiology and spatially specific interactions usually absent from classical models as well as their variance across individual organisms. Justus admits that this attention to details has a cost, and the quantity of variables can become analytically intractable; but, at the same time, this is a crucial advantage of IBMs. Grimm (1999) offers an extensive review of some IBMs studies published in the 1980s and 1990s, arguing that two distinct motivations were the basis for the modelers using the individual-based approach: one is that important features of individuals are not taken into account in state variable models, as I have related above, which he calls the pragmatic motivation; the other is that the theory emerging from state variable approaches has severe deficiencies, a paradigmatic motivation. In particular, Grimm (1999) considers that the latter motivation means that IBMs are driven by the suspicion that much of what we have learned from state variable models – in classical population ecology – would have to be revised if the discreteness, uniqueness, life cycles and variability of individual organisms were to be taken into account, including the nature of most interactions, which are local. I tend to agree with Grimm, and believe that IBMs, driven by the pragmatic motivation, aim to refine and avert the limits of classical theoretical population ecology. One major advantage of IBMs is that this approach opens up the possibility of modeling by relying on directly collected data; indeed, IBMs allow integrating observations directly into a model (Grimm, 1999; Justus, 2014).

More generally, Justus (2014) argues that, appropriately construed, MI *does not require* ontological individualism, the thesis that only individual organisms exist, while aggregates, collections and other wholes do not, or do not somehow exist "over and above" their individual constituents.<sup>10</sup> MI and reductionism are frequently considered to be synonymous (Justus, 2014); at the very least, reductionism is taken to require MI, but if MI condones appropriating extra-individualistic information when modeling systems, for instance in the form of taking into account interactions between individual organisms, this seems to preclude, in a sense, rather than facilitate strict reduction.

*Supervenience* and *compositionality* are the most plausible, and least controversial, points of support of MI in ecology, making *emergence* a more contentious issue (Justus, 2014).<sup>11</sup> On the grounds of supervenience relationship, no alleged obstacle threatens the thesis that population and community facts supervene on properties of individual organisms, their interactions, and their relations to the environment. In other words, population and community phenomena are determined by

<sup>&</sup>lt;sup>10</sup> Justus (2014, pp. 773-776) argues that MI is not the same as *methodological atomism*, the idea that wholes are only explainable by parts' properties, without considering their interrelations. Unlike methodological atomism, which is more restrictive, the epistemic priority MI places on individual organisms does not necessitate that particular representations of systems be individualistically pure, free from any influence of extra-individualistic factors. IBMs establish how properties and interactions between individual organisms, which in turn may depend on input from extra-individualistic sources, can account for higher-level phenomena. Whether the phenomena can be fully accounted for ultimately depends on whether this input might be accounted for individualistically.

<sup>&</sup>lt;sup>11</sup>Supervenience is a notion in analytical philosophy that states that a set of properties A supervenes upon another set B just in case no two things can differ with respect to A-properties without also differing with respect to their B-properties. Thus, there cannot be an A-difference without a B-difference. So, for instance, community facts supervene upon individual organisms' facts because one cannot have a difference in the community without a difference in the individual organisms. Compositionality is the notion that a set of entities constitutes an entity at the hierarchical level above than that of the constituent entities. For instance, communities are composed by populations.

properties of individual organisms, and their biotic and abiotic interactions, providing an adequate methodologically individualistic basis for reduction. However, these kinds of relations between individual organisms (parts) can *only* change them *quantitatively*, and *never qualitatively*, according to MI. That is, parts cannot gain or lose properties because of their relations; only the quantities of its intrinsic properties can change according to MI. If one allows a qualitative change in the parts of a system because of their relations, MI falls apart: in this case, individual parts remain; however, the focus of explanation becomes the set of structuring relations in the system, and the new relational properties that each individual organism (part) manifest as a function of that same set.

Another uncontroversial claim is the fact that individual organisms compose biological populations and communities, which facilitates, in a sense, reduction, because one is able to bridge different hierarchical levels. All this makes emergence controversial in ecology, even though the issue is far from settled; in fact, some population, community, and ecosystem-level properties are considered emergent and thus impervious to reductionist analyses, as I have anticipated in section 1.2.

One prominent and fairly well-studied candidate for ecological emergence – that has garnered increased attention and illustrates, according to Justus (2014), some underrated merits of MI, moreover clearly revealing how IBMs can contribute to reductionist accounts of putatively emergent properties – is the phenomenon of *community stability*. The concept of community stability is related to that of "balance-of-nature" (Egerton, 1973). Maclaurin and Sterenly (2008) argue that stability constitutes an emergent property immune to reduction. On this basis, these authors criticize an individualistic view of communities in which abundances and distributions of individual organisms are largely controlled by abiotic factors rather than by inter-organismal interactions. In contrast, Justus (2014) argues that this kind of emergence does not pose any special conceptual difficulty to MI, thus allowing that communities are "real" or that there are causally efficacious properties usually described at the community level. Justus contends that Maclaurin and Sterelny do not show that stability is a phenomenon meriting the label of emergence, as the thesis defended is just that community properties "are not just an extrapolation of" or "are not simple reflections of" the properties of individual organisms. Emergence so conceived, Maclaurin and Sterelny argue, challenges the reductionist view that "all important system-level behavior can be explained, and can only be explained, by explaining the behavior of the parts" (Maclaurin et al., 2008, pp 120). Conversely, Justus (2014) contends that what is missing from this kind of implicit methodologically atomistic analysis is an account of how temporal stability is different, because it depends on the biological interactions between individual organisms shaping a community. This view, criticized by Maclaurin and Sterelny, and embodied by Gleason's perspective, reflects a long-standing theoretical orientation in ecology, as I have related in section 2.1, according to which ostensibly community-level properties simply derive from patterns of abiotic factors impacting different species; organismal interactions are causally negligible or fail to produce anything novel at the community level. The marked difference between this austere conception of individualism and MI should be clear, according to Justus. While MI countenances interactions between individual organisms in accounts of higher-level phenomena, the conception that Maclaurin and Sterelny criticize corresponds most closely to methodological atomism, not MI. However, few ecologists would doubt that biological interactions such as competition, predation, mutualism, and others shape the composition and structure of communities. The argument, according to Justus, is that MI takes into account the latter biological interactions, being able, supposedly, to capture the emergent property of community stability. This point is crucial and captures a somewhat different position from Gleason, because, even if the latter argues that organismal interactions with the abiotic factors are causally relevant, Gleason nonetheless neglects, conspicuously, the biotic interactions between individual organisms. As I will show in section 2.2 – discussing some examples

of reductionist mechanistic approaches to ecology – emergent properties can become a major impediment to reduction, even using IBMs accordingly with MI precepts. Thus, this is a point on which I disagree with Justus's perspective.

Justus (2014) argues that there are several unification aims in ecology and that, perhaps, the most appreciated is the elusive integration of organismal and population ecology within community/ecosystems ecology, reducing the latter to the former, an approach I shall discuss next in section 2.2.1. Biological entities are the primary focus of the former and its models address issues concerning species composition, intraspecific dynamics and interspecific interactions between coexisting species. Abiotic factors rarely have an explicit role in these models. In contrast, energy and material flows through biotic interactions and abiotic mechanisms are the main focus of ecosystems ecology, like tracing nutrient cycles processed by organisms. There have been some attempts pursuing the reductionist approach, i.e., to integrate several models of organismal and population ecology within community/ecosystems ecology, which involve making connections between intratrophic-level species diversity and ecosystem functioning, interactions in food web and ecosystem functioning, indirect mutualism and nutrient cycling, populations stability and ecosystem stability. The foundation of such approaches is a theoretical insight about how population, community and ecosystem perspectives can be bridged, and, crucially, the connection concerning the mass and energy budgets of individual organisms. Justus (2014) argues for the possibility of ecophysiology being the link between population/community and ecosystems approaches (in which abiotic factors would have a role). As I will show in section 2.2.2, the Metabolic Theory of Ecology is a unification of population, community and ecosystem approaches, rooted in the ecophysiology of individual organisms, in particular on the constraints governing the acquisition, allocation and disposal of materials and energy; its formulation is based on the premise that the structure and dynamics of ecological communities are inextricably linked to individual metabolism, in a reductionist fashion, in the sense that interactions between organisms and environment are constrained by individual metabolic rates.

In summary, the units that are relevant for explaining ecological phenomena, according to the individualistic position, are the *individual organism* and the *population*. Communities, according to this position, are not well-delineated aggregates of individual organisms, as they are randomly determined by the factors of migration and by the environmental conditions. Nothing makes a community or ecosystem sufficiently cohesive and, moreover, the assemblage of species in an ecological grouping does not reflect any kind of organicity. Succession does not proceed towards a particular end state; it is rather random, involving change but not development, in disanalogy with the ontogenetic dynamics characterizing organisms. The ecologist can solely explain the community and the ecosystem properties through the analysis of assemblies of populations and the dynamics of populations' interactions, which are ostensibly well studied first, as if they were components. As a consequence, individual and population phenomena determine the properties of higher levels of ecological phenomena, which can ultimately be seen as resultant properties rather than emergent ones.

I will now critically analyze in more detail the reductionist mechanistic approach, trying to identify the relevant elements that I will endorse in order to support a moderate approach in ecology.

#### 2.2 The Reductionist Mechanistic Approach in Ecology

Biologists and ecologists converge on a basic mechanistic account, in which a mechanism is construed as generating a phenomenon through a start-to-finish sequence of qualitatively characterized operations performed by component parts (Bechtel *et al.*, 2005; Bechtel, 2011). It is important to note the processes by which scientists decompose mechanisms *structurally* into their *parts* and *functionally* into their *operations*. The basic account of mechanistic explanation differs in many ways from the more traditional deductive-nomological model of explanation, in which explanation is provided by derivations from laws, as I have referred in section 1.1, providing a distinct perspective. The mechanistic perspective starts from some different assumptions that I will now briefly describe.

Firstly, the crucial component of a mechanistic account is not the formulation of the relevant law; it is, instead, the determination of the parts of the mechanism, the operations they perform, and how they are organized (Bechtel, 2011; Craver et al., 2019). Secondly, although these parts and operations can be described linguistically, it is often more productive to represent them in diagrams (Bechtel, 2011). Thirdly, the demonstration that the mechanism can produce the phenomenon does not rely on logical derivations, but rather on mental simulations of the mechanism in operation, later ascertained by empirical research. Fourthly, mechanistic explanations are inherently reductionist insofar as they require specifying the parts of a mechanism and the operations they perform (Bechtel et al., 2005; Bechtel, 2011). However, they also require consideration of the organization of the whole mechanism and its relation to conditions in its environment, since it is only when appropriately situated that a mechanism will produce the phenomenon of interest. Mechanistic explanations are always multilevel accounts, integrating information about parts, operations, and organization within the mechanism with characterization of the phenomena exhibited by the whole mechanism. Finally, although some philosophers of science have eschewed examining the process of scientific discovery, limiting their focus to justification, mechanism discovery is a rich topic of philosophical analysis (Bechtel, 2011).

Therefore, mechanisms are *decomposable* in the sense that the behavior of a system as a whole can be broken down into organized interactions among the activities of parts. There are numerous characterizations of mechanisms in literature, and a "consensus concept" has been adopted: "A mechanism for a phenomenon consists of entities (or parts) and activities (or operations) organized in such a way that they are responsible for the phenomenon" (Craver *et al.*, 2019). All characterizations contain four basic features: a phenomenon, parts, causing and organization.

The *phenomenon* is the behavior of the mechanism as a whole, being all mechanisms the mechanisms of some phenomenon. The boundaries of a mechanism are fixed by reference to the phenomenon that the mechanism explains. The components in a mechanism are components in virtue of being relevant to the phenomenon. New mechanists speak variously of the mechanism as producing, underlying, or maintaining the phenomenon (Craver *et al.*, 2019). The language of production is best applied to mechanisms conceived as a causal consequence terminating in some end product. In contrast, for physiological mechanisms, it is more appropriate to says that the mechanism underlies the phenomenon. I shall prefer, for ecology, the idea that a mechanism might *maintain* a phenomenon, in a homeostatic sense. In this case, the phenomenon is a state of affairs, or a range of states of affairs, that is held in place by the mechanism. An area of active discussion is whether the relationship between the mechanism and the phenomenon must be regular. Machamer *et al.* (2000, pp. 3) stipulate that mechanisms are regular, in that they work "always or for the most part in the same ways under the same conditions". I converge with this position, even though this is not a universal agreed position.

There has been a great struggle to find a concise way to express the idea of what is a *part*, a crucial concept required to define the components of a mechanism. Formal mereologies are difficult to apply to the material parts of mechanisms in the life sciences. The axioms of mereology, such as reflexivity (i.e., everything is a part of itself) and unrestricted composition (i.e., any two things form a

whole) do not apply in standard life sciences' uses of the "part" concept (Craver *et al.*, 2019). Glennan's proposal (2006, pp. 53), for example, is that: "The parts of mechanisms must have a kind of robustness and reality apart from their place within that mechanism. It should in principle be possible to take the part out of the mechanism and consider its properties in another context".

Mechanists have disagreed with one another about how to understand the concept of mechanistic *cause* (Craver *et al.*, 2019). New mechanists have been at pains to liberate the relevant causal notion from any overly austere view that restricts causation to only a small class of phenomena, generally associated with physics, such as collisions, attractions or repulsions. Another difficulty has been to distance themselves from the regularist conception of causation, in the Humean sense, common among the logical empiricists. Four ways of discussing the concept of cause have been prominent in this debate (Bechtel, 2011; Craver et al., 2019). The first way defends a transmission account in which causation involves the transmission and propagation of marks or conserved quantities. This view has been unpopular in the life sciences because, within this domain, causal claims usually do not involve explicit reference to conserved quantities. The second account sees causation as derivative from the concept of mechanism, in the sense that causal claims are claims about the existence of a mechanism. The truth-maker for a causal claim at one level of organization is a mechanism at a lower level, that is, mechanisms are the hidden connection Hume sought between cause and effect. The third account embraces the view that causation should be understood in terms of productive activities. This account has been criticized because it fails to say what activities are and to account for the relationship of causal and explanatory relevance. The last account has the central commitment that models of mechanisms describe variables that make a difference to the values of other variables in the model and to the occurrence of a phenomenon. Difference-making in this manipulationist sense is understood as a relationship between variables in which interventions on cause variables can be used to change the value of effect variables. I shall explore in more detail this latter account in section 2.2.2, because I think that this account is the most robust in ecology.

The characteristic *organization* of mechanisms is also the subject of considerable discussion (Wimsatt, 1997; Bechtel, 2011; Craver et al., 2019). It is relevant to contrast mechanistic organization with aggregation, a distinction that mechanists have used to articulate how the parts of a mechanism are organized together to form a whole. This distinction will be crucial in the following analysis of some reductionist mechanistic approaches to ecology (section 2.2.1). Aggregate properties are properties of wholes that are simple sums of the properties of their parts. In aggregates, the parts can be rearranged and intersubstituted for one another without changing the property or behavior of the whole; the whole can be taken apart and put back together without disrupting its behavior, and the properties of the whole change linearly with the addition and removal of parts. Organization can be conceived as non-aggregativity, allowing a mechanistic form of emergence (Wimsatt, 1997). Mechanists have also detailed several kinds of organization characteristic of mechanisms (Craver et al., 2019), in particular spatial organization (including location, shape, position and orientation) and temporal organization (including order, rate and duration of component operations). Other important points about organization are modularity, meaning that it should be physically possible to intervene on a putative cause variable of a mechanism without disrupting the functional relationships among the other variables; jointness, a property that characterizes the interdependent relationship between parts of a mechanism in the sense that components in a mechanism often form a more complex unit by virtue of the individual properties uniting them; and, finally, mechanists emphasize the hierarchical organization of mechanisms and the multilevel structure of theories in the special sciences, such as ecology, demanding an analysis of mechanistic relations across levels organization (Craver et al., 2019), as it will become evident in the mechanistic approaches illustrated in the next sections.

Concerning the issue of explanation, while in the covering-law model explanations are arguments showing that the event to be explained is to be expected on the basis of the relevant laws of nature and antecedent and boundary conditions, mechanists, in contrast, insist that explanation is a matter of elucidating the causal structures that produce, underlie, or maintain the phenomenon of interest (Craver *et al.*, 2019). Thus, the philosophical problem is largely about characterizing or describing the worldly or ontic structures to which explanatory models must refer if they are to count as genuinely explanatory. The phenomenon must be situated in the causal structure of the world, and the explanation is an account of how the phenomenon is produced by entities and their properties.

Most mechanists recognize two main aspects of mechanistic explanation (Craver *et al.*, 2019): the etiological, which reveal the causal history of the *explanandum* phenomenon; and the constitutive, which explain a phenomenon by describing the mechanism underlying it. With increased attention to the latter, mechanists realized the need for an account of constitutive relevance, a principal need for sorting relevant from irrelevant factors within a mechanism. One central research problem is to say which of these entities, activities and organizational features contribute to the phenomenon and which do not. In a sense, the challenge is to define the boundaries of a mechanism: of saying what lies within and outside the mechanism.

It is relevant that in much of the literature on mechanisms, these are contrasted explicitly with laws of nature (Machamer *et* al., 2000; Craver *et al.*, 2019). This contrast grew out of an emerging consensus in philosophy of science that there are few, or perhaps no, laws in the life sciences, as I have related in section 1.1. The empirical generalizations found in biology and ecology tend to be hedged by *ceteribus paribus* clauses; whether they hold or not depends on background conditions that might not hold and on conditions internal to the mechanism that might fail. In short, these generalizations are mechanistically explicable, and what necessity they have derives from a mechanism. Thus, mechanisms seem to play the role of laws in the life sciences, because one seeks mechanisms to explain, predict, and control phenomena in nature even if mechanisms lack many of the characteristics that define laws in the logical empiricist framework, such as universality, inviolable necessity or unrestricted scope.

The work on mechanisms has also helped to clarify the idea of levels of organization and its relation to other forms of organization and non-mechanistic forms of emergence. Many mechanists emphasize that biological and ecological systems are hierarchically organized into near-decomposable<sup>12</sup> structures (Craver *et al.*, 2019): mechanisms within mechanisms. This view leads to the conclusion that the evolved structures, such as biological and ecological ones, are more likely to be nearly decomposable into hierarchically organized, more or less stable structures and sub-structures. An important objection has been raised against this perspective, stating that it is misleading because evolution does not construct organisms from scratch, piece by piece. I shall develop further this criticism in section 2.2.2 because it is relevant to analyze the Metabolic Theory of Ecology. However, there have been some attempts to reconstruct this argument and tackle this kind of criticism, as a way of showing that evolved systems are more likely to be modular, as described above: systems made of independently manipulable parts that can quarantine the effects of changes to specific parts, giving them flexibility to make local changes without causing great side-effects.

The near decomposability of mechanisms is directly related to the idea that mechanisms span multiple levels of organization. The behavior of the whole is explained in terms of the activities and interactions among the component parts. These activities and interactions are themselves sustained by

<sup>&</sup>lt;sup>12</sup> Near-decomposable because sometimes, in life sciences, is extremely difficult to identify all the components of a mechanism.

underlying activities and interactions among component parts, and so on. Levels of mechanisms can be defined in terms of a relationship between the behavior exhibited by a system and the activity of some component part of that system (Craver *et al.*, 2007). On this account, the activity of a component is at a lower level of mechanistic organization than the behavior of the system if and only if the component is a part of the system, and its activity is part of the system's behavior. In short, to say that something is at a lower mechanistic level than the mechanism as a whole is to say that it is a working part of the mechanism.

For some mechanists, one implication of this view of levels, combined with certain familiar assumptions about causal relations, is that there can be no causal relationships between items at different levels of mechanisms (Craver et al., 2007; Craver et al., 2019). There can be causal relationships between things of different sizes, and there can be causal relationships between things described in very different vocabularies; but conjoined with certain assumptions about the temporal asymmetry of cause and effect and the independence of cause and effect, there cannot be causal relationships between the behavior of a mechanism and the activities of the parts that jointly constitute that behavior (Craver et al., 2019). This is a position that is contrast with the holistic methodological approach, which necessarily does not limit the analysis to the constitutive parts of -or their relations within - a specific level of organization, as I have argued in section 1.2. For the holistic approach, both the higher levels ("downward causation") and the lower ones ("upward causation") participate in determining the properties of specific levels. Claims about inter-level causation concerning mechanisms are expressed as hybrid claims combining, on the one hand, constitutive claims about the relationship between the behavior of the mechanism as a whole and the activities of its parts and, on the other hand, causal claims concerning relationships between things not related as parts and whole (Craver et al., 2007).

The fact that phenomena at higher levels of mechanisms depend upon the organization of component parts entails that the properties or activities of wholes are not simple sums of the properties or activities of the parts. Levels of mechanisms can thus be contrasted with levels of mere aggregation. Because, in this sense, the whole is greater than the sum of the parts, some mechanists have found appropriate to describe this as a kind of *emergence*. From this perspective, *mechanistic* (or organizational) *emergence* thus understood is ubiquitous and banal but extremely important for understanding how scientists explain things (Craver *et al.*, 2019). Also common is the concept of *epistemic emergence*, the inability to predict the properties or behaviors of wholes from properties and behavior of parts (Humphreys, 2006; Craver *et al.*, 2019). This kind of emergence can arise as a result of ignorance, such as failing to recognize a relevant variable, or from failing to know how different variables interact in complex networks. It might also result from limitations in human cognition abilities or the available representational tools. Then, there is an urgency and practical necessity of studying mechanisms by decomposing them into component parts and the epistemic challenge of putting the parts back together again in a way that actually works.

The mechanists' emphasis on *mechanistic emergence* and *epistemic emergence* contrasts with their desire to distance themselves from *ontological emergence*, a position according to which emergent phenomena must be objective features of the world and independent of human knowledge (Humphreys, 2006), which some mechanists found as "spooky" (Craver *et al.*, 2019). They see it as spooky because they argue that it involves the appearance of new properties with no sufficient basis in mechanisms. Accordingly, it is not clear that emergent properties are properly said to be properties of the necessary mechanisms; and it is not clear in what since the emergent property is "emergent" rather than a fundamental feature of the causal structure of the world. I shall return to this discussion, in section 4, when arguing in favor of a moderate approach to ecology, since this is a fundamental issue.

One of the major successes of the life sciences has been not just to identify numerous biological mechanisms but also to decompose them into their component parts and operations, with successful examples in different domains. Even though there are limitations in the basic account of mechanisms, I believe that one has to acknowledge that it describes the conceptual framework in which the vast majority of productive research in the life sciences has been conducted.

After this brief introduction of a mechanistic account, I will now illustrate three prominent attempts to reductionist mechanistic analysis in ecology, discussing hereafter their possible virtues and limitations. Firstly, I will analyze the possibility to reduce ecosystem and community ecology to the ecology of individual organisms. Secondly, I will present the Metabolic Theory of Ecology, which is a unification of population, community and ecosystem approaches rooted in the ecophysiology of individual organisms and using metabolism as the unification concept between levels. Thirdly, I shall study the possible contribution of the New Mechanicist Philosophy to ecological explanation. My objective is, in discussing some examples of reductionist mechanistic approaches to ecology and, second, that using metabolism as a great unifying process in ecology, connecting all levels of organization, can raise philosophical concerns. In the end I would try to show how the New Mechanicist Philosophy can provide good insights to ecological explanations, solving some of limitations of the other reductionist mechanistic attempts, holding promise to contribute to a moderate approach.

#### 2.2.1. Aggregation and Reductionism

As I have anticipated in section 2.1, in the 1970s and 1980s, making use of valuable mathematical developments, a reductionist mechanistic approach in ecology came to prominence. Some ecologists used some individual-ecological concepts, those of behavioral ecology, ecophysiology and ecomorphology, as the basis for constructing a theoretical framework within which to interpret reductively the phenomena of ecosystems and community ecology, trying to formulate predictions by identifying a series of causal relationships (Schoener, 1986). The basic aim was to provide a reduction of ecosystems and community ecology to individual ecology, through the decomposition of "megaparameters" into behavioral and physiological parameters.

Some authors argue that there are two kinds of megaparameters: *sufficient* parameters and *aggregative* parameters (Levins, 1998; Raerinne, 2017).<sup>13</sup> The two are associated with different approaches, holism and reductionism respectively, which some view as incompatible and explanatorily contradictory. Aggregation is tied to reductionist research strategies, whereas sufficient parameters are associated with holistic research strategies (Wimsatt, 1986).

In the case of a sufficient parameter, one investigates whether different lower-level causes have similar or robust effects. If they have similar effects, then the ecologist forms a sufficient parameter, which is used in models instead of different specific causes. Sufficient parameters function as abstract, general, or higher-level causal or explanatory surrogates for different lower-level causes or mechanisms that have similar effects in models of a common phenomenon. For example, when studying niche breadth, ecologists observe that in an unstable environment species will evolve broad niches and tend toward polymorphism but that a stable and diverse environment leads to specializations. Temporal variation, patchiness of the environment, productivity of the habitat, and

<sup>&</sup>lt;sup>13</sup> I am referring to the use of parameters as simplifying assumptions or abstractions in ecological models. Models make use of simplifying assumptions, which function as approximations and abstractions.

mode of hunting can all have similar effects. And they do this by way of their contribution to the stability of the environment, rendering this instability a sufficient parameter (Raerinne, 2017).

In aggregation, one integrates different lower-level causal components with different or similar effects in order to extrapolate what their combined effect is. The ecologist forms a parameter, which combines the effects of different causal components into a single monadic coarse component, i.e., the aggregative component. The aggregative parameter is then used in a model as a causal or explanatory surrogate for the different causal components while the latter's organization is abstracted away in the parameter. For example, in ecological mechanistic reductionism, ecologists consider that the aggregate parameters of interest concern the various species populations, such as species diversity and abundance distributions (Raerinne, 2017).

Let me clarify that I use the term "reductionism" in the mechanistic sense, namely, the requirement for mechanistic models and explanations for ecological phenomena, rather than for the nomological reduction (Nagel, 1961) of ecology to more basic sciences. A reductionist mechanistic explanation is in this respect a *micro-explanation* or *micro-reduction*, whereby a property of a system is completely explained by, or reducible to, a certain composition relation between some part's properties. This is how ecologists understand the difference between holism and reductionism as modeling heuristics, which is evident in Schoener (1986) and Grimm (1999), two notable defenders of reductionist models in ecology. Nomological reduction, in the Nagelian sense, amounts to explaining the higher-level laws, theories and phenomena in terms of lower-level laws, theories, or phenomena. Note that mechanistic reductionism in its extreme form – e.g., ecological systems being nothing but mere aggregates – would amount to the epistemic and methodological elimination of ecology. That is, it would amount to the replacement, not the reduction, of ecological theories to lower-level theories. Schoener (1986) comes close to this position defending what he considers, erroneously in my opinion, a form of nomological theory reduction in ecology. With this distinction in mind, let us now consider how reduction is pursued in ecology within this account.

With an aggregative parameter, an ecologist builds a composite abstraction of different causal components with different or similar effects, using a function that combines the effects of different components together into one causal proxy (see note<sup>26</sup>) having a compound effect. An aggregative and abstract function or relation is then used in mechanistic models. Given that different components or forces are typically responsible for the system-level properties in ecology, many authors, such as Schoener (1986) and Vellend (2010), seek a synthesis of ecology by means of aggregative parameters.

There are general problems with aggregation (Raerinne, 2017). Different individual causal components might fail to be operative in different background conditions. Thus, their combination is not stable or projectable if the background conditions change. Addition of components and their subtraction often have the result that a qualitatively different compound effect is produced. Change in the organization of components can produce unpredictable effects. In general, when one rearranges, substitutes, adds, or subtracts some of the individual components, the compound effect might be qualitatively different (Wimsatt, 1986), a problem partially related to the modularity of the organization of a mechanism, as I have described above.

In his defense of mechanistic reductionist models, Schoener (1986) proposes a strong form of mechanistic reductionism in ecology (even though, as anticipated above, he is actually thinking in reductionism in a nomological sense). Namely, his proposal is that "The phenomena of interest in population ecology are aggregate properties of the individuals composing the population (...) Community ecology deals with a group of populations in some place. Here the aggregate properties of

interest concern the various species populations: abundance distributions, species diversity, speciesturnover rates, and so on." (Schoener 1986, pp. 91). Schoener uses the term "mechanistic" for studies primarily employing the "particularization", as he says, of population and community ecology, in which biological differences between various systems are emphasized rather than ignored, seeking a reductionist mechanistic explanation: an explanation of why a whole has a certain property exclusively on the basis of its constituents and differentiated microstructure; thus, using methodological individualism as the methodological precept in the quest for a micro-explanation. Schoener's goal is to demonstrate how individual behavioral and physiological information can be used in order to improve the epistemic status of community ecology (Schoener, 1986; Justus, 2014).

Schoener (1986) evaluates whether the conditions for a "nomological" reduction, as he sees it, were met by the mechanistic approaches to community ecology listed in his paper, arguing that even though community ecology has not been totally reduced, there are certain aspects that appear to satisfy the conditions of reduction, without excessive complexity and formalism, and that the reduction achieved is usefully explanatory. However, the critical issue becomes that, given that theory reduction proceeds from higher to lower sciences, the sub-disciplines of ecology must be arranged, inasmuch as possible, into a hierarchy of levels, in order to achieve the reduction. Therefore, Schoener pursues a uncontroversial hierarchy that satisfies the formal conditions for a perfect reduction: *individual ecology*, in which the parts are individual organisms; *population ecology*, in which the parts are populations, defined as those individual organisms located in a specific place and belonging to a single species; *community ecology*, in which the parts are collections of populations occurring in some place.

Thus, according to Schoener (1986), one should tackle directly the possible reductive relations between the sub-disciplines of ecology. The author then shows that the population dynamical approach to modeling ecological community phenomena makes a reduction of community to population ecology plausible; after that, he attempts to show that the theoretical model structure of population ecology might be reduced to individual ecology, following an individual based model (i.e., an IBM, see section 2.1). In short, Schoener (1986), using the arguments of nomological reduction, argues that community ecology is in principle reducible to individual ecology via a reduction through population ecology, and he thinks that there is nothing but complexity barring the way for this theory reduction to be possible.

However, as I have anticipated above, I shall consider reductionism as the quest for mechanistic explanations for ecological phenomena (as I have characterized them at the beginning of section 2.2), rather than a nomological theory of reduction. Moreover, as a general thesis, I would argue that Schoener's claim that the properties of ecological systems are aggregates of their component's properties (individual properties) taken in isolation is implausible and lacks empirical support. Consider the example of predation,<sup>14</sup> which is a causal factor of prey mortality and with an effect on population density, more specifically, a positive causal factor of prey mortality and a negative (regulatory) causal factor of prey population density. Predation is an abstraction of the components of the predator-prey systems.

In a classical study on predation, Holling (1959) focuses not only on the components of predation, but on how the components of predation *make up and interact* to produce a total predation response. The total predation response expresses the total proportion of mortality rate of prey by its predators, determining whether the density of prey population is regulated by its predators. The shape of the total predation response curve helps to determine whether the predators are able to control their prey population density. Expressed in the terminology of this paper, Holling's idea was to study

<sup>&</sup>lt;sup>14</sup> Predation is a biological interaction where one organism, the predator, kills and eats another organism, its prey.

whether the total predation response is an aggregative property of its components' properties in isolation and how the total predation response, as a biotic density-dependent factor, regulates the density of prey species populations. Holling's study originally started as a field investigation of a simple predator-prey system in a uniform and homogenous environment, which was causally isolated from abiotic and biotic background conditions that could interfere with the system. The ingenuity of Holling's study was that he stripped down this simple predator-prey system into its basic components to see how the components produced the supposedly aggregate property of the system, namely, the total predation response.

His investigations showed that the total predation response is more than the sum of the properties of predator-prey systems' components' properties in isolation, i.e. it is an *emergent* rather than a simple aggregative property. Using the terminology of his paper, the results were as follows. Holling's study was originally concerned with the predation of cocoons of a sawfly species by three mammal species. Due to the simplicity of the predator-prey system and the uniformity of the background conditions, there initially seemed to be two main additive components to the total predation response: 1) how predators respond dietarily to changes in prey density, such as by consuming their prey in fewer or greater numbers (the so-called functional response of predators) and 2) how predator density is affected by the density of their prey (the so-called numerical response of predators). A functional response (C1) is the change in predator's consumption as a function of change in prey density, whereas a numerical response (C2) is the change in predator density as a function of change in prey density. The total predation response is a combination of functional and numerical responses. Were the total predation response an aggregative property of predator-prey systems, then the effects (E1) and (E2) of predators' numerical (C1) and functional (C2) responses on the mortality of their prey could be combined as independent (additive) elements, and the aggregative function (C1  $+C2 \rightarrow E1 + E2$ ) could be applied to predator-prev systems to model total predation responses. However, as Holling notices, prey density has different kinds of effects on the functional response of predators. There is no typical or general response, although some qualitative general results can be stated. The numerical response is more varied, and there are species that show no numerical response, whereas other species show a marked positive or even negative numerical response vis-à-vis changes in the density of their prey. The total predation response is thus a combination of two possible continua: "a negative numerical response to a marked positive numerical response" and "no functional response to a marked positive effect in functional response." Thus, there is no general or universal total predation response, because the components vary and/or are taxon or system specific. The results of his investigations apply to predator-prey systems in general. In fact, later studies on predation have elucidated different ways in which the total predation response is not an aggregative property of predator-prey systems in general.

The conclusion is that the total predation response is typically not an aggregative property of its components' properties in isolation, but an *emergent property* of a predator-prey system. The way the components interact, how they are organized, what are the biotic and abiotic background conditions, do matter and produce qualitatively different or emergent total predation responses. Total predation is mechanistically decomposable, but is more than the sum of its components' properties considered in isolation. Most of the higher-level properties of ecological systems cannot be treated as mere aggregates of their components' properties taken in isolation, in contrast to what seems to be suggested by Schoener in the passage quoted above. Therefore, the total predation response is a property that cannot be completely described by mechanistic (or organizational) emergence.

#### 2.2.2. The Metabolic Theory of Ecology

The Metabolic Theory of Ecology (henceforth MTE) claims to provide a mechanistic explanation for known allometric relationships between biomasses and metabolic rates, postulating that these patterns of allometry and scaling relationships<sup>15</sup> are driven by constraints of transport of energy and materials (West *et al.*, 1997; Enquist *et al.*, 2003; Brown *et al.*, 2004; Allen *et al.*, 2004; O'Connor *et al.*, 2007).

This theory was advanced on the philosophical premises that allometric phenomena required a mechanistic explanation and that a MTE could elucidate that mechanistic basis based on physical, chemical, and physiological principles. The formulation is based on the theoretical hypothesis that the structure and dynamics of ecological communities are inextricably linked to individual metabolism, in a reductionist way, in the sense that interactions between individual organisms and their environment are constrained by metabolic rates, which depend on factors like body size, body temperature and resource availability and that, as a consequence, these interactions will explain some characteristics of higher ecological levels.

Therefore, the reason for considering MTE a mechanistic approach is that metabolism is assumed to be mechanistically explained in terms of biochemical reactions. According to the basic mechanistic account that I have described in section 2.2, decomposability is clearly possible in MTE. The metabolism of a community (or ecosystem) is the behavior exhibited by the entire system (i.e., the whole mechanism), and the metabolisms of the populations that compose it are the components' activities of that entire system (i.e., the sub-mechanisms). In the same way, the metabolism of a population is the result of the metabolisms of the individual organisms, its components 'activities. Thus, the levels of the mechanism are defined in terms of a relationship between the behavior of a system and the activities of component parts. That is, to say that a population is at a lower mechanism. The same is true for individual organisms being the working parts of a population.

Metabolism provides a basis for using basic principles of physics, chemistry and biology to link the biology of individual organisms to the ecology of populations, communities and ecosystems. A calculation is said to be from basic principles if it starts directly at the level of established laws of physics. Thus, the ecology of populations, communities and ecosystems can be studied starting from the physical laws concerning the movement of gases, chemical elements, compounds and fluids; and the laws of diffusion and evaporation. Onwards, ecologists can use the laws involving the kinetics of chemical reactions. Finally, ecologists can analyze the variation in the rates and specificity of biochemical pathways of metabolism among different kinds of organisms and environmental settings.

Metabolic rate i.e., the rate at which organisms take up, transform and expend energy and materials, is, according to this approach, the most fundamental biological rate. Advocates of this approach have developed a quantitative theory for how metabolic rate varies with body size and temperature (West *et al.*, 1997; Enquist *et al.*, 2003; Brown *et al.*, 2004; Allen *et al.*, 2004; O'Connor *et al.*, 2007). This metabolic theory predicts how metabolic rate – by setting rates of resource uptake from the environment and resource allocation for survival, growth and reproduction – controls ecological processes at all levels of organization from individuals to ecosystems (Brown *et al.*, 2004).

<sup>&</sup>lt;sup>15</sup> In allometries and scaling relationships, body size (or mass) is used as an independent variable of different dependent variables representing anatomical, physiological, morphological, behavioral, social, ecological traits. See Annex 1.

Within this perspective, the complex, spatially and temporally varying structures and dynamics of ecological systems are consequence of individual metabolism because individual organisms transform energy to power their own activities, convert materials into uniquely organic forms, and thereby create a distinctive biological, chemical and physical environment. Metabolism might be generally characterized as the biological processing of energy and materials whereby organisms take up energetic and material resources from the environment, convert them into other forms within their bodies, allocate them to the fitness-enhancing processes of survival, growth and reproduction, and excrete altered forms back to the environment. Metabolism therefore determines the demands that individual organisms place on their environment for all resources, and simultaneously sets powerful constraints on allocation of resources to all components of fitness. The overall rate of these processes sets the pace of life. In particular, body size, temperature and chemical composition affect biological structure and function at various levels of organization (West et al., 1997; Enquist et al., 2003; Brown et al., 2004). This is because metabolism obeys physical and chemical basic principles that govern the transformation of energy and materials; therefore, much of the variation among ecosystems – including their biological structures, chemical compositions, energy and material flows, population processes and species diversity - depends on the metabolic characteristics of the present organisms. Much of the variation among individual organisms, including their life history, characteristics and ecological roles, is constrained by body sizes, operating temperatures and chemical composition (Brown et al., 2004). These constraints of allometry, biochemical kinetics (rates of biochemical reactions) and chemical composition lead to metabolic scaling relations that, on the one hand, can be explained in terms of well established principles of biology, chemistry and physics and, on the other hand, can explain many emergent features of biological structure and dynamics at all levels of organization (Brown et al., 2004).

This theory explicitly shows how many ecological structures and dynamics can be explained in terms of how body size, chemical kinetics and resource supply affect metabolism. The MTE builds on them by providing a quantitative framework to better understand how these three variables combine to affect metabolic rate, and how metabolic rate, in turn, influences the ecology and evolution of populations, communities and ecosystems. This quantitative framework is explained in Annex 1.

The mathematical structure of the theory provides two concise mathematical expressions of interest: equations A1.5 and A1.6 (see Annex 1). The first correlates the variation of B, the mass specific rate of metabolism,<sup>16</sup> with the combined effect of size and temperature in a single quantitative expression. What is observed is that B is negatively associated with body size and positively (exponentially) with temperature. The second correlates the variation of K, the carrying capacity of individual organisms,<sup>17</sup> with the combined effect of size, temperature and the available quantity of a limiting resource. What is observed is that the carrying capacity is negatively associated with body size, and positively with the resource concentration (linearly) and temperature (exponentially).

Since the above referred studies of Lotka-Volterra in the section 2.1, ecologists have tried to understand how pairs of competing species or of predators and prey stably coexist in the same environment. Empirical evidence suggests that a number of interactions rates and times, including rates of parasitism and predator attacks, are inversely related with temperature. It has been argued that MTE predicts the pace of these interspecific interactions, because the rates of consumption and

<sup>&</sup>lt;sup>16</sup> Mass specific rate of metabolism is the rate at which organisms consume energy per unit of body weight.

<sup>&</sup>lt;sup>17</sup> The carrying capacity of an environment or given place is the maximum population size of a biological species that can be sustained by that specific environment, given the food, habitat, water, and other resources available. The carrying capacity is defined as the environment's maximal load, which in population ecology corresponds to the population equilibrium, when the number of deaths in a population equals the number of births.
population growth are determined by the rates of individual metabolism and have the same body size and temperature dependence (Brown *et al.*, 2004; Allen *et al.*, 2004). Moreover, the scaling of rates of ecological interactions has important implications for coexistence and species diversity, because the qualitative empirical patterns of biodiversity would suggest that the processes that generate and maintain species richness scale similarly to other biological rates, as shown in equation A1.5. Other things being equal, there are more species of small organisms than larger ones and more species in warm environments than colder ones.

The corroborated hypothesis that species diversity varies inversely with body size suggests, according to MTE, that metabolism plays a central causal role in determining ecosystems' species composition. It has been long known that diversity of most taxonomic and functional groups is highest in the tropics, but this has usually been attributed to higher productivity or reduced seasonality, rather than to the kinetic effect of higher temperature (Pianka, 1966).<sup>18</sup> However, empirical evidence suggests that species richness in many groups of animals and plants has the same relationship to environmental temperature than metabolic rate does (Brown *et al.*, 2004). This result holds true not only along latitudinal gradients, but also along elevation gradients, where variables such as light intensity, seasonal changes in day length and biogeographic history are held relatively constant. The implication is that much of the variation in species diversity is directly attributable to the kinetics of biochemical reactions and ecological interactions (Brown *et al.*, 2004; Allen *et al.*, 2004). Clearly, much additional work on the relationship between metabolism and biodiversity is needed, but a metabolic perspective, as proposed by MTE, demonstrates the centrality of many of these questions and has suggested where to look for in pursuit of appropriate answers.

Some of these questions can be addressed by probing more deeply the effects of biological metabolism on the fates of energy and materials in ecosystems (Brown et al., 2004). Biologically regulated whole ecosystems' stores and fluxes of elements and compounds can be seen as simply the sums of the stores and fluxes of the constituent organisms. Thus, MTE makes explicit predictions about the contribution of the biota to biogeochemical cycles. Specifically, equation A1.6 provide the basis for predicting how body size, temperature, and stoichiometry,<sup>19</sup> determine specific magnitudes of stores and rates of flux within and between "compartments" such as primary producers, herbivores, predators and detritivores. It is possible to derive from equation A1.6 expressions for the stored biomass, the energy flux and biomass production, the biomass turnover, and for trophic dynamics (Brown et al., 2004). This metabolic framework could also be applied to address more precisely and quantitatively some of the questions raised by Odum concerning the dynamics of succession (see section 3.1).<sup>20</sup> The MTE also provides a framework for more explicitly incorporating stoichiometry and understanding the effects of limited water and nutrients supply on variation in productivity and other processes across biomes (i.e., collections of organisms that have common characteristics in respect to the environment they inhabit) and physical gradients. For the supporters of MTE, regressions<sup>21</sup> incorporating these variables are able to account for much of the observed variation.

In summary, the MTE: 1. conjectures that a complex structure of distributional networks of essential nutrients and chemical elements, such as the circulatory systems in metazoans (multicellular

<sup>&</sup>lt;sup>18</sup> Pianka's (1966) paper is, according to most authors, maybe the first attempt to explain mechanistically some ecological phenomena.
<sup>19</sup> Stoichiometry, in ecology, refers to the quantities, proportions or ratios of chemical elements in different entities, such as

<sup>&</sup>lt;sup>19</sup> Stoichiometry, in ecology, refers to the quantities, proportions or ratios of chemical elements in different entities, such as organisms or their environments.
<sup>20</sup> Odum (1969) raised the issue of understanding how productivity, biomass and materials turnover rates change with

<sup>&</sup>lt;sup>20</sup> Odum (1969) raised the issue of understanding how productivity, biomass and materials turnover rates change with increasing plant size during transition from herbaceous-dominated to tree-dominated ecosystems.

<sup>&</sup>lt;sup>21</sup> Regression analysis is a set of statistical techniques for estimating the relationships between a dependent variable and one or more independent variables.

animals), requires an allometry in order to explain the need to minimize transport costs of energy and materials as body size increases; 2. argues that minimizing these transport costs requires a scaling exponent of  $-\frac{3}{4}$ , as defined in equation A1.5; 3. links metabolism and temperature, via the Boltzmann factor (see Annex 1), used to predict the rate of simple biochemical reactions, essential to the living processes, as defined in equation A1.5.

The theory was advanced on two philosophical premises: that allometric phenomena *require* a mechanistic explanation and that MTE would *identify* that mechanism, based on physico-chemical, biochemical and physiological basic principles; that the proposed mechanism motivates and justifies renewed and expanded work on the ecological implications of allometry. I think these premises are valid, with the caveat that allometries and scaling relations are not universal or exceptionless laws, in the way that I described in section 1.1. If it is true that allometries and scaling relationships do not represent biological laws, the covering-law account (Hempel, 1965) cannot be used to explicate how and under what conditions they function in articulating explanations and inferring predictions. Thus, some other account is needed to salvage the putative explanatory and predictive roles of allometries and scaling relationships: the feasible alternative is provided by a mechanistic approach, because, as I have related in section 2.2., in such account mechanisms are contrasted explicitly with laws of nature (Machamer *et al.*, 2000; Craver *et al.*, 2019).

The proposed mechanistic explanation has energized the consideration of allometric effects in ecology, producing a number of substantial hypotheses. Therefore, the expectation was that this theory would provide a quantitative framework to better understand how the variables of resource availability, body size and temperature combined to affect metabolic rate, and how metabolic rate, in turn, influenced the ecology of populations, communities and ecosystems. However, there is a considerable debate regarding the support for the predictions articulated by the MTE as well as the validity of the theory's underlying assumptions. This issue shall be explored below, starting with the virtues and limitations of MTE. Then I will move to the possible mechanistic nature of the theory.

O'Connor *et al.* (2007) recognized two putative advantages of MTE: being based on basic principles of physics, chemistry and biology and, secondly, depending on fewer assumptions and parameters than other explanatory frameworks. However, these authors also note that the notion of first principles is not well defined and additionally argue that freedom from assumptions is hardly an advantage in itself. In fact, while well-elaborated ecological models based on physical laws and relationships have the virtue of depending on processes whose dominant dynamics are well understood and, additionally, have the virtue of clearly outlining the assumptions made, they are not free of such assumptions. In fact, the application of simple physical principles to ecological systems requires a lot of assumptions because of the complex series of organizational levels, from macromolecules to ecosystems, through which physical effects are filtered to produce their ecological effects.<sup>22</sup>

Thus, MTE is hardly free from or independent on fewer assumptions. I would also argue that some of these are untenable. Characterizing MTE as based on first principles does not mean that the assumptions are easily identifiable and the consequences of violating them are easily understood. Moreover, all this should not confer special status on MTE as an explanatory mechanism.

 $<sup>^{22}</sup>$  O'Connor *et al.* (2007) contend that the potentially limiting assumptions of the MTE regarding metabolic allometry include: that metabolic rate is primarily limited by distributional networks of nutrients (such as circulatory systems); that circulatory transport costs will indeed be minimized; that capillary diameters of such networks are size invariant; that the simplified description of the circulatory system is inadequate, even for organisms with open circulatory systems or no cardiovascular systems; that branching in real bodies sufficiently approximates the simplifying assumptions to justify MTE arguments; and that the normalization constants in the allometric power equations are unimportant in comparing to scaling exponents.

In spite of these possible limitations, some authors disagree with O'Connor et al. (2007), arguing that the proposed mechanisms underlying the body size and temperature dependencies of individual metabolic rate represented in the equation A1.5 can be accurately described (Allen *et al.*, 2007). O'Connor et al. take issue with the Brown et al. 's network model as a mechanistic explanation for the <sup>3</sup>/<sub>4</sub> power scaling of metabolic rate (2004), but Allen et al. (2007) argue that this model is indeed mechanistic because: it invokes a few simplifying assumptions that allow causes to be postulated; it yields quantitative predictions by explicitly linking organism structure to function based on these assumptions; it can be extended to predict how deviations from assumptions affect model predictions. This network model represents a manifestation of general principles that entail maximizing the number of metabolic units where metabolism occurs, as respiratory complexes, while minimizing the transport distances to those metabolic units (Allen et al., 2007). These general principles are geometric, and they assume that natural selection will lead to evolutionary optimization of network geometry, subject to physical, evolutionary and physiological constraints. Given this evolutionary optimization assumption, quarter-power scaling of metabolic rate is predicted to apply at multiple levels of biological organization, in agreement with empirical data. O'Connor et al. (2007) do not agree with the general hypothesis that natural selection results in the network optimization in organisms. For these authors, the minimization of transport costs is a tenable criterion for evolutionary optimization, although it is clearly not the only factor upon which selection operates, and this simple optimization criterion is not sufficient to describe the variety of selective forces that likely operate in determining metabolic rates. Thus, for O'Connor et al. (2007) the degree to which minimizing a subset of costs of metabolite transport determines metabolic rates needs further attention. To whatever extent selection might optimize bulk transport via distributional networks, the specific mechanism proposed by the MTE (i.e., isolated minimization of fluid transport costs) is a poor subject for minimization because it is unlikely that transport costs map in a uniform and simple manner onto fitness. In my opinion, natural selection optimizes organismal fitness (and not the fitness of isolated organismal parts), implying that the optimal design hypotheses must consider costs and benefits of parts optimization (O'Connor et al. 2007). What is actually required in order to maximize fitness is that simultaneous optimization, of both the costs and benefits, is expressed in a common currency, organismal fitness being the logical candidate.

In my opinion, this is the correct perspective: true optimization of isolated physiological systems (like metabolism) is difficult, if not impossible to achieve in nature. Pleiotropy,<sup>23</sup> multiple use for structures, and variable selective environments all constrain optimization of physiological systems. Selection optimizes the expected lifetime reproductive success of entire organisms rather than the efficiency of a particular component of metabolism, although the two may well be correlated. Many aspects of metabolism, active and resting, could conceivably affect the fitness of an organism. Therefore, the idea that natural selection would optimize circulation transport costs (in isolation from other systems), which would then come to dominate metabolism allometry, seems unlikely. When conflicting demands are placed on a system, biologically optimal solutions are context dependent and the results of optimality analysis depend on optimization criteria. Rarely can any of a set of criteria be confidently identified with the fitness of an organism. This is the issue raised, as I have anticipated in section 2.2, by the supposed near-decomposability of structures into sub-structures, piece by piece.

O'Connor *et al.* (2007) present evidence that shows that predictions made by the MTE regarding single cells are poorly supported by data and that empirical evidence disputing the main

<sup>&</sup>lt;sup>23</sup> Pleiotropy occurs when one gene influences two or more seemingly unrelated phenotypic traits. A gene exhibiting multiple phenotypic expression is called a pleiotropic gene. Mutation in a pleiotropic gene may have an effect on several traits simultaneously, due to the gene coding for a product used differently by a population of cells or having different functions in different tissues.

predictions of MTE with regards to the mechanism of metabolic standing and transport systems in vascular plants is mounting. However, Allen *et al.* (2007), opposing this criticism, argue that there is considerable empirical evidence to support the network model assumptions and predictions in unicellular organisms, plants and a variety of animal taxa.

Another criticism advanced against the MTE by O'Connor *et al.*(2007), and with which I concur, is that, although these authors agree that most components of metabolism are affected by temperature, proposing Boltzmann relationships as the explanatory mechanism for the temperature dependence of metabolism is untenable because no macroscopic equivalent of activation energy exists (see annex 1). At the level of the cell, with its complex, feedback controlled network of reactions with numerous metabolic checkpoints, each of which responds to several controllers and external conditions, no equivalent of activation exists. Furthermore, at this level the simplicity of control implied by the Boltzmann relationship does not exist (O'Connor *et al.*, 2007).

As one moves to considers organ systems, entire individual organisms, populations and ecosystem levels of organization, the complexity and diversity of the organization networks and their responses to temperature all increase progressively. Any putative relationship based on activation energies for the processes of the different levels of organization can be, at best, an observed correlation with temperature, but not a mechanism. Mechanisms demand causational reduction adequate to describe phenomena, both qualitatively and quantitatively, a connection between the dependent effect and the causative process, and I think it would be impossible to identify a causative process that could explain the effect of temperature moving across all the levels of ecological organization. Moreover, as I have reported in section 2.2, the near decomposability of mechanisms is directly related to the idea that mechanisms span multiple levels of organization, however, this view, according to some mechanists, have the implication that there can be no causal relationships between items at different levels of mechanisms (Craver *et al.*, 2007; Craver *et al.*, 2019), making it difficult to postulate the role of a causative process moving across all the ecological levels.

Thus, according to O'Connor *et al.* (2007), correlative relationships like those proposed by the MTE cannot be regarded as mechanistic, because they are merely couched in a mathematical form, lacking the causative linkage between the postulated mechanism and the temperature dependence of metabolism. The authors argue that the reservation about Boltzmann's relation arises from a poor fit to thermal physiology, particularly the short and long term variation of metabolism in response to changes in body temperature. O'Connor et al. (2007) concentrate on ectothermic responses, presenting data from the literature on acclimation,<sup>24</sup> particularly acclimation of metabolic rates to varying temperatures in ectotherms,<sup>25</sup> showing that the dependence of metabolism on temperature is both subject to selection among animal taxa and physiologically adjustable within a single organism. Thus, this range of variation is inconsistent with Boltzmann's relation. O'Connor et al. (2007) do not argue that temperature does not affect metabolism, but that the proposed Boltzmann relationship cannot encompass the patterns of variation commonly seen in nature. On the contrary, Allen et al. (2007) argue that the Boltzmann relationship can capture the complexities of metabolism, claiming that a large and growing body of empirical evidence supports the commonality of temperature response rather than the ability of individual species to overcome the physical constraints of temperature. These authors argue that Boltzmann's relation is firmly based in statistical thermodynamics and present

<sup>&</sup>lt;sup>24</sup> Acclimation is the process in which an individual organism adjusts to a change in its environment (such as a change in altitude, temperature, humidity or pH), allowing it to maintain performance across a range of environmental conditions.

<sup>&</sup>lt;sup>25</sup> An ectotherm is a type of organism in which internal physiological sources of heat are of relatively small or of quite negligible importance in controlling body temperature. Such organisms (for example frogs) rely on environmental heat sources, which permit them to operate at very economical metabolic rates.

empirical data relative to heterotrophic organisms (diverse taxa of insects and marine larvae), showing that the temperature dependence of metabolic rate reflects the temperature dependence of respiration on individual mitochondria, according to equation (A5); and that for plants this same temperature dependence is expected to hold over the short term.

Another point of contention is that, according to O'Connor *et al.* (2007), these attempts to link individual metabolic rate to the structure and function of higher levels of biological organization are neither useful nor valid: MTE only describes "pre-existing" patterns and these patterns are dissociated from underlying mechanisms. Allen *et al.* (2007) argue that these claims are false and reflect a poor understanding of the MTE; in fact, these authors argue, the vast majority of MTE studies have been motivated by new questions that have resulted in the generation of new hypotheses, models, and empirical relationships. In each of these studies, new patterns have been described and directly linked to individual metabolic rate.

Thus, as I have showed, a significant debate about the capacity of MTE to explain and predict ecological phenomena is taking place. I shall now discuss the issue of the mechanistic nature of MTE because a central question needing clarification is whether the explanation in terms of allometric relationships provided by the MTE is actually mechanistic (O'Connor *et al.*, 2007). In this discussion, it is crucial to distinguish between different types of explanatory models (O'Connor, 2007; Pâslaru, 2009; Raerinne, 2011; Raerinne, 2013): a *phenomenological* type, which requires an empirical, but not a mechanistic, relation between variables – e.g., regressions of metabolic rate on mass fall in this category –, and this implies that maybe there are hidden variables creating the pattern, thus engendering a problem of extrapolation and prediction; a *mechanistic* type, in which the input variables are linked to output variables by a series of causal relationships. The models proposed by the MTE are a compromise between these two types of models; in fact, proxy variables<sup>26</sup> for factors of likely mechanistic importance are embedded within a statistical framework.

In spite of a long and useful history in the physiological explanation of ecological processes, the extent of variation to which such regressions provide broadly generalizing mechanisms such as thermal environments and physiologies, distributional systems of chemical elements and its constraints, and selection forces, is an open question. Likewise, in my opinion, the extent to which the linear equations,<sup>27</sup> fitted by regression, constrain the mathematical form of a generalized mechanism is unclear, particularly in systems whose dynamics result from multiple, interacting, non linear

<sup>&</sup>lt;sup>26</sup> In statistics, a proxy or proxy variable is a variable that is not in itself directly relevant, but that serves an epistemic function in place of an unobservable or immeasurable variable. In order for a variable to be a good proxy, it must have a close correlation, not necessarily linear, with the variable of interest. This correlation might be either positive or negative. For example, in antelope species, body size is positively correlated with group size, and the two variables covary from small, almost solitary antelope species, such as the species in the genus Cephalophus, to large herding species, such as Oryx beisa (Raerinne, 2013). A qualitatively similar correlation between body size and group size has been found in primates too. In the regression for antelope species, however, body size is a proxy for or a correlate of other variables, such as the available food supply in the home range of these species or the level of predation threat. The latter two, rather than body size, seem to represent the true causes or explanatory factors for differences in group sizes among antelope species. Body size is therefore used as an independent variable for *convenience*: it is more easily quantifiable and measurable than the putative true causes of the phenomenon. For instance, species' home ranges can be notoriously difficult to estimate, let alone to measure. Presenting a proxy as a cause is not only inaccurate but also misleading insofar as we are searching for ways to control and understand nature. Of course, the use of proxies is unobjectionable if the authors acknowledge this limitation and do not present proxies as causal factors. However, proxies are sometimes used because the true causes or effects are not easily definable as variables, in which case, proxies can be used to hide the fact that the allometries and scaling relationships in question are non-change-relating as generalizations (see below).

<sup>&</sup>lt;sup>27</sup> In mathematics, a linear equation is an equation that may be put in the form:  $a_1x_1+...+a_nx_n+b=0$ . Where  $x_1...x_n$  are the variables, and b,  $a_1...a_n$  are the coefficients, which are often real numbers. The coefficients may be considered as parameters of the equation, and may be arbitrary expressions, provided they do not contain any of the variables. To yield a meaningful equation, the coefficients  $a_1...a_n$  are required not to be all zero.

subsystems, as ecosystems.<sup>28</sup> Therefore, some critics argue that most putative MTE mechanisms must be regarded as mere statistical models based on plausibly mechanistic variables. According to O'Connor *et al.* (2007), arbitrarily assigning some components of interspecific allometric variation to the scaling, while assigning others to the normalization constant, is a reification of assumptions of statistical fitting and not a real mechanism. Such speculations may ultimately be justified by the discovery of genuine mechanisms, but so far they are merely statistical and, as such, they do not possess the robustness of mechanisms and cannot be justified by the very patterns to which the statistical models fit.

In this sense, I would argue that it is difficult to understand how allometries and scaling laws, such as those exemplified by West et al. (1997), Enquist et al. (2003), and Brown et al. (2004), represent generalizations with causal or explanatory relevance for ecology, in the sense of representing a causal or explanatory relation between variables, dependent and independent, with well-defined values. Even though it is well known that correlation does not necessarily amount to causation or provide explanation, in practice this point is often forgotten in the literature on allometries and scaling relationships, whereby body size or mass as an independent variable is claimed to explain a major part of the variation in the dependent variable. In this respect, I agree with Raerinne (2011), who defends an interventionist account of explanation, which I have anticipated in section 2.2, in which *invariance* should be the correct relation of explanatory relevance in the case of causal explanations, and that explanations should be descriptions of objective dependency relations between entities or variables. Raerinne (2011) claims that an invariant generalization is one that continues to hold under a special change - an intervention - that alters the value of its variables. According to this interventionist account of explanation, regressions or correlations,<sup>29</sup> by themselves, are not explanatory, regardless of how strong the correlation between the two factors is.<sup>30</sup> For a correlation to count as genuinely explanatory, an intervention must be performed, whereby the relationship between factors actually remains invariant. In order for there to be an intervention and a possibility of manipulation, at least some of the predicate terms of a generalization are required to be representable as variables. If a generalization cannot be tested for how it might behave during interventions in or manipulations of its variables, the claims made about its explanatory status should be treated with suspicion.

Therefore, accordingly, many large-scale ecological generalizations are not explanatory for the reason that they do not describe invariant relations. Even though some of these relationships represent change-relating generalizations,<sup>31</sup> it is quite possible that they might be joint correlation effects, because of their common causes or the causal influence of certain background conditions. That is, they would amount to cases of spurious causation (Raerinne, 2013). Moreover, even if one finds that some of these generalizations are change-relating and invariant, allometries and scaling relationships seem to offer rather phenomenological explanations that seem to require, in order to be genuinely explanatory, to be supplemented with information about the *mechanisms* that underlie them.

 $<sup>^{28}</sup>$  In mathematics, a nonlinear system is a system in which the change of the output is not proportional to the change of the input. Nonlinear dynamical systems, describing changes in variables over time, may appear chaotic, unpredictable, or counterintuitive, contrasting with much simpler linear systems. Typically, the behavior of a nonlinear system is described in mathematics by a nonlinear system of equations. The point of interest, in my opinion, is that higher ecological levels, such as communities and ecosystems, behave as nonlinear systems – thus, one cannot fit complex ecological data in a linear regression (which uses linear equations), even using plausible mechanistic variables such as temperature, for example.

<sup>&</sup>lt;sup>29</sup> In statistics, correlation or dependence is any statistical relationship, whether causal or not, between two random variables or bivariate data. In the broadest sense correlation is any statistical association, though it commonly refers to the degree to which a pair of variables is linearly related.

<sup>&</sup>lt;sup>30</sup> See Annex 1.

<sup>&</sup>lt;sup>31</sup> A change-relating generalization describes how changes in the value of its variable or variables are related to the changes in the value of other of its variables. Change-relating generalizations typically describe dynamic or active relationships between variables.

Allometries and scaling relationships with ill defined variables are non-explanatory as generalizations. Indeed, in ecology, phenomenological or superficial explanations – in which one has an invariant relation between variables but no account as to why or how the relation holds between variables – are abundant (Raerinne, 2011).

In the interventionist account of explanation defended by Raerinne (2011), causes are difference-makers. Causes and effects should be understood as representable variables. Causes are difference-makers in that they can be intervened upon to control or manipulate their effects. A change in the value of a cause makes a difference in the value of its effect. It is useful to distinguish between two kinds of causal explanation in the philosophical literature: simple causal claims and mechanistic explanations. A simple causal claim describes the causal connection between the phenomenon to be explained and the thing that does the explaining. It refers to a phenomenological or superficial causal explanation in which one has an invariant relation between variables, but no account – or mechanistic explanation – as to why or how the relation holds between variables. This account of explanation describes how simple causal claims function by identifying what is required of a causal dependency relation in order to be considered explanatory. That is, simple causal claims need to be invariant during interventions. Describing a mechanism of a phenomenon is not something that is contrary to the spirit of describing what the causal dependency relation of a simple causal claim actually is. Instead, a mechanistic explanation is a complement to a simple causal claim, since it describes how the dependency relations produce the phenomenon to be explained. In particular, a mechanistic explanation describes the internal causal structure of the phenomenon to be explained, as I have explained in section 2.2. It describes the underlying mechanism *within* the system by showing how the system is constituted and how the mechanism produces the phenomenon to be explained. Mechanistic explanations are causal and bottom-up reductionist explanations; they are causal explanations as a result of their invariance - they, or representations of them, are true if they correctly describe the mechanisms in nature (Raerinne, 2011).

Describing an "underlying mechanism" becomes, henceforth, a paramount complement to an invariant causal relationship because it shows *how* the relationship produces the phenomenon (Raerinne, 2013). A causal explanation complemented with mechanistic details provides us with possibilities of more precise interventions and information about the extrapolability of a causal relationship, because with mechanistic details we obtain information about how the parts of a system are related to one another and under what conditions parts of the system fail to operate. In brief, one gains explanatory depth (Raerinne, 2013). Many ecological mechanisms are not well known (Raerinne, 2011). In fact, most mechanistic explanations in ecology are either underdetermined by the available data or by their absence (Raerinne, 2011, 2013). Thus, many causal explanations in ecology are simple causal claims in the sense that there are no known or confirmed mechanistic explanations. When one contrasts ecology with genetics, molecular biology or neuroscience, disciplines where mechanistic explanations seem to be more prominent, ecological causal explanations appear to be merely phenomenologically invariant generalizations.

In this sense, in my opinion, allometries and scaling relationships should be understood as elucidating phenomena from available data. That is, they must be used to discover, describe, and classify the phenomena or *patterns* to be explained rather than being the things that do the explaining. Let me illustrate this point with an example.

Homeotherms (i.e., the organisms that exhibit the specific thermoregulation capacity of maintaining a stable internal body temperature regardless of external influence), poikilotherms (i.e., the organisms whose internal temperature varies considerably, being the opposite of a homeotherm)

and unicellular organisms have different i<sub>0</sub> values (is the normalizing constant independent of body size in the equations that relate their metabolic rates to their body mass - equation A1.2) (Raerinne, 2013). The values of i<sub>0</sub> are 4.1, 0.14 and 0.018 for, respectively, homeotherms, poikilotherms, and unicellular organisms. The questions raised are why the unicellular organisms have the lowest value of i<sub>0</sub>, and how and why do homeotherms metabolize at a higher rate (and therefore seem to use and exhaust relatively more resources) than do poikilotherms and unicellular organisms of similar size. These are questions demanding an explanation, because the allometries spur this kind of question without, however, providing a direct answer. Nonetheless, allometries and scaling relationships may serve a heuristic role by suggesting new research questions, prompting the postulation of new explanatory hypotheses and by helping to discover regular connections between body size and other biological variables. Rather than providing explanations, many allometries and scaling relationships represent interesting objects of explanation, giving ecology interesting phenomena to be explained and the potential to progress and mature. This is a position close to the one that I illustrated in section 1.1, according to which ecologists seek regular patterns in nature even though they do not try to organize them within a body of theoretical explanations (Lawton, 1996). The reason is that they assume that ecology has no universal laws but just observable *tendencies* that cannot be derived from basic principles. Accordingly, I would argue that ecologists accept patterns of dependence as mere descriptions (as it seems to me with allometries and scalings), but not as explanatory relations. Instead, what they take to be explanatory is a description of the mechanism that produces these patterns. I shall now argue that MTE cannot generally elucidate this mechanistic basis.

In summary, even though MTE has been praised for reinvigorating the study of metabolic and other allometries in ecology because they aim to capture interesting explanatory hypotheses, criticisms have arisen. The theory aims to show how the metabolism of individual organisms affects the structure and dynamics of ecological systems, assuming that, at all levels, from individual organisms to ecosystems, the processing of energy and materials is linked through metabolic constraints and that the biogeochemical processes in ecosystems are largely consequences of the collective metabolic processes of the constituent organisms. Some ecologists (West *et al.*, 1997; Enquist *et al.*, 2003; Brown *et al.*, 2004; Allen *et al.*, 2004) think that metabolism is one of the great unifying processes in biology, making connections between all levels of organization possible, a theoretical hypothesis that I consider very robust.

Notwithstanding, I would argue that the proposed mechanistic bases of MTE are inadequately tested and supported, and that they are also inconsistent with fundamental aspects of ecology and physiology. My opinion is underpinned by two criticisms: that the cost of transport minimization is an untenable form of optimization by natural selection and that the Boltzmann normalization of thermal effects on metabolism requires a uniform response to temperature not observed in most organisms. Due to these concerns, it is difficult to resist the conclusion that the mechanisms underlying metabolic allometries postulated by MTE are not the only ecologically relevant ones. From this point of view, the main problem of MTE is that its mechanisms are treated as presumptively validated as well as mutually exclusive of other mechanisms proposed to explain allometries.

Thus, I find MTE lacking a universal explanatory mechanism for allometries and scaling relationships because: the proposed mechanisms are disconnected from the hypotheses they motivate, the putative mechanisms seem biologically implausible and the proposed universality of the mechanisms is untenable. The theory, at best, highlights potential physical constraints imposed on the allometry of metabolic rates, and might be considered as a result an oversimplified and insufficient description of the mechanisms underlying metabolic allometries. The upshot is that it cannot be considered a unifying model of mechanistic explanation for the simple reason that one must

acknowledge that multiple mechanisms are likely to be involved in metabolic allometries. I would also argue that we cannot suppose that the so far illustrated criticisms are based, instead of on the analysis of available empirical data, on purely philosophical grounds. The "metaphysical" critics of MTE seem to operate under the belief that unifying principles in biology and ecology, as metabolism surely is, do not exist and that all species are unique, arguing that the optimization of physiological traits is almost impossible in nature and that all aspects of natural selection are idiosyncratic and therefore unpredictable. I would argue that this latter critical perspective leaves no room for general predictive theories and, for this reason, it is not a sufficiently strong criticism of MTE. The MTE approach, in contrast, is based on the theoretical assumption that ecology is well served by the development of general quantitative theories yielding testable predictions, including how organisms will respond to environmental change. This theory is formulated on the premise that organisms share many common attributes, particularly with respect to metabolism, assuming that there are general principles governing the process of evolution, and that these are inextricably linked to individual energetics, therefore embracing the principle of evolutionary optimization. I am not a "metaphysical" critic and I think that ecologists should not abandon unifying principles. The crucial issue, in my opinion, as I have already argued, is the oversimplification in describing the putative mechanisms of the MTE, which is conspicuous in the insufficiency of empirical evidence in support of MTE.

I think we have to recognize that a general theory as MTE will never be able to explain *all* the variation of biological phenomena due to the inherent complexity of biological systems and that, necessarily, further work is required, testing all assumptions and predictions of its models. Nevertheless, I believe that MTE has succeeded in explaining a good range of phenomena at various levels of biological organization and eventually holds some promise for somehow linking individual organisms to populations and then to communities and ecosystems using metabolism. This can turn out to be a valuable contribution to a moderate approach in ecology, since it provides a deep study of *components* at various levels of ecological organization. I shall explore, in the next section, starting from some limitations of the MTE, the new perspective provided by the New Mechanicist Philosophy in explaining ecological phenomena.

### 2.2.3. The New Mechanicist Philosophy and Mechanistic Explanation in Ecology

MTE is founded on the promise of providing a mechanistic explanation for allometric phenomena based on the application of physical, chemical, biochemical and physiological principles. We have seen in the previous section that empirical evidence is lacking in order to vindicate its explanatory pretensions, while its theoretical assumptions are arguably invalid or at least difficult to evaluate.

Following Raerinne's suggestion that mechanisms are networks of invariant causal relationships (Raerinne, 2011, 2013), as outlined in section 2.2.2, mechanisms should not only capture the overall relationship of dependence of the mechanism's phenomenon on its components, but should also show *how* this relationship arises. The preceding discussion on MTE showed that the explanatory goal of ecologists goes beyond documenting putative dependencies between variables, such as allometries and scalings. Rather, they seek to uncover *how* stable dependency relations between variables arise. Ecological explanations require more than just specification of invariant generalizations about the behavior of components and how the overall output of the mechanism varies under interventions on the input to each component.

Pâslaru (2009), following Tilman's work on what counts as an acceptable mechanistic explanation in ecology (Tilman, 1987), suggests that the New Mechanicist Philosophy (henceforth,

NMP) is a promising starting point to delve with these issues. According to Tilman, one has a good mechanistic explanation in ecology (in this illustration for the specific case of competition) "(...)if it includes both the direct processes by which competition occurs and information on physiology, morphology, and/or behavior of individual species or functional groups relevant to that direct processes (...)" (Tilman, 1987, pp. 771). In order to make sense of Tilman's suggestion, Pâslaru (2009) presents a simple example of niche complementarity, which is one of the mechanisms articulated to account for the dependence of ecosystem functioning on biodiversity. This mechanism is based on species differences and their interactions. In this case, niche complementarity occurs when there is a shade-tolerant species and a shade-intolerant species.<sup>32</sup>

Niche complementarity requires that organisms of different species are different in their functional traits, whereby this difference determines species' differential use of resources and nutrient use efficiency. Furthermore, ecosystems' composition with species with different functional traits, allowing them to more efficiently uses a greater amount of resources from different ranges, increases ecosystem productivity. Hence, the greater the number of functional groups, the greater the overall ecosystem productivity is. Organisms of different functional groups occupy distinct niches and can exploit their resources differently; this differential exploitation, in turn, increases their body mass and, consequently, the overall productivity of the ecosystem.

Let me now consider the more general issue regarding the nature of mechanistic explanation in order to apply it to ecology. The supporters of NMP, such as Machamer *et al.* (2000), Glennan (2002) and Bechtel *et al.* (2005), have different conceptions, but they are all committed to the following tenets, as explored in a more detailed way in section 2.2: a) mechanisms produce phenomena, and describing the mechanism responsible for the phenomenon under scrutiny amounts to an explanation of that phenomenon; b) mechanisms are compositional, in the sense that they have working parts, which are relevant to the working of a mechanism in virtue of some of their properties but not all of them; c) all mechanisms are constituted by causal relations, in the sense that the components of a mechanism that act and interact in a particular way are able to produce a behavior; d) the components of mechanisms must be organized because, in order to produce a phenomenon, the components and their causal relations must be spatially (location, shape, size, orientation, connection, and boundaries of components) and temporally (order, rate, duration, and frequencies of activities) related.

According to Pâslaru (2009), these tenets of NMP capture some important facets of ecological mechanisms, as illustrated in the previous example. For instance: a) Ecologists see mechanisms as being responsible for a certain output and, in this respect, the niche complementarity mechanism may explain why ecosystem productivity increases with diversity; b) From the viewpoint of NMP, the components of the niche differentiation mechanism would be the individual organisms and their

<sup>&</sup>lt;sup>32</sup> In Pâslaru's niche complementarity example (2009, pp.826-828), each leaf layer consists of leaves that photosynthesize at a rate corresponding to the light conditions of that layer and respire at a rate of a unit per leaf. Net assimilation is positive for the upper layers but turns negative for lower layers. At the lower layer, the shade-intolerant species does not find adequate conditions. By contrast, the shade-tolerant species is able to develop well. Thus, lower layers represent a different niche that is suitable for the shade-tolerant species but not for the shade intolerant species, which finds its adequate conditions in the niche represented by upper levels. When both species occupy their niches—which amounts to niche complementarity—solar radiation is utilized more efficiently such that photosynthesis, respiration, and net assimilation rates are increased for both species. And this translates into higher biomass production and higher ecosystem productivity. This happens, however, only when the shade-tolerant species is present, and not simply if the shade-intolerant species grows more leaves. The shadetolerant species positively affects the shade intolerant species by preventing the leaves of the lower leaf layer from being a respiratory drainage on the shade-intolerant species. Plant morphology is a further determinant of this interspecific interaction and of how efficiently available solar radiation is utilized. In particular, different leaf morphologies and the number of leaves on each level determine differentially the percentage of the occupied leaf area at that level. If the total percentage across all levels is higher, then the total light assimilation and, ipso facto, biomass production is higher.

interactions with sunlight. This focus on the organismal level is consistent with the claim of ecologists that certain mechanisms - for instance the mechanism of competition-operate at this level. If photosynthesis or respiration were the relevant activities, then relating them to the organismal level is supported by the fact that these activities require certain physiological systems found at that level. Yet, ecologists extrapolate from the organismal level to the population level and often speak about species, or functional groups, as being the relevant components. However, the species as a collection of organisms does not have the proper physiological system able to perform photosynthesis or respiration. Thus, c) Respiration, photosynthesis, assimilation etc. are activities or operations whose specification is the key to articulating an explanation of the interaction between the organisms of two species; d) The organization of components is central in ecologists' discussion of niche differentiation. The shade-tolerant plant has to be in close proximity to the shade-intolerant plant so that it can be protected from excess sunlight. Thus, the plants have to be spatially organized. Duration and variation of sunlight during the day as well as the rates of respiration, of photosynthesis, and of assimilation are instances of temporal organization and, in addition, they are measured at each layer, which is a facet of spatial organization. The geometry of leaves is considered as well in genuine mechanistic explanations because their shape and size are decisive for the ability of plants to interact in a manner that creates niche complementarity.

Pâslaru (2009) argues that NMP successfully captures the above mentioned aspects of the mechanism of niche complementarity; however it recognizes that NMP encounters difficulties when it tries to account for what is remarkable about mechanisms, namely, that they always work or, for the most part, that they work in similar ways under different conditions (Machamer et al., 2000). Niche complementarity functions despite various changes in its components and background conditions. For example, organisms of various shade-tolerant species can play the role of the shade-tolerant plant. Moreover, the relationship between biodiversity and ecosystem processes holds despite variations in the number of species involved, their identity, the number of functional groups and variations in the environment. This compositional variation implies variations in the organization of the mechanism and in the activities and interactions of its components; yet ecologists would think that it is the same mechanism. This aspect of the mechanism is difficult to capture with NMP because its supporters defend a formulation of a more specific account of the causation exhibited in each particular case. To fulfill this aim, NMP requires that the activities or interactions that take place must be specific. This obscures the fact, however, that there is a more general causal relationship between biodiversity and ecosystem functioning that is not affected by various changes in components. In order to overcome this impasse, Pâslaru (2009) proposes a mixed solution by relying on the notions of *invariance* (i.e., causal relationships remain invariant, that is, they remain stable across various changes in the values of variables of the causal relationship, as proposed by the interventionist account of explanation seen in section 2.2.2), insensivity (i.e., causal relationships are also insensitive, meaning that they are not affected by modifications in the background conditions of variables or by changes in the actual circumstances of the relationship) and the conception of mechanisms in terms of causal networks.

Invariance characterizes the niche complementarity mechanism in several respects (Pãslaru, 2009). The overall relationship between biodiversity occupying complementary niches and ecosystem processes is invariant within a certain range of variation, for instance in species composition. Productivity will vary under interventions that change the number of species, the number of functional groups in a community, or the identity of species in functional groups, yet the overall causal relationship between these factors and productivity will hold. The activities of organisms involved could be photosynthesis, nutrient uptake, or foraging. Niche complementarity would still occur among these organisms.

The biodiversity-productivity relationship turns out to be often insensitive to these changes in the background, indicating that more diverse ecosystems withstand environmental stresses and are still able to support ecosystem processes. The same reasoning applies to variations in other abiotic factors (Pãslaru, 2009). The biodiversity-productivity relationship would occur and thus be insensitive to variations, within a range of tolerance of organisms: in temperature, sunlight, or chemical composition of the air. The limiting resource could be sunlight, or water, nitrogen or calcium, or other nutrients. The biodiversity–ecosystem processes relationship is insensitive to all the above-mentioned types of variation, since species will have to be organized in complementary niches in order to maximize resource intake.

Following Pâslaru argumentation, I think that an account of ecological explanation would benefit by integrating the contribution of the New Mechanistic Philosophy and Raerinne's notions of invariant and insensitive causal relationships. After all, the objective of ecological explanations is to reveal the invariant and insensitive causal structure of the ecological phenomenon under examination and to show, in the light of the available knowledge of the properties of components, their causal roles and organization, how this structure causes the phenomenon, exactly as NMP suggests. Thus, these two perspectives are complementary because when one specifies only the causal dependence without the mechanistic details, one sacrifices the realism of the general model. Conversely, if one describes all the mechanistic details, the model turns out to be realistic but at the cost of limited applicability. I would argue that ecology is interested in models that are, at the same time, general and realistic, as I have discussed in section 1.1.

In short, I would argue that the most important merit of mechanistic reductionism in ecology is the claim that we need to go "inside" an ecological phenomenon. This phenomenon can present itself, in the first approach, as an immediate and vague complex or whole and, in order to disentangle it, one has to find its constitutive dimensions, parts, causes, organization and relations, and to study their specific properties and contributions to the production of the ecological phenomenon as a whole, in an analytical way. This, I would argue, is the most relevant contribution of mechanistic reductionism for a moderate approach. Otherwise, as I have emphasized above, there would just be an external, phenomenal description of what the whole does as a whole, but no explanation of why it acts and behaves the way it does. However, as I have also referred above, ecologists extrapolate from the organismal level to the population level and often speak about species populations, or functional groups, as being the *relevant components* for explanation. This is an abstraction that reflects a choice, chosen for reasons of convenience. In spite of losing information about individual variability and locality, as I have already illustrated, in not using IBMs and preferring a population-centered approach, ecologists assume to resort to processes of abstraction that can give rise to useful models. I think that the important thing is to recognize their status as abstractions, both legitimate and at the same time incomplete, as intellectual constructs that are an approximation to reality. As I will illustrate in the empirical example for a moderate approach, the data that is used is all about species populations and, sometimes, taxonomic groups.

In summary, there are some limits to the reductionist approach. I think that the most relevant is the expectation that an ecosystem can be fully explained by studying the parts as if they were isolated or previous to their integration, i.e., in terms of their intrinsic properties and respective relations, and just add certain laws of composition to account for the global organization of those parts. To explain any organized whole one needs laws of composition, but these laws do not belong, nor are directly derivable from the micro-laws concerning the parts; the latter describe how the components would behave if they were *isolated*. But they are not isolated and, as a consequence, one needs to assert how the behaviors of parts combine. Furthermore, in a particular class of organized wholes called

integrative wholes (Santos, 2020), such as ecosystems, even laws of composition (e.g., concerning the organization of mechanisms) are not enough. It is not sufficient to know how the parts compose or combine at one particular temporal stage. One needs also to study the transformations and interdependencies of the parts via their intra-systemic relations. So, there is a partial and reciprocal *co-determination* between parts and wholes – between the properties of the parts and the system's structure of relations – that is crucial to understand the emergent properties of the ecosystem. I will further develop this dynamic relational ontology in section 4. But before doing this, let me first describe the theoretical developments in ecology stemming from the holistic approach, founded on comprehending the properties of an ecosystem as a whole.

# 3. The Holistic Approach in Ecology

In this section I will start by illustrating the foundations of the holistic position in ecology and, afterwards, by relating how this position has driven the construction of classical ecosystems ecology and, consequently, the latter developments in post-classical ecosystems ecology. The objective of this section is to identify the holistic elements that I consider more relevant to elaborate the moderate approach to ecology that I shall defend in section 4.

### 3.1. The Classical Holistic-Organicist Position

According to organicist holism, supra-organismic units are collections of organisms that are determined primarily by relationships of dependency between organisms (Looijen, 2000, Bergandi, 2011; Trepl *et al.*, 2011).

The whole depends heavily on the activities of the parts. In a stable end state or "climax", however, the relation between parts and whole consists essentially in each individual part being brought forth by all the others, and therefore in a reciprocal bringing forth of the parts and the whole. Thus, individual organisms, or even units made up of several organisms, such as functional groups of producers, consumers and decomposers, exercise certain functions within the community as a whole, much like, by analogy, organs in an organism. These functions need to be carried out in order to preserve not just the whole but also the organisms themselves which carry out the functions. Thus, populations, communities and ecosystems are regarded as analogous to organisms in the sense that they have the capacity for self-regulation (Trepl *et al.*, 2011) through various feedback mechanisms and also in the sense that they are connected through a network of interactions analogous to that realized by the physiological mechanisms that maintain organismal homeostasis.

Every ecological entity is a whole, which exists objectively, just like an individual organism, and can be individualized in space and time, if somewhat less clearly than an individual organism (Trepl *et al.*, 2011). The methodological consequence of this perspective is that the characteristics and behavior of individual organisms need to be examined according to the contribution they make towards the functioning or adaptation of the community as a whole.

Thus, the holistic view in ecology is that the entities at higher levels of organization – like communities or ecosystems – are discrete, integrated wholes with their own emergent properties which cannot be derived from properties of the component species populations and individual organisms (Looijen, 2000; Bergandi, 2011; Trepl *et al*, 2011). One relevant characteristic of this view is that it is primarily organismic or physiological.

The organicist-holistic theory is also a theory of development.<sup>33</sup> Therefore, the image of nature in holistic ecology is erroneously seen as static whenever ecological balance occurs. Just like an individual organism, the community develops according to internal rules of development through different "stages" to reach a state of maturity – i.e., the climax – and it maintains itself in this state or else embarks anew on the process of development. Thus, communities and ecosystems show a development from a young to a mature stage, in analogy to the ontogenetic development of organisms. The standard example of this view is due to Clements, who described plant communities as superorganisms that, analogously to real organisms, have a certain physiological integrity that comes into existence, growing and then ripening until the stable "mature stage" or climax (Clements, 1916). His theory, according to Phillips (1935a,b), is meant to explain a phenomenon known as "succession", i.e., the development of a plant community starting with the first plant growing on a previously bare soil and which runs in the direction of a more or less stable end phase, the above referred climax.<sup>34</sup>

Succession was mainly seen, by the earlier holistic ecologists (for instance Clements and Forbes), as the result of interactions between species, in particular competition; the species were constantly being displaced by other species until in the end only a few dominant survived.<sup>35</sup> The succession of different species at a certain site became an act of self-sacrifice on the part of pioneer species for the benefit of the community at later stages and, ultimately, the climax community. From the perspective of community, this process of replacement means that it adapts as a whole to environmental conditions. This occurs through a change in the composition of its species, prompted by competition and through internal differentiations, in particular in the number of species and in the number of interactions. At the same time, the community adapts the local environment to itself, and one can say that the community adapts it to its own future constitution. In this way, the community becomes increasingly independent from specific site factors – from those that existed initially but no longer exist, and from those that will exist in later phases in the sense that they will influence the organisms indirectly, through the community. Thus, the development of a community is simultaneously a process of adaptation and detachment in the holistic approach (Trepl *et al.*, 2011).

The later concept refers to the fact that the dependency of the whole on external factors decreases as the dependency of the parts on one another and the way they adjust with each other increases. The climax stage is such that it no longer engenders changes to the external and internal conditions of the species in the community. Instead, each individual organism processes the impact of external factors through their interactions in such a way that the state of the whole remains unchanged.

Differentiation, as an increase in diversity, internal functional dependency and mutual adjustment, as well as independence from external factors – in line with the homeostasis of an individual organism –, all occur together in a necessarily common context. This theory of development implies two different concepts of environment: first, the many and varied small-scale, temporally different site factors– edaphic (i.e., soil characteristics and conditions) and microclimatic – where the community lives, which in the course of succession relinquish their influence on the development of the community, and which the community then adapts to; secondly, the regional climate, over which it

<sup>&</sup>lt;sup>33</sup> Phillips (1935, pp. 211-216) made an exhaustive analysis of the concept of development in the context of ecology and its relation with the concept of succession, investigating its most relevant features.

 $<sup>^{34}</sup>$  For Phillips (1934, pp. 556-565), ecological succession may be defined in terms of three parameters: it is an orderly process of community development that is reasonably directional and, therefore, predictable; it results from modification of the physical environment by the community – that is, succession is controlled by the community even though the physical environment determines the pattern, the rate of change, and often set limits as to how far development can go; it culminates in a stabilized maximum biomass.

<sup>&</sup>lt;sup>35</sup> Forbes (1887) presents a somewhat teleological perspective, claiming that equilibrium is reached and maintained and that this idea is "solid ground for a belief in the final beneficence of the laws of organic nature".

has no influence and to which the community itself adapts in the course of its development. Adaptation is complete in the climax state (Trepl *et al.*, 2011).

Thus, in organicist holism, succession is conceived as *goal-oriented*. Even if we were not to interpret it in explicitly teleological terms, it is still a teleological process at least in the sense that it proceeds towards a final state conceived as fixed from the start, in a *deterministic* way. The implication of this is that the organicist approach faces the accusation of having an inadequate methodology, in the sense that the study of nature should provide causal explanations and avoid teleological ones. This criticism highlights that values or goals can only be attributed to nature by us, while everything that is viewed from a genuine scientific perspective is actually value-free and without purpose. Nonetheless, it is worth noting that, particularly in the life sciences, it is common to "contravene scientific method" along similar lines; for instance, teleological terminology is often used to describe the physiology and behavior of an organism, while terms like benefit, optimum, and developmental goals, though betraying a teleological connotation, can be meaningfully applied in the scientific context. The organism is conceived of in such a way that each of its parts owes its presence to the agency of all the other parts and exists for the sake of the others and of the whole: the parts are organs of the whole. Thus, when one speaks of the function of the organs being to maintain the organism, one is making a teleological judgment. The term self-maintenance, when applied to an organism, assumes that the state of life is the purpose and desirable goal of the organism. In this way, I suggest that it is possible to attribute a value to living phenomena that is at the same time objective and not related to a specific external value system.

At the same time, we can discuss if it is fruitful in science to assert that things in nature happen according to some purpose. The orientation toward purposes presupposes the idea of a preceding goal, of an action based on intention, even though we cannot insinuate that nature has intentions. At the same time, it is important to note that even the individualistic position is vulnerable to the same criticism, in the sense that it too considers individual organisms as organic wholes, that is, as entities with the goal of self-maintenance.

Thus, I believe that the mechanistic criticism of teleology is unjustified when teleological explanations are intended *heuristically*. Indeed, it is biologically useful to regard the individual organism as a whole and to think of its parts as elements that serve the function of maintaining it in order. Surely, if the life sciences are to be natural sciences, they must use causal explanations. I would argue that heuristic teleological judgments might be genuinely causal in the above sense. At least, they betray allegiance to methodological holism. In my opinion, this can be held against mechanistic reductionism: if the self-maintenance of an organism was not conceptualized as constituting the purpose of the physiological processes going on within it, even if only heuristically, then one would not be able to find a starting point for physico-chemical explanations, couched in reductionist terms.

The holistic approach in ecology not only conceives the individual organism as an individual whole. Also the community, the ecosystem and even the entire biosphere are conceived as wholes. These wholes, on their part, consist of hierarchically interacting individual wholes. It is the function of the parts in the service of the whole to work in such a way that everything supports everything else – just like the relation between organs and organism. In analogy with the criticism of organismal teleology presented above, it might be equally difficult to understand how ecological explanations couched in terms of the function parts have in relation to the community as a whole should be considered scientific. As a matter of fact, the nature of the criticism seems stronger: while organs cannot live outside an organism, organisms can live outside their respective population or community, for instance in others or in complete isolation. I accept that it is highly questionable, therefore, whether

a teleological judgment relating to the whole community or ecosystem makes sense, even if it is only intended heuristically. In brief, I recognize that it is a big problem for ecological holism justifying its physiological approach.

Phillips (1934, 1935a,b) tried to make philosophical sense of Clements' concept of biotic community as a complex organism, tackling the above polemical issues concerning the essential nature and direction of succession and development, the nature of climax, the existence of a possible superorganism, and its inherent oneness as a biotic community. Phillips sought support for the concept of the superorganism from philosophy, turning to the concept of holism, arguably originated in its contemporary form by Jan Smuts in a 1926 book, *Holism and Evolution*. This author identifies unified structures, which he called *wholes*, created by a process of creative synthesis, in which the whole is the synthesis of the parts. Smuts (1926) stressed that the whole is not a simple object, but a complex one, consisting of many interacting parts, even arguing that the concept of the ecological community.

It is important to emphasize that ecology, as structured within a holistic ontological framework, takes the form of an organicist worldview. This is chiefly because, according to Clements (1916), the climax formation is, as a matter of fact, an organic entity, which grows, develops, and dies like an organism. Clements created an inspiring concept of nature that was deterministic, all-inclusive and internally coherent. Later, Phillips (1935b), pursuing his committed organicist position, concluded, following Clements, that an ecological succession is always the result of biotic interactions on the environment and that it is always progressive, converging toward an end-point. The upshot of this view is that the same biotic community is a complex organism (Phillips, 1935b). I think that the phenomenological reading (in the sense of a interpretation of observable phenomena not requiring explanations in terms of deeper underlying entities and relations) of this ecological organicism hides a more essential level of interpretation, because these authors, in reality, wanted to point out the holistic ontological dimension of ecological entities, i.e., they sought to underscore the "organizational" idea that is inherent in biotic entities, in the sense that organization is the core idea behind a whole. However, it is noteworthy that while Forbes (1887) supported a conception of biotic community that, while certainly holistic and expressed in organicist terms, is substantially pre-emergentist, Clements (1916) and Phillips (1934, 1935a,b) were proponents of an organicist perspective that clearly involved the concept of *emergence*:

"Very briefly and generally stated, it is the view of the authors and disciples of this concept that there is a creative synthesis and emergence of properties, structures, forms, stages or levels; such newness, springing from the interaction, interrelation, integration and organization of qualities-whether these be inorganic, organic, or psychic-could not be predicted from the sum of the particular qualities or kinds of qualities concerned; integration of the qualities thus results in the development of a whole different from, unpredictable from, their mere summation (...)For the ecologist it appears to offer a vantage point from which to survey characteristics of novelty, of integration, of wholeness, emergent from succession and development in biotic communities. Direct contact is thus seen to be possible, nay, essential, with the thesis that communities are not mere summations of individual organisms, but are integrated wholes with particular emergents." (Phillips, 1935b, pp. 489-490)

I suggest that this affirmation of *emergentism* is extremely important, since it holds, as I have anticipated in section 1.2, that the various levels of organization are characterized of new and specific properties increasing the degree of complexity of a given level compared with the various levels of which it is composed. It is noteworthy that, for Philips, emergence seems an essential conceptual tool in ecological research.

Currently, the radical holistic Clementsian approach at the level of communities has been abandoned in favor of reductionist approaches, which I have described in section 2, even though it remains alive with regard to ecosystems ecology. Around 1960, a strong movement in ecology arose that applied the holistic approach to ecosystems, a concept coined by Tansley (1935).<sup>36</sup> The vision of these earlier systems ecologists showed a great resemblance to the Clementsian view of plant communities. Nevertheless, by contrast, Tansley (1935) departed from the referred Clements' and Phillips's organicist perspective by proposing a more integrative holistic entity, i.e., the physical system constituted by the individual organisms and the physical factors, in which the former "cannot be separated from their environment due to the constant interchange of the most various kinds within each system, not only between the organisms but between the organism". Tansley's ecosystem concept identifies specific systems as elements in a hierarchy of physical systems ranging from the universe to the atom. In the ecological sense, the basic system of ecology is composed of both the "complex organism" and the physico-environmental complex.

In my opinion, Tansley's "Use and Abuse of Vegetation Concepts and Terms" (1935) aimed to defend ecology from extreme philosophizing approaches and to maintain its connection to mechanistic and reductionist science, thus protecting its reputation within the life sciences by avoiding vitalism, an idealistic concept widely debated at the end of 19<sup>th</sup> and the beginning of the 20<sup>th</sup> centuries. At that time, vitalistic concepts were frequently used in biology to explain phenomena that appeared to be unexplainable in materialistic terms. However, one after another, these phenomena were explained by conventional research founded on materialistic principles, and, as a result, the vitalist argument was discredited. Tansley, aware of these arguments, probably became suspicious of certain strands of holistic thinking, whose conceptual resources were at odds with standard ecological methods of analysis. Another interesting perspective developed by Tansley was the idea that holism could be described in a less idealistic form. He was a *materialistic holist*, concerned about how parts are organized to create wholes, that is, about the rules used to assemble parts into functional wholes. Thus, he not only accepted the value of reductionism, agreeing that it is necessary to understand the parts and how they act in isolation, but also added that it is essential to understand the rules of assembly allowing the parts to make a whole. Both Phillips and Tansley were materialists. Phillips was a materialist using a more idealistic holistic philosophy to support the concept of the complex of organisms. Tansley, aware of the split between reductionist and holistic materialism that was tearing apart ecology, sought a common ground. His ecosystem concept was a bridge, avoiding organismic theory. He presented a physical theory that was founded on the concept of *equilibrium*. Within this context, equilibrium and stability provide the foundation for assembly rules, in the sense that the more stable the system, the more likely it is to persist.

Although Tansley's 1935 paper was mainly concerned with the terms and concepts reviewed by Phillips – i.e., succession, development and the quasi-organism, climax, the complex of organisms, and biotic factors – the new idea he offered was the *ecosystem concept*, emphasizing its physical character and its relation to physical systems in general, based on the concept of equilibrium and making relevant the interactions between physico-chemical and biological components. I think that Tansley's emphasis on the interaction between the biota and the abiotic environment was an important conceptual advance and opened the door for the later wider use of energy theory and matter cycling in ecology, as I shall illustrate in section 3.2 in more detail.

<sup>&</sup>lt;sup>36</sup> Tansley (1935, pp. 297-300) thought, in accordance with the holistic position, that the webs of life adjusted to particular complexes of environmental factors were real wholes. However, he preferred to regard them, together with the whole of the effective physical factors involved, simply as "systems", in the sense that they were not properly described as "organisms".

According to Tansley (1935), even though the community is composed of organisms in mutual association, examination must be conducted using an *analytical and anti-emergentist* perspective, because of the "necessity for investigation of *all* the components of the ecosystem and of the ways in which they interact to bring about approximation to dynamic equilibrium" (Tansley, 1935, pp. 305). Tansley's rejection of the Clementsian worldview followed, in a way, in the footsteps of a certain atomistic and individualistic point of view that I have explored in section 2, in the context of classic individualistic-reductionist approach. The lack of sharp limits and structure of communities was the fundamental reason pushing Tansley to see in these ecological entities the result of random immigration and environmental variations. This non-oriented, random juxtaposition of organisms determined structurally different forms of associations, whose study required analytical methods.

A more recent approach pursing the original ideas in Tansley's theory of equilibrium is due to Eugene Odum (1969, 1971), probably the most important representative of the earlier strand of holistic systems ecology. Odum (1969) argued that ecosystems are generally stable and have a "strategy", showing a development (succession) from a young to a mature end phase (climax). However, a major difference between Clements and later systems ecologists is that, while the former view was primarily physiological and can therefore rightly be called superorganismal, the vision of modern systems ecologists has some reductionist mechanistic elements, not in a sense of a strictly mereological approach (according to Hagen's 1989 distinction, see p. 5), but rather following Tansley's vision and methodology, that is, in the sense of an application of thermodynamics, information theory and general systems with the capacity of self-regulation, something analogous to homeostasis in organisms. I shall develop these points in section 3.2. For now, I would just like to reinforce Odum's argument that ecosystem studies should be based on *a whole before the parts* approach – the ecosystem concept should be a broad one, and its main function in ecological thought lies in emphasizing interdependence and causal relationships (Phillips, 1935a).

This emphasis on interdependencies and relationships, and the associated ideas about stability and self-regulation, can be seen as modern expressions of the much older concept, already referred to in section 1.1, of "balance of nature" (Egerton, 1973). These relations form the core of holism in ecology. Parts, whether they are organs in organisms, organisms in populations or populations in communities and ecosystems, are seen as functionally related in the whole. Holistic systems ecology is thus generally equated, by both proponents and opponents, with "functional" ecology.

Yet, it is not the individual organisms or populations as parts of the whole that form the units of ecosystems research. The units of this research are the so-called *trophic levels*, or food levels, such as primary producers, first-order consumers, second-order consumers and decomposers, as proposed by Lindeman (1942). This ecologist was the first to implement Tansley's ecosystem concept explicitly in a quantitative effort to define the system and describe and understand its dynamic behavior. The trophic levels are conceptual black boxes, theoretical compartments through which energy and matter flow. The information on the content of these boxes does come from metabolic studies of individual organisms and populations, which as a consequence are not objects of study in themselves, as they are in the reductive mechanistic approach. Ecosystem research is specifically targeted at estimating the amounts of energy and matter entering into each trophic level and the efficiency with which they are used, a topic I shall explore in more detail in section 3.2. Thus, with Lindeman (1942), the ecosystem became the fundamental unit of trophic-dynamics, which can be organized into trophic levels. Lindeman also demonstrated that one could identify an ecosystem as an object in the physical environment, defined by boundaries, which can be studied as a system. This system has a structure composed of living species and non-living material. It also has a metabolism and converts input

energy from the sun into heat energy or energy stored in inorganic matter. It can receive nutrients, and recycle them through the biota and non-living materials, transforming them into water, atmospheric gases and food for living beings. It has also a developmental pattern, changing through time, in the course of the above mentioned process of succession, the latter being a function of the interactions of the biota and non-living material with external climate, nutrients, and human disturbance.

Tansley's ecosystem concept has had a decisive influence in the development of ecology. His categorization of the "basic unit of nature" was rendered dynamic by Lindeman's energetic approach, which was based on an analytical and additive methodology tailored to explain ecosystem dynamics in terms of energy exchanges among the different compartments in the biotic community and between the community and the physical environment. Lindeman's focus was on the dynamic processes of the system, expressing it in the language of energy. Lindeman (1942) introduced most of the major questions and concepts of modern ecological energetics, including questions about the length of food chains, the efficiency of trophic transfers, the storage of energy at different levels, the rates of primary productivity, the problems of correcting energy values for losses due to respiration, predation, and decomposition, and the role of bacteria and microorganisms in recycling dead organic matter. In addition, Lindeman made clear the idea that ecosystems develop through ecological succession and are tied to the energy dynamics of the system and the concept that nutrient cycling, such as food cycling, is linked to the wider biogeochemical cycles coupling one ecosystem with another.

Henceforth, Odum, following the works of Tansley and Lindeman, developed an ecological paradigm that combines this energetic ecosystem framework with a holistic and emergentist ontology, according to which ecosystems are complex entities characterized by emergent properties that cannot be predicted by strictly applying the analytical method, a claim that I am to defend. This holistic approach takes into account the ecosystem as a whole. It is important to note that, although Odum denies too much value to epistemological reductionism, at the same time he locates the theoretical core of systems ecology in energetic analysis, which involves the study of components, as Tansley did.

From then onwards, ecology has been perceived, in a sense, as the chief holistic science. The holistic position outlined in this Odumian perspective provides a hierarchical worldview where every level of organization is characterized by a specific degree of complexity and by properties that are not predictable, or explicable, from the study of the lower levels alone. Emergence and emergentist ontology are the cornerstones of the Odumian ecosystems paradigm, and will be, as I shall try to argue, the main foundation for the chief claim I would like to defend in my thesis concerning the explanatory power of the systems approach to ecology. The reason is that, as I shall argue, the *strictly* reductionist and mechanistic approach is not able to tackle the issue of emergent properties, and that all systems with emerging properties cannot be described by listing all the components and their properties.

In summary, the units that are relevant for explaining ecological phenomena, according to the holistic position, are the *community* and the *ecosystem*. This choice is underpinned by the endorsement of a holistic and emergentist ontology, which is based on the thesis that these complex entities are objective, real, and endowed with emergent properties. They are therefore conceived as wholes, composed of parts. These wholes depend heavily on the activities of their parts and on the interrelations between them. This position does not dismiss the need to decompose wholes, but it contends that this methodology is not sufficiently explanatory to understand their behavior and properties. In analogy with an organism, the idea that these ecological entities develop deterministically, into a mature and stable stage, named climax, through a process called succession is evident. According to the chosen analytic purpose, the ecologist can establish the boundaries of the

physical system under study. This physical system or ecosystem is thought to be composed by trophic levels, whose study allows analyzing the energetic ecosystems framework and the flux of energy and chemical elements through the ecosystem.

I will now critically analyze in detail the recent developments of the holistic approach, namely, the formulation of classical and post-classical ecosystems ecology, trying to identify the relevant elements that I will endorse in support of the moderate approach in ecology defended in this thesis.

### 3.2. The Modern Holistic Ecosystems Approach in Ecology

In this section I shall start to analyze how the ecosystem concept has evolved and its importance for the construction of classical ecosystems ecology. Afterwards I will describe different perspectives in the description of ecosystems such as ascendency, eco-exergy and the ecological law of thermodynamics, which are all concepts of post-classical ecosystems ecology.

### 3.2.1. The Ecosystem Concept in Classical Ecosystems Ecology

As described in section 3.1, Lindeman (1942), by harnessing Tansley's (1935) ecosystem concept, provided the outline of a research program that would occupy holistic ecologists for the following decades. This program was founded on the thesis that nature is organized into ecological systems, which are recognizable objects having an origin and developing to a steady state or dynamic equilibrium. These systems have a structure, defined as a network of feeding relationships among their species' populations that can be simplified by grouping the populations into food chains or trophic levels. According to this view, the ecosystem has a characteristic behavior, beyond that of developing, involving the processing of energy received from the sun or other ecosystems into work or heat as well as the processing of chemical elements imported into the system. These are the energy flows and the nutrient cycles occurring between the species' populations and between them and the nonliving parts of the system. The structure and the function of the system can be expressed mathematically as a series of equations describing the interactions between the systems' components.

In brief, Lindeman (1942) introduced another way to view the natural world. The species' populations constituting the community were to be identified and their biomass was to be determined. This information was then organized into a model that showed how they interact with each other (based on their feeding, predation and parasitic relations), and with the abiotic environment. He assumed that the species could be aggregated into groups (trophic levels) of species either feeding on each other. The amount of energy or food flowing from one trophic level to another – represented either as the amount stored in a group at one time or as rates of flow – could then be compared using ratios of efficiency. Lindeman's use of energy to express the relations between trophic levels linked ecology with thermodynamic theory in physics.

On the theoretical basis provided by Lindeman's contribution, Eugene Odum (1971), as I have anticipated in section 3.1, eventually developed an ecological paradigm that combines an energetic ecosystem framework with a holistic and emergentist ontology. An important concept that much influenced Odum and later systems ecologists was that *of integrative levels* (Novikoff, 1945; Feibleman, 1954; Rowe, 1961), which is a description of the evolution of matter through successively higher orders of complexity and integration. Accordingly, what are wholes at one level of biological organization become parts at a higher one, and each level of organization possesses unique structural and functional properties that, though dependent on the properties of the constituent elements, appear

only when these elements are combined in the new system. One important epistemological point is that knowledge of the laws of the lower level is necessary for a complete understanding of the higher level; however, the unique properties of phenomena at the higher level cannot be predicted merely from the laws of the lower level, because the laws describing the unique properties of each level are distinct, and their discovery requires methods of research and analysis appropriate to each level. The concept also recognizes as essential, for the purpose of analysis, both the isolation of parts of a whole and their integration into the structure of the whole (Novikoff, 1945).<sup>37</sup>

The proponents of the concept, despite assuming the weakness of atomistic and mechanistic perspectives in the life sciences, criticized the fact that Clementsian-style organicism was pervaded by non-materialistic concepts, failing to picture the whole as developing through the integration of individual units of matter into a single system. Organicists try to describe the living system solely in terms of the higher level, the whole, omitting the discussion of the organizing relationships of the parts. As a result, the impression was that no material basis existed for the part-whole relation. Novikoff (1945) instead contends that all levels – cells, tissues, organs, organs-systems, organisms and populations – need to be studied. This research cannot be solely pursued by means of an organicist agenda because it is the reciprocal relationship of elementary units to each other and to the system that must be understood. Yet, this research cannot be merely pursued by means of a mechanistic agenda either because the methods for studying the higher levels (among which Odum 1971 would include communities and ecosystems) will not be exhausted by those necessary to study the lower ones.

In the context of my analysis and argument, what is important in this concept is the idea that the laws of a lower level are *inadequate* to describe the higher level. The laws unique to the higher level can only be discovered by approaches appropriate to that particular level. When we stress the material interrelationships and integration of parts and whole and the qualitative uniqueness of each level, I think that the concept of integrative level can be helpful. Feibleman (1954) attempted to systematize some of the structural uniformities and interrelationships between integrative levels developed by Novikoff, arguing that each level organizes the level below and that the complexity of the levels increases upwards.

What is presupposed in the theory of integrative levels is that each level must be an *object*, discriminated from its surroundings in space and time, and that objects at successive levels must be structurally related (Rowe, 1961). The object of study of a level must contain, volumetrically and structurally, the objects of the lower levels, and must therefore be itself a part of the levels above. Each object will constitute the immediate environment of the object at the level below while forming a structural-functional part of the object at the level above.

In the context of this perspective, the ecosystem is an objective level of organization that stands above population and communities, volumetrically including, and internally structured by, these levels. While in the definition given by Tansley (1935) the concept of ecosystem has only epistemological meaning (as it is defined as a physical system whose size and structure is determined according to research purposes and methods), in contrast Lindeman (1942) argued that the ecosystem is a *genuine* system composed of physical, chemical and biological processes active within a space-time unit of any magnitude, as reported in section 3.1. I would argue that for sure we should be pragmatic in using the criteria for selecting ecosystems. However, I also recognize that there is an

<sup>&</sup>lt;sup>37</sup> According to Novikoff (1945, p. 209), the concept neither reduces phenomena of a higher level to those of a lower one, as in the reductionist mechanistic approach, nor describes the higher level in vague non material, vitalistic terms. Both parts and wholes are material entities, and integration results from the interaction of the parts as a consequence of their properties. The study of the organizational interrelationships of parts and whole is thus pivotal.

element of subjectivity in the delineation of ecosystem boundaries. The important issue here, I think, is the fact that each ecosystem can encapsulate successively smaller levels of organization down to the level of individual organisms. The shift in attention from individual organisms to populations to community and, finally, to ecosystem, can give deeper meaning to ecosystem structural and functional analyses by providing the operational framework of modern systems ecology by assuming ecosystems as *ontological categories*. Indeed, the concept of integrative level of organization was illuminating and inspiring for Odum, providing him with a basis for relating the objects of study at successive levels according to the principles of *spatial inclusiveness* and *structural relatedness*. The object of each level could then be seen as the environment of the objects at the levels below and as a specific structuralfunctional part of the object at the level above. The ecosystem, a geographically life-filled space, became an object of study divisible into structural parts or components, such as plants, animals, microorganisms, climatic and soil environment, etc. This development was fundamental and instrumental for Odum because, even though he denied too much value to epistemological reductionism, at the same time he located the theoretical core of systems ecology in energetic analysis, which involves the study of components, as Tansley defended (see section 2.1).

The very influential textbook *Fundamentals of Ecology*, whose first edition was published by Odum in 1953, had a prominent role in popularizing the ecosystem concept defined according to the theoretical developments referred above. The approach was conceptually clear and permitted Odum to highlight principles and concepts he felt were the fundamental elements of systems ecology within a logical and coherent framework. He explains the concept of ecosystem as follows:

"(...) any entity or natural unit that includes living and nonliving parts interacting to produce a stable system in which the exchange of materials between the living and nonliving parts follow circular paths is an ecological system or ecosystem. The ecosystem is the largest functional unit in ecology, since it includes both organisms (biotic communities) and abiotic environment, each influencing the properties of the other and both necessary for maintenance of life as we have it on the earth. " (Odum, 1971, pp. 9)

The book unfolds from this beginning to consider limiting factors, energetics, the food chain, biomass, productivity and then ecological principles at the level of populations and communities. Thus, by the 1960s, the ecosystem concept had become an *organizing idea* in ecology.

When looking at the structure of ecosystems, ecologists realized that careful counts of species were extremely important to ecology as a whole. Nonetheless they were only indirectly relevant to ecosystem studies. The crucial issue was not how many species there were but *how* species used food and energy. Lindeman (1942) proposed a solution to this problem by focusing on the ecological role of dominant species, determining their food habits, feeding coefficients, metabolism and growth, then extrapolating from the dominant to the rare species under the assumption that the rare species acted similar to the dominants. Concerning the functional studies of ecosystems, it was then becoming evident that the ecosystems approach provided the basis for a *functional analysis* of nature. Most ecologists in the 1960s divided this functional or dynamical aspect in two parts: one was concerned with the *energetic of the systems* and the other was involved with *organic productivity*.

Ecological energetics became an extremely relevant autonomous subject of research in seeking a deeper understanding of ecosystems (Odum, 1968). As outlined in section 3.1, the energy flow approach was central to Lindeman's trophic-dynamic aspect of ecology. However, even though Lindeman recognized that energy permitted an integration of diverse activities, he used energy as a currency rather than making energetics the fundamental theory of ecology. Odum (1971) reviewed the fundamental concepts related to energy, stating that the behavior of energy is described by the laws of

thermodynamics,<sup>38</sup> then proceeding to apply energy theory to the food chain, biomass and productivity. The generalizations Odum developed from these concepts almost all relate to the ratios of energy or biomass in trophic levels. Thus, the energy flow approach that entered ecology, as a way to compartmentalize diverse biological processes, was transformed into a theoretical foundation for ecosystem function. This energy approach provided two useful tools for ecological analysis: first, by following the first law of thermodynamics, ecologists studying the energy flow in a system could expect that all the energy entering the system would equal all the energy leaving the system, plus that stored in it – thus ecologists gained a balance sheet that could be used to check the accuracy of the measurements of inputs, outputs and storages; second, according to the second law, at each transfer of energy in the food cycle, energy is degraded and is no longer available to do further work – ecologists gained here the notion that ecosystems could spontaneously degrade their initially contained energy and increase their entropy, corresponding to a loss of order and organization, and increase in "randomness". I shall develop these concepts in section 3.2.2.

Ecologists began to apply these ideas to all levels of ecological organization. The first issue in ecosystems energetics concerned the balance of the whole system, as required by the first law of thermodynamics, questioning if the inputs of energy to an ecosystem or component of an ecosystem equal the outputs – the balance between the energy input and output become expressed by the ratio of production and respiration.<sup>39</sup> A second question introduced by this approach concerns the relative significance of the rate of energy transfer across a food link and the efficiency of that transfer, according to the second law of thermodynamics. The concept of *production*, as the quantity of biomass produced, is of great importance for ecologists, because of the need to measure production and apply this measurement to understanding populations and communities in terms of flow of energy. Ecologists have always attempted to assess the definitions of *production* and *productivity*, being the second the amount of biomass produced per time (and even area or volume).

When one applies ecosystems concepts to ecology, *stability* is one of the most complex and important ones. It involves more than a balance of energy flow and production. According to Odum, the stability principle states that "any ecosystem with energy flowing through it (...) tends to change until a stable adjustment, with self-regulating mechanisms (...)" (Odum, 1971, pp. 45). Thus, self-regulation provides the mechanism to achieve the equilibrium state postulated by Tansley (1935, see section 3.1), maintaining the climax of the ecosystem.

However, the crucial question for ecologists was about the nature of that mechanism, in a real ecosystem. The first approach to the issue was that the control was produced by *feedback*, as in systems engineering. Bertalanffy's Systems Theory was embodied in ecology in the 1950s. The

<sup>&</sup>lt;sup>38</sup> The first law of thermodynamics states that energy may be transformed from one type to another but is never created or destroyed. The second law of thermodynamics states that no process involving an energy transformation will spontaneously occur unless there is the degradation of the energy from a concentrated form into a dispersed one.

<sup>&</sup>lt;sup>39</sup> In ecology, primary production is the synthesis of organic compounds from atmospheric or aqueous carbon dioxide. It principally occurs through the process of photosynthesis, which uses light as its source of energy, but it also occurs through chemosynthesis, which uses the oxidation or reduction of inorganic chemical compounds as its source of energy. Almost all life on Earth relies directly or indirectly on primary production. Ecologists distinguish primary production as either net or gross, the former accounting for losses to processes such as cellular respiration. Ecosystem respiration is the sum of all respiration occurring by the living organisms in a specific ecosystem. The two main processes that contribute to ecosystem respiration are photosynthesis and cellular respiration. Photosynthesis uses carbon-dioxide and water, in the presence of sunlight to produce glucose and oxygen whereas cellular respiration uses glucose and oxygen to produce carbon-dioxide, water, and energy. Cellular respiration is the process by which organisms combine oxygen with foodstuff molecules, diverting the chemical energy in these substances into life-sustaining activities and discarding, as waste products, carbon dioxide and water. The coordination of inputs and outputs of these two processes creates a completely interconnected system, constituting the underlying functioning of the ecosystems overall respiration. Ecosystem respiration is the overall relationship between autotrophs and heterotrophs.

suggestion that systems analysis was the proper methodology for the life sciences, such as physiology and ecology, became common, and was crucial to accommodate the radical reductionist and holistic positions, within the framework of the systems theoretical conception of the ecosystem concept. In all these subjects, phenomena represented by the concepts such as coupling, accumulation, transformation, and efficiency started to being treated within a single and unified perspective – *a general systems perspective* (Bertalanffy, 1950), which applied a new organic, holistic metaphor to nature. It demonstrated that all natural and human-built systems had a fundamentally similar structure and function. This approach was in sharp contrast to the organic metaphor of Clements and his theoretical concept of the whole, because it was physical and had a more machine-like character.

Bertalanffy (1950) argued that there were some laws in science characterized by the fact that they hold generally for certain classes of complexes or systems, irrespective of the special kind of entities involved. Accordingly, there exist general laws that apply to any system of a certain type, irrespective of the particular properties of the system or the elements involved. Such considerations led Bertalanffy to postulate a new discipline, *General Systems Theory*, a logico-mathematical field, the subject matter of which is the formulation and deduction of those principles that are valid for systems in general. The main issue spurring Bertalanffy (1950) was the need to expand our conceptual schemes if we wish to deal with complex realms, such as biology or ecology, and to make it possible for them to be included in the exact sciences. Given the then predominant methodology of the physical sciences, it was thought that, in order to state exact laws for any non-physical discipline and to render them exact sciences, they had to be reduced to physics and chemistry. Opposing this reductionist conception, Bertalanffy (1950) was led to a different view. He thought that the task of science is to state laws for the different levels of reality and that, taking the individuals at each level as units, one will eventually get a system of laws which is not physical but that is of the same form as those of the exact physical science, that is, a mathematical hypothetico-deductive system.

To apply this procedure consistently, Bertalanffy (1950) emphasized the need to establish the principles applying to those entities which are called systems and of which physical systems are only subclasses, thinking that the problems of biology and ecology, such as individuality, competition, interrelations etc., require exact treatment as the exact sciences. He also thought that General Systems Theory should be, methodologically, an important mean of controlling and instigating the transfer of principles from one field to another. According to Bertalanffy (1950), it is also necessary to formulate the concept of *wholeness*, which has a central position in biology, ecology, psychology and sociology, in an exact language. What is meant by this concept in these sciences is indicated by expressions such as system, *gestalt*, organism, interaction, "the whole is more than the sum of its parts", and the like. However, these concepts have been often misused and misinterpreted and are thus of a vague, muddled and somewhat mystical character. In order to avert these confusions, Bertalanffy proposes General Systems Theory as the new scientific doctrine of *wholeness*.

If one takes any realm of biological phenomena, argues Bertalanffy (1950), whether metabolism, growth, communities or ecosystems dynamics, one will always find that the behavior of an element is different within the system from what it is *in isolation*: we cannot sum up the behavior of the whole from that of the isolated parts; thus, we have to take into account the relations between the various subordinated systems and the systems which are above them in order to understand the behavior of the parts. It is the basic characteristic of every organic system that it maintains itself in a state of perpetual components' change; the characteristic state of the living organism is that of being an open system because there is constant inflow and outflow and, therefore, constant change of the component materials. Closed systems must eventually reach a state of equilibrium, according to the second law of thermodynamics. By contrast, open systems, provided certain conditions are given,

appear also to be constant, though this constancy is maintained in a continuous change, inflow and outflow of materials. This constant state is called steady state.<sup>40</sup> Accordingly, living systems are the most important examples of open systems and steady states, as they depend on continuous flows of materials, energy and information.

Another interesting concept developed by Bertalanffy (1950), instrumental to understand the equilibrium state postulated by Tansley (1935), is that of *equifinality*: if in most physical systems the final state is determined by the initial conditions, living phenomena show a different behavior: here, to a wide extent, the final state may be reached from different initial conditions and in different ways; such behavior is *equifinal*.<sup>41</sup>

A further important distinction articulated by Bertalanffy (1950) that contributed to the analysis of self-regulation in the ecosystems approach is that between static teleology – meaning that an arrangement seems to be useful for a certain purpose – and dynamic teleology – meaning a directedness of processes. In the latter the author distinguishes different phenomena: direction of events towards a final state which can be expressed as if the present behavior was dependent on the final state; directedness based upon structure, meaning that an arrangement of structures directs the processes in such a way that a certain result is achieved. Bertalanffy (1950) argues that an important part of these processes is represented by *homeostasis* – those processes through which the material and energetic state of the living system is maintained constant. These regulations are governed, in most cases, by *feedback* mechanisms. By feedback is meant a process that, given the output of a system, the system uses a certain amount of this output as information in order to monitored back to the input, so as to regulate the latter and thus to stabilize or direct the action of the system. Feedback mechanisms appear to be responsible for a large part for the organic regulations and phenomena of homeostasis, as was also emphasized by cybernetics at the time, an issue on which I shall return below.

Bertalanffy (1950) argues that equifinality can be another basis for organic regulation. There is, finally, true finality or purposiveness, meaning that the actual system's behavior is determined by the foresight of the goal. I agree with Bertalanffy's argument that vitalism is essentially the attempt to explain organic directedness by means of intelligence given foresight of the goal, by feedback mechanisms or by equifinality. I also think that phenomena of organic directedness are consequences of the characteristic state of the living system – an organism, a population or an ecosystem – as an open system, which is accessible to scientific analysis and interpretation, rather than requiring vitalism. Bertalanffy's analysis and concepts were crucial to the development of systems ecology because systems ecologists started studying stability as maintained by feedback control.

<sup>&</sup>lt;sup>40</sup> In systems theory, a system (or a process) is in steady state if the variables, the state variables, which define the behavior of the system (or the process), are unchanging in time. A steady state is a more general situation than dynamic equilibrium. While a dynamic equilibrium occurs when two or more reversible processes occur at the same rate, and such a system can be said to be in a steady state, a system that is in a steady state may not necessarily be in a state of dynamic equilibrium because some of the processes involved are not reversible.

<sup>&</sup>lt;sup>41</sup> The author emphasizes that closed systems cannot behave equifinally; however, in open systems, which are exchanging materials with the environment, in so far as they attain a steady state, the latter is independent of the initial conditions and thus equifinal. Therefore, in an open kinetic system, irrespective of its initial or subsequent material composition, the steady state values will always be the same, because they are determined only by constants of reaction and of inflow and outflow. Steady state systems show equifinality in contrast to closed systems in equilibrium where the final state depends on the components given at the beginning of the process. Therefore, Bertalanffy claims that equifinality is at the basis of organic regulation, and that one finds it realized whenever biological events are determined by the dynamic interactions of parts. The author adds that the equifinal form of directedness, which is so characteristic of biological phenomena and has been considered the vitalistic essence of life within some holistic traditions is, in fact, a necessary consequence of the steady state in living systems.

Ecosystem concepts continued to be applied to studies of ecological succession (Odum, 1969). For the ecologists of the 1960s there was an obvious connection between the systemic concept of steady state and the Clementsian concept of climax, as defined in section 3.1. It was Whittaker that presented a more modern view of ecological climax,<sup>42</sup> a modern concept of ecological succession and climax that could be used to interpret the patterns of succession observed in the field from the vantage point of ecosystems theory perspective.

In summary, the community of ecosystem ecologists, since the 1960s, made a choice, defending the concept of ecosystem against attacks by reductionists. In a sense, the ecosystem concept became established as a scientific paradigm in ecology. This paradigm described an ecosystem as an ecological machine constructed of trophic levels that were coupled by energy flows. Ecosystems were in steady state when the input and output of energy was balanced and no accumulation of biomass through productivity was observed. If there were an accumulation of energy and materials, as in successional ecosystems, the system would expand in biomass and species diversity until a steady state was reestablished. Tansley's concept of a system made up of the "organisms complex" and the "environment of the biome" had been applied to a well-defined object of research, ignoring the impediment in the application of the concept to ecological systems of all sizes and complexities. Ecosystems theory was developed through the articulation of the concepts of structure, function and of energy flow. Odum asserted that the ecosystem was a whole greater than the sum of its parts and had emergent properties that could not be explained solely from a knowledge of the parts.

Fundamentally, ecosystems theory was a perspective that used *energy* as the currency of exchange between components. Because there was no method available to keep track of the exchanges between all species in an ecosystem, it was necessary to aggregate species into functional groups, the trophic levels. This analytic technique simplified the task of organizing data and opened the door to the use of system analysis in ecosystem studies. But the choice of aggregating organisms into trophic levels entailed some disadvantages, related to the fact that most of the biological variability encompassed by species was lost in abstraction, an issue that I have explored in section 2.1. Aggregation analysis cut ecosystem studies off from biology and linked them more closely to engineering, physics and mathematics. While admitting this is a valuable link, it has costs. In my opinion, the choice of the trophic level aggregation model meant that the field could surmount some problems related with taking into consideration excessive biological detail, potentially profiting from advances in systems engineering, information theory and computer science. Most importantly though, I would argue that the pivotal point about the articulation of the ecosystem concept was that, for the first time, ecologists identified a specifically ecological object of study. Although the ecosystem contains biological species and environmental physical and chemical processes, ecologists moved away from biology, chemistry and physics to become members of a new scientific discipline, which Odum (1964) labeled the "new ecology". The ecosystem concept has arguably provided order in the complex and multidimensional science of ecology; the word emphasizes the system, which is both a modern and technical concept, and it conveys the idea of an ecological machine, a metaphor that in Western societies has had and still has a strong impact and appeal. Whatever the cause, Tansley's invention has had a great appeal and success in ecology.

<sup>&</sup>lt;sup>42</sup> According to Whittaker (1953, pp. 61): 1) The climax is a steady state of community productivity, structure and population, with the dynamic balance of its populations determined in relation to its site; 2) The balance among populations shifts with change in environment, so that climax vegetation is a pattern of populations corresponding to the pattern of environmental gradients, and more or less diverse according to diversity of environments and kinds of populations in the pattern; 3) Since whatever affects populations may affect climax compositions, this is determined by, or in relation to, all "factors" of the mature ecosystem – properties of each of the species involved, climate, soil, and other aspects of site, biotic interrelations, floristic and faunistic availability, chances of dispersal and interaction, etc. There is no absolute climax for any area, and climax composition has meaning only relative to position along environmental gradients and to other factors.

After the 1960s, holistic ecologists approached ecosystems through the analysis of components, which would then be linked together into a system in a computer model theory or as a natural object that could be studied using conventional methods. In this latter case, the ecosystem object would be observed, a pattern of behavior identified and questions about the origin of this behavior posed. These questions would then require the ecosystem to be dissected into components or subsystems and their linkages or interrelations, and their behaviors observed and explained. In this way, a mechanistic explanation of ecosystem behavior could be framed in terms of biological, chemical or physical principles. This is the position that I shall illustrate and partially defend in section 4: that a mechanistic notion of reduction, crucial in the context of the moderate approach, is necessary, but in itself insufficient, in the explanation process of ecological phenomena. An essential complement is provided by ecosystem theory, which allows tackling the crucial issues of inter-level and systemic integration within ecosystems.

One important challenge to the ecosystem concept and theory is to surmount the idea that this concept is a continuation of the *superorganism notion* espoused by Clements (1916) and that, as a consequence, it should not be dismissed as a the latest form of organic holism. The superorganism was a metaphor that attributed the properties of individual organisms to supra-organismal entities (such as a bee or ant colony) or even to the biome as a whole. It was an appropriate metaphor for that time; however it was a misleading one, because, for instance, between an individual plant and vegetation there is scarcely anything in common, even considering the analogy provided by development. One problem with this metaphorical form of reasoning was that the plant community was thought of as an abstraction (distinct from concrete patches of living plants) and it was then possible to attach the abstraction to idealistic concepts such as those of John Philips (1934, 1935a, 1935b, see section 3.1). This was the issue Tansley (1935) addressed when he formulated the ecosystem concept as an alternative to the superorganism concept. That ecologists still confuse the superorganism and ecosystems testifies to the persistence of outdated concepts in ecology. But I think we have to understand the heuristic role of such metaphors as something that we hold onto in the absence of more scientific concepts, as I have argued in section 1.1.

Another important challenge in ecology concerns the question of *determinism*. I have presented before a continuum of ecological views ranging from the more deterministic to the more contigentist. Deterministic theory was strongly associated with vegetation classification and ecological succession, especially with Clements (1916). Although Gleason (1917, 1926) put forward a contigentist theory of vegetation development by means of his individualistic concept, it was first rejected and subsequently revived only after the Second World War. Afterwards, occurred a time of transition, characterized by an initial emphasis on determinism, then moving to an emphasis on relativity and contigentism. Some criticisms, such as those advanced by Simberloff (1980), can be interpreted as against the deterministic outlook seemingly implicit in the concept of ecosystem, that is, the assumption that ecosystems are goal-directed and self-regulated. In contrast, Simberloff thinks they are stochastic and indeterminate. Prominent systems ecologists, such as Patten and Odum (1981), have asserted that ecosystems are self-regulating and goal-seeking systems, but others have described stochasticity in ecosystems behavior (Schindler *et al.*, 1985). Thus, it is not true that the ecosystem approach requires that ecosystems function deterministically.

Finally, a related and crucial challenge is that stemming from the *cybernetic character* of the ecosystem. Rather than being describable by the state equilibrium of Tansley (1935), the ecosystem is better described as a response system, which is in a dynamic relation with its environment. The state of the system at any particular time is contingent upon its history and the environment. This a relativistic theory of ecosystem behavior and it contrasts strongly with Tansley's deterministic

concept. The changing environment in which the ecosystem is placed creates its dynamic response as a whole. If the environment is changing in a consistent way, then the ecosystem is said to track the pattern. Furthermore, the ecosystem may have a damping and controlling influence on the environment; it has a reciprocal relation to its environment and it is not merely responding to it. A more modern approach to the existence of equilibrium should involve, I would argue, the concepts of resistance and resiliency, which describe how an ecosystem might respond to or recover from disturbance. I would argue that describing ecosystems as cybernetic systems, in accordance with the non-teleological model as described in Annex 2 (see figure A.1b), in which a diffused, decentralized and indistinct informational subsystem regulates the primary energy-matter subsystem in order to achieve order, is the best way to describe how systemic models tend to be established so that components or set of components are linked together in a network, such as an ecosystem. While, admittedly, the analysis of information in ecology can be greatly complex, I believe the crucial question is, rather, how the control of ecosystem dynamics is mediated in this non-teleological model. In ecology, an important theoretical debate - summarized in annex 2 -concerns the cybernetic nature of ecosystems. This is a point on which I shall return in the next section in order to understand the "agencies" that impart directionality to ecosystems in their development. In looking for directionality in natural systems, one must consider feedback within living systems. Feedback has a central role in the theory of self-organization, and central to control and directionality in cybernetic systems is the concept of the *causal loop*. The causal loop is any concatenation of causal connections whereby the last member of the pathway is a partial cause of the first, a hypothesis that is relevant in the postclassical ecosystems approach, as I will illustrate.

To conclude this section, I think that a new relational ontology, along the lines proposed by Santos (2015), can hold promise to tackle the three main challenges facing ecosystems theory seen so far: the role of the metaphor of the superorganism, the issue of determinism and the cybernetic character of ecosystems. If, according to Santos proposal, the qualitative and causal identity of any ecological entity, as well as its very existence and persistence conditions, must be ultimately explained as constructed and transformable by the interplay of its endogenous and exogenous relations, including those instantiated in the context of higher-level relational structures (such as those composing an ecosystem), this is a good premise to understand the way that the components are linked together in a network. After pursuing a mechanistic understanding of the ecosystem's activity through the decomposition and localization of the ecosystem's components and activities, their recomposition as a global combination of components and the situating of the system as a whole in its environment, the ecologist would try to profit from describing ecosystems' regulation and control, according to this new relational and emergentist ontology.

Following this proposal, and endorsing this dynamic relational view, I would argue that there are structural networks of transformative and interdependent relations within an ecosystem, then a system that *seems* an organismal, deterministic and teleological entity. To develop further this integrated notion of inter-level emergence in ecosystems, in which individual properties of the components are determined by their relations and are not independent or immutable, I will in the following section focus on some elements of a new dynamical perspective emerged in ecosystems ecology in the last years that will be relevant for the construction of a moderate approach in ecology.

## 3.2.2. The Post-Classical Ecosystems Ecology: Eco-exergy and Ascendency

As related above, under the influence of the energetic ecosystems models, elaborated by Odum, classical ecosystems ecology has been guided by mechanistic and equilibrium assumptions about

ecosystems dynamics. In my opinion, these are the main aspects of this classical perspective: the expectation by default of equilibrium, with its corresponding requirement of explanation for departures from equilibrium; and the expectation that patterns of energy flow through an ecosystem would be mechanistically accountable. Recently, some ecologists have been focusing on some elements of a new dynamic perspective that is emerging from the application of self-organizing and complex adaptive systems in ecology (Yin and Herfel, 2011). I will hereby try to show how some traditions in complex systems research have come to influence contemporary studies in systems ecology, such as the Ecological Theory of Thermodynamics, Eco-exergy, Maximum Power Principle and Ascendency.

#### Eco-exergy and the Ecological Law of Thermodynamics

Of great relevance is the *far-from-equilibrium thermodynamic tradition* (Yin and Herfel, 2011; Jørgensen, 2012; Jørgensen *et al.*, 2020). Its starting point is that classical thermodynamics only applied to either static or reversible systems, which indeed do not occur in nature. It is desirable to work with *availability* of energy, because in a real natural process we have energy degradation while in a reversible process energy would remain the same. Recent developments in thermodynamics have allowed some accurate predictions of irreversibility, which will have significant relevance to ecosystems ecology, since ecologists think that ecosystems are irreversible systems working far from thermodynamic equilibrium<sup>43</sup> (Yin and Herfel, 2011; Jørgensen, 2012; Jørgensen *et al.*, 2020).

Ecosystems are able to grow and develop in spite of energy and matter needing to be conserved (according to the first law of thermodynamics), in spite of all processes being irreversible, and in spite of the basic fact that all biological components have to obey biochemical constraints. Ecosystems are capable to evade the thermodynamic and biochemical constraints by being open to energy flows and by the use of *four possibilities to grow and develop: increasing their boundaries, their biomass, the complexity of their ecological network and their information flow* (Jørgensen, 2012; Jørgensen *et al.*, 2020).

Ecosystems models focus on the energy and mass flows in the ecosystem, because these flows determine the further development of the ecosystem and characterize its present condition. The ecosystem has a flow of matter under the drive of a thermodynamic force. The flux is the flow of food through a food chain and the force is some function of the concentration gradient of organic matter and biomass (Jørgensen, 2012; Jørgensen *et al.*, 2020).

The developments and reactions of ecosystems in general are, however, not only a question of energy flow (Jørgensen, 2012). Matter and information also play a major role. No transfer of energy is possible without matter and information, and no matter can be transferred without energy and information. This implies that not only matter recycles but also energy and information recycle through the ecological network.<sup>44</sup> The higher the levels of information, the higher the utilization of

<sup>&</sup>lt;sup>43</sup> In accordance with classical thermodynamics, all isolated systems will move toward thermodynamic equilibrium, a state of equal distribution of components. This means that all the gradients have been eliminated, i.e., there are no differences in any energy potentials such as concentration of chemicals or temperature differences, and structures in the system will have ceased to exist: a homogenous dead system will be the result. This is expressed thermodynamically as follows: entropy will always increase in an isolated system. As work capacity is a result of gradients in certain intensive variables such as temperature, pressure, and chemical potential, etc. a system at thermodynamic equilibrium can do no work.

<sup>&</sup>lt;sup>44</sup> One way to measure the organization is the information content of the material, which can be the complexity at the genetic, organismal, or ecosystem level. Jørgensen *et al.* (2020) express the organizational aspect using Kullbach's measure of information based on the genetic complexity of the organism, and understands information in thermodynamic terms, trying to relate eco-exergy and information in an ecosystem, as I explain in more detail in annex 3.

matter and energy for further development of ecosystems away from the thermodynamic equilibrium. Odum (1969) describes the development of ecosystems from the initial stage to the mature stage as a result of continuous use of self-design ability, emphasizing that the content of information increases in the course of ecological development. According to Odum, an ecosystem encompasses an integration of all the modifications that are imposed on the environment. Thus, it is on the background of genetic information that systems develop allowing an interaction of information with the environment. Herein lays the importance of the feedback from the organism to the environment; this means that an organism can only develop in an evolving environment. The differences between the two stages include entropy and exergy (see annex 3), two concepts that I will develop below. The conservation laws of energy and matter (see annex 3) set limits to the further development of energy and matter, while information may be amplified almost without limits (Jørgensen, 2012; Jørgensen *et al.*, 2020).<sup>45</sup> It is theoretically possible to divide most of Odum's attributes of an ecosystem (1969) into groups, defining the four different growth and development forms for ecosystems referred above.<sup>46</sup>

In order to understand the growth and development of ecosystems, it is relevant to consider the *maximum power principle*. Boltzmann said that the struggle for existence is the struggle for free energy available for work and Schrödinger pointed out that organization is maintained by extracting order from the environment (Jørgensen *et al.*, 2020). These principles can be interpreted in terms of behavior of systems able to gain the most free energy under the given conditions, i.e., to move away from the thermodynamic equilibrium (see annex 3). Such systems will gain most biogeochemical energy available for doing work and therefore have most energy stored to use for maintenance and buffer against perturbations. As I describe in annex 3, in equation A3.11, the maximum power principle is defined as the maximization of useful power, summing up all the contributions to the total power, found as the sum of all flows expressed in energy terms. The maximum power principle is embedded in the irreversibility of natural systems (Jørgensen *et al.*, 2020).<sup>47</sup>

Also important is the concept of *emergy* (embodied energy), which calculates how much solar energy (which is the biosphere's ultimate energy resource) it costs to obtain one unit of biomass of various organisms (Odum, 1983; Jørgensen, 2012; Jørgensen *et al.*, 2020). It is determined by the biogeochemical energy flow into an ecosystem component, measured in solar energy equivalents, as

<sup>&</sup>lt;sup>45</sup> Jørgensen *et al.* (2020) defend the view that information has some properties that are very different from mass and energy: information, unlike matter and energy, is not conserved; the disappearance and copying of information, that are characteristics processes for living systems, are irreversible processes, and information exchange is communication, which brings about the self-organization of life. See in more detail in annex 3.

<sup>&</sup>lt;sup>46</sup> Boundaries growth refers to the capture of energy input by the ecosystem and bringing it in across its system boundaries, being this the basic prerequisite for all further activities in the ecosystem and maintaining them as open far-from-equilibrium systems; biomass growth refers to the increase of biomass substance of the ecosystem; network growth refers directly to the increased complexity of the ecological network, more complex life and mineral cycles, a slower nutrient exchange rate, and a more narrow niche specialization, and it also implies a longer retention time in the system for energy and matter - this is not only an increase in the network connectivity but also the placement or articulation of those links; information growth refers to the evolutionary advances that explain the higher diversity, the appearance of larger animals, of longer life spans, of more symbiosis and feedback control, and a shift from r-strategists (organisms that live in unstable environments, with the ability to reproduce rapidly) to K-strategists (organisms that live in more stable environments, larger and with greater life expectancy, whose reproductive strategy is to grow slowly, live close to the carrying capacity –K- of their habitat and produce a few progeny each with a high probability of survival).

<sup>&</sup>lt;sup>47</sup> These authors show that the highest process efficiency can be obtained by reversible conditions within the ecosystems, meaning that all irreversibilities are located in the coupling of the system to its surroundings. However, in this case the power will be zero, and if one wants to increase the process rate, one also increases the irreversibility and thereby decrease the efficiency. The maximum power is a compromise between internal reversible processes and very fast completely irreversible processes. See pp.118-119.

presented in equation A3.12. It is an important concept to account for the quality of the energy in the ecosystem,<sup>48</sup> as is the concept of *exergy*, which I will introduce below.

The growth and development of ecosystems follows the first law of thermodynamics: thus, mass and energy are conserved (see annex 3). This means that it is possible, by bookkeeping the exchange processes between the system and the environment, to calculate the system's gain or loss of energy and matter. As I have formulated in annex 3, most chemical processes in nature are carried out at constant temperature and pressure, implying that dG = -dW, presuming constant temperature and pressure for processes in ecosystems. Thus, Gibbs free energy, G, covers the work, W, that is done. At thermodynamic equilibrium, all gradients are eliminated according to the definition, expressed in equation A3.10. This means that no work can be performed, and implies that dG=0, which is an important consequence of the energy conservation law. A general dynamic equilibrium, but not a thermodynamic equilibrium, is possible by equal process rates in opposite directions to ensure that steady state is maintained.

A further important concept that I describe in annex 3 is *eco-exergy*, which measures the distance from thermodynamic equilibrium and equals the content of work capacity relative to the thermodynamic equilibrium. Exergy density can be found as biomass times RTK, as explained by equation A3.19.49 According to Boltzmann, as I have referred above, competition in nature is a struggle for free energy and information embodies free energy (Jørgensen, 2012). By the use of statistics, Boltzmann expresses entropy as  $S = R \ln W$ , and free energy as  $-RT \ln W$ , where W is the number of microstates that originate a macrostate. If we presume that we know the present probability distributions of biomass' components, it is possible to understand that eco-exergy = Biomass \* RTK is close to what Boltzmann considered free energy. The difference is that free energy is not a state function for far from equilibrium systems such as ecosystems, while one has accepted that eco-exergy is not a state function, and that it is a relative measure of the work capacity (relative to the ecosystem at thermodynamic equilibrium), as I describe in annex 3 and illustrate in figure A.2. Strictly speaking, eco-exergy is a measure of the useful work that can be performed by the ecosystem. Conceptually, this obviously includes the energetic content of the material, i.e., biomass, but also the state of organization of it. One way to measure the organization is the information content of the material, which could be the complexity at the genetic, organismal, or ecosystem level. The organizational aspect of exergy is expressed in equation A3.19, and we can also calculate the information that the organism carries, which is the basis for the organism's eco-exergy (see equation A3.20). The important point is that ecoexergy can be related to entropy (S), which measures the disorder of the system, and the work capacity (W):  $-TS = kT \ln W$ . Entropy (S) measures the information one *needs* to get while eco-exergy measures the work capacity of the information that one has about the system. Thus, eco-exergy expresses the development of an ecosystem by its work capacity, and will be a relevant conceptual tool in the moderate approach.

However, the total eco-exergy of an ecosystem cannot be calculated exactly, as we cannot measure the concentrations of *all* the components or determine all possible contributions to eco-exergy in an ecosystem; neither does it include the information of all interactions. One can calculate the contributions from the *dominant biological components* in an ecosystem, for instance, using a model covering the most essential components for a focal problem, and this can be a limitation for the realism of the model. As I will illustrate in the empirical example (section 4.1), the difference in

<sup>&</sup>lt;sup>48</sup> Energy quality is a measure of the ease at which a form of energy can be converted to useful work or to another form of energy.

 $<sup>^{49}</sup>$  B is the biomass, R the gas constant, T the absolute temperature, and K the Kulback measure of information. See in more detail in annex 3.

exergy by comparing different possible structures (species composition) is decisive. Moreover, ecoexergy computations always give only relative values, as the eco-exergy is calculated relatively to the reference system. For now, it is important to emphasize the metaphorical relevance of the eco-exergy concept, because even with some short-comings, eco-exergy gives an approximate, relative measure of how far an ecosystem is from thermodynamic equilibrium and thereby how developed it is. As it will become evident with the empirical example, such assessment of important holistic ecosystem properties is important in systems ecology as well as in environmental management.

When one introduces the second and third law of thermodynamics in systems ecology, there are consequences for our understanding of ecosystems. Ecosystem growth and development, as proposed by Odum (1969), can be described under the constraints of the thermodynamic laws by the use of eco-exergy (Jørgensen, 2012; Jørgensen *et al.*, 2020).

Ecosystems present physical openness, as they receive an input of energy with a high content of exergy and a low content of entropy, which is applied to cover the maintenance of the ecosystems far from thermodynamic equilibrium (Jørgensen, 2012; Jørgensen *et al.*, 2020). The energy is conserved in ecosystems, but the outflow of energy has a lower content of exergy (energy that cannot do work) and a higher content of entropy than the inflowing energy (solar radiation).

As I describe in annex 3, in accordance with the second law of thermodynamics, all the processes in ecosystems will inevitably imply a loss of exergy to heat at the temperature of the environment, which means that the energy that can do work is lost to energy that cannot do work. All processes therefore imply loss of exergy and production of entropy, and all processes are irreversible. According to equation A3.24, creation of order in a system must be associated with a greater flux of entropy out of the system than into the system. This implies that the system must be open or at least non-isolated. Using free energy, this means that an ecosystem requires input of free energy to compensate for the loss of free energy and corresponding formation of heat due to maintenance processes, i.e., respiration and evapotranspiration. If the system is not receiving a sufficient amount of free energy, the entropy will increase (Jørgensen, 2012). If the entropy of the system continues to increase, the system will approach thermodynamic equilibrium and the system will die. Hence, life without the input of free energy or energy that can do work is not possible. The entropy produced by the life processes can be exported by three processes (Jørgensen, 2012; Jørgensen *et al.*, 2020): transfer of heat to the environment, exchange of material with the environment and biochemical processes within the system. The first process is, quantitatively, of particular importance.

As ecosystems are not isolated, they are able to maintain a certain concentration of lowentropy compounds against the second-law dissipation gradient. Ecosystems receive a continuous supply of free energy from outside to compensate for the positive entropy produced internally as a consequence of the second law of thermodynamics. On earth, solar radiation is the main source of this input of free energy, or low-entropy energy. The incoming energy has low entropy, while the outgoing energy has higher entropy.

All ordered structures require low entropy for maintenance, and therefore for a system to maintain structure or increase its internal order it must receive input of low-entropy energy from external sources. Structure, in this context, is a spatial or temporal order describable in terms of *information theory* (Ulanowicz, 1997; Jørgensen, 2012; Jørgensen *et al.*, 2020). The term *dissipative structure* can be used to denote self-organizing systems, thereby indicating that such systems dissipate energy (produce entropy) for the maintenance of their organization (order). Hence, all ecosystems, because they are subject to the second law of thermodynamics, are *inherently* dissipative structures. To

offset the dissipative processes they require inputs of low-entropy energy to maintain or produce a more internally organized structure, measurable in terms of information content. Thus, again, ecosystems must be open.

Ecosystems, in common with all natural systems, have a global attractor state, the thermodynamic equilibrium (Jørgensen *et al.*, 2020). Through their openness they avoid reaching this state by importing low entropy or matter carrying information from their surroundings. This anabolism compensates for the deterioration of the structure due to catabolism; the two processes operate against each other. It is important to stress that the equilibrium attractor represents a resting state, one that is passively returned to if system openness or non-isolation is compromised (Jørgensen *et al.*, 1999).

The third law of thermodynamics defines the relation between entropy production and temperature, as stated in equation A3.28. As I have mentioned above, it is necessary for an ecosystem to transfer the generated heat (entropy) to the environment and to receive low-entropy energy (solar radiation) from the environment for the formation of a dissipative structure. Ecosystems can remain in their organized state by exporting entropy outside the system but are dependent on outside free energy fluxes to maintain their organization, as I have already mentioned and emphasized above. The organization is inexorably torn down according to the second law of thermodynamics. Only a flow of free energy can compensate for this decomposition of the organization, since, according to the second law, all systems have loss of exergy or work capacity, especially as loss of heat energy at the temperature of the environment.

The dissipative structure of an ecosystem can be interpreted using the concept of eco-exergy (Jørgensen, 2012; Jørgensen *et al.*, 2020). As an ecosystem is non-isolated, the entropy changes during a time interval can be decomposed into the entropy flux due to exchanges with the environment and the entropy production due to the irreversible processes inside the system, such as diffusion, heat conduction and chemical reactions. The equation A3.29 is equation A3.23 being expressed by the use of exergy, and shows that systems can only maintain a non-equilibrium steady state by compensating the internal exergy consumption with a positive energy influx, thus having the system a surplus energy input, which may be used to construct further order in the system: the dissipative structure. The point is that there is a fundamental tension between order and disorder, between ordering processes (work) and disordering trends (increasing entropy), which is emphasized by thermodynamics. Energy can never be entirely translated into order (through work), but always entails some dissipation. The conditions for life, ordering processes out of disorder (more specifically chemical order by formation of complex organic molecules and organisms from inorganic matter) are then deduced from the laws of thermodynamics related above.

Thus, assuming all these conditions, it is inferred that more or less complex ecosystems will *emerge* open to an energy flow. If this flow is bigger than the needed to cover the maintenance, this surplus will be used for growth and development, in terms of increase in boundaries and biomass, network complexity and information storage. The seasonal variations of the inflow of free energy by the solar radiation show clearly what is happening when the free energy flow exceeds the need of free energy for maintenance: ecosystems develop and grow during spring and summer. So, ecosystems can move away from thermodynamic equilibrium, meaning they are growing in spite of the constraints of the three thermodynamic laws and the biochemical constraints. These four growth forms, defended by Odum (1969), are at the root of how ecosystems move away from thermodynamic equilibrium. Thus, what can be denoted as the *Ecological Law of Thermodynamics* (henceforth, ELT) would be valid (Jørgensen, 2012; Jørgensen *et al.*, 2020): when an ecosystem received more free energy than it needs to cover the maintenance of the system far from thermodynamic equilibrium, then the surplus free

energy or exergy is utilized to move further away from thermodynamic equilibrium, meaning that the system gains eco-exergy. There are, however, many possible pathways to move away from thermodynamic equilibrium, because ecosystems have many components and are linked in a complex ecological network. This implies that the four growth forms can be used by the ecosystem to move away from thermodynamic equilibrium in a huge number of ways. Jørgensen (2012) argues that the answer to how these numerous possibilities can be restricted is through the process of natural selection, that is, the species that have properties that are best fitted to the prevailing conditions, determined by the constraints, will survive and grow. Survival is represented by biomass and information maintenance or increase. Survival in the latter sense concerns the survival of the genes, which ensures that the processes, the biomass and the functions of the ecosystem are conserved to the next generation. The more biomass, the more difficult it will be to eliminate the species, while more information means that resources are used more effectively. Biomass and information, as related above, are expressed by eco-exergy, and as all the organisms in a ecosystem are interrelated and dependent on each other through a complex network, the eco-exergy of the ecosystem can be used to account for the survival of the entire ecosystem, being these holistic considerations included in the translation of Darwin's theory to thermodynamics by the ELT (Jørgensen, 2012; Jørgensen et al., 2020). Thus, the ELT is a translation of Darwin's theory to thermodynamics and at the same time an expansion from the individual organisms to the ecosystem.

The putative law, according to the latest formulation, asserts that (Jørgensen *et al.*, 2020): a system that receives a throughflow of exergy (high-quality energy) will try to utilize the exergy flow to move away from thermodynamic equilibrium, and if more combinations of components and processes are offered to utilize the exergy flow, therefore, the organization that gives the system as much exergy content (storage) as possible, i.e., maximizes dEx/dt (see annex 3),<sup>50</sup> will be selected.

#### Ascendency and Ecodynamics

As I have related in section 3.1, in the Odumian energetic framework that has been dominant since the 1970s, ecosystems are conceptualized as energetic systems with biological properties and interactions being "gathered" in black-boxes: instead of modeling individual organisms, as by IBMs (see section 2.1), this approach focused on trophic groups linked by a food chain or web, which was expected to behave in a somewhat mechanistic way. The machine or heat engine was the central metaphor for the Odumian framework, which has come under increasing criticism because of its limited success in providing the necessary conceptual tools in order to account for the unruly complexity of ecological systems (Ulanowicz, 1986; Ulanowicz, 1997; Yin and Herfel, 2011).

Ulanowicz (1997) criticizes the mechanistic framework, arguing that it cannot support adequate modeling and analysis of the self-organizing and self-regulating organizations emergent in ecosystems. This author proposes a phenomenological description of the ecosystem structure,<sup>51</sup> i.e., a

 $<sup>^{50}</sup>$  One can express preference for a formulation where the flow of eco-exergy (dEx/dt) is replaced by a flow of free energy, which is fully acceptable and makes the formulation closer to classical thermodynamics. However, eco-exergy cannot be replaced by free energy because it is a free energy difference between the actual system and the same system at thermodynamic equilibrium.

<sup>&</sup>lt;sup>51</sup> According to Ulanowicz, one can conceive of a totally self-consistent and coherent body of phenomenological observations that explicitly mentions only agencies at the focal level, e.g. to consider the growth and development and ecosystems without explicitly mentioning the genomes embedded in them. Ulanowicz believes in the sufficiency of a macroscopic narration (which is not intended to constitute a full explanation), even though he does not dismiss the contribution of the lower levels. The point is that, accordingly, ecologists must concentrate in the phenomena that are proper to ecological description. Ecologists are entitled to choose their own focal level and are free to search causes appropriate to that level.

formal pathway network of the energy and material flow in ecosystems, based on far-from-equilibrium thermodynamics (see annex 3) and information theory. He argues that such a model can offer a more adequate framework to model and analyze the self-organizing order emerging from ecosystems:

The flows make possible the higher level behaviors, which in turn help to order and coordinate the flows. So reflexive is this couple that the description of one member lies implicit in the description of the other element. It is in this reflexive sense that a key postulate in the development of the current thesis should be understood; to thermodynamically describe an ecosystem, it is sufficient to quantify the underlying networks of material and energy flows. A more general form of the postulate would read: *the networks of flows of energy and material provide a sufficient description of far from equilibrium systems*. (Ulanowicz, 1986, pp. 30, Italic in original)

Therefore, according to Ulanowicz, the phenomena that describe an ecosystem are the transformations of materials and energy that accompany processes such as feeding, decay, excreting, etc., and the account for the flow network of these transformations is sufficient to describe ecosystems' behavior.

Ulanowicz tries to distinguish two states, i.e., thermodynamic equilibrium and a dynamical steady state, in order to account for the fact that ecosystems, even if they have an unchanging balance that could be regarded as an equilibrium state, are not nevertheless at thermodynamic equilibrium. Instead, they are in a dynamic steady state (see note 40, pp. 51) with constant energy and material throughput (see annex 3). According to Ulanowicz (1997), only if there is no dissipation occurring in the system (that is, if no entropy is being created), can we regard it as at equilibrium. In this sense, he is arguing that there are no living systems among these thermodynamic equilibrium systems, and that ecosystems (as organized ensembles of living systems), are not at thermodynamic equilibrium. Instead, they are far from equilibrium systems with a dynamically stable flux network (Ulanowicz 1997; Jørgensen, 2012; Jørgensen *et al.*, 2020). Furthermore, these flux networks are emergent self-organizing *dissipative structures* (Ulanowicz, 1986), as I describe in annex 3.

Ascendency emerges largely from the thermodynamic perspective, which from its very inception has provided a counterpoint to Newtonian mechanistic thought. Thermodynamics emphasizes the fundamental tension between order and disorder, between ordering processes (work) and disordering trends (increasing entropy). The orthodox, or Newtonian, worldview is that of a closed universe, wherein only material and mechanical agencies may act. If any novelty can arise in the world, it can do so in the atomic world or in the vast reaches of the remote cosmos: from these peripheries, causes are propagated in closed fashion to intermediate scales, such as that of the ecosystem. Against such a background, ecosystems integrity would be regarded either as an epiphenomenon or as a pure metaphor, as other purported emergent properties, rejected as a metaphysical or transcendental construct.

Following Ulanowicz's (1997, 2005) argumentation, when focus turns to ecosystems, parsed into a number of essential components, these components respond to some degree to constraints arising outside the ensemble. However, these exogenous constraints are insufficient to determine the behavior of the component, because the components themselves interact with one another. That is, each component is constrained by, and on its own constrains, other components. And here we are moving away from the systems studied by Boltzmann in thermodynamics, composed of non-interacting elements<sup>52</sup>. In ecosystems and other biotic groups the boundary constraints of any element arise in part within the system itself as engendered by other proximate elements.

Accordingly, it is not the equations of conservation of mass and energy that are of interest in ecodynamics. These are nearly satisfied in relatively short order. Nor are energy-based constraints so

 $<sup>^{\</sup>rm 52}$  In an ideal situation, gas molecules that don't react with each other.

relevant, because, as I have described above, ecosystems develop so as to store the maximal amount of exergy possible alone sufficient to dictate the final outcome. The focus must thus be upon the interactions among the (mostly hidden) internal constraints, which change more slowly with time (Ulanowicz, 1997, 2005). Therefore, the control of ecodynamics appears to be *relational* in nature: how much any change in one constraint affects others with which is linked. This is a position which corresponds to a dynamical relational view, proposed by Santos (2015), according to which the qualitative and causal identity of any entity, as well as its very existence and persistence conditions, must be ultimately explained as constructed and transformable by the interplay of its endogenous and exogenous relations, including those instantiated in the context of higher-level relational structures, such as an ecosystem. *Relations* are thus posited as the primary objects of research (Santos, 2015).

The issue, as in thermodynamics, is the difficulty to follow the actions of every component in detail: so, rather than attempting to quantify the trajectories of each component, attributes of the *entire* (macroscopic) ensemble are measured (such as temperature or pressure in thermodynamics). Applying the same stratagem to ecosystems, one attempt to measure, or at least estimate, more aggregated processes, such as how much material or energy passes from one ecosystem component to another in an interval of time. All such estimated transfers can then be arrayed as a network of ecosystem material and/or energy linkages. Just as aggregated effects of individual agents are captured by the macroscopic variables of thermodynamics, so does an ecosystem flow network embody all the consequences of the hidden constraints (Ulanowicz, 1986, 1997, 2005). Before quantifying these constraints, however, one must analyze some considerations concerning these essentially different dynamics undergone by ecosystems, such as *contingency, autocatalysis*, and *causality* (Ulanowicz, 1997, 2005).

Ulanowicz (1995, 1997, 1998, 2000, 2005) argues that we must reconsider our conceptions of causality, defending an open world and invoking another form of dynamical cohesion. The subject at issue is the ontology of nature or what science assumes as its metaphysics. The Newtonian assumptions that should be discussed are that Newtonian systems are conceived as: *causally closed, atomistic, reversible, deterministic and governed by universal physical laws*.<sup>53</sup>

Ecosystems ecology assumes a hierarchy of integrative levels, as I have described in section 3.1, and this hierarchy theory rejects the Newtonian postulate that causes are propagated universally without attenuation, that is, an event at any scale is ramified to all other scales. On the contrary, within the hierarchical perspective, the consequences of an event at a given scale are attenuated at adjacent levels and become inconsequential at remote scales. Popper (1990) suggests that causes do not propagate intact between scales, because there are "interferences" or stochastic events that have the effect of opening the universe. However, Popper's world is not without form: this author calls *propensities* those agencies that keep reality from dissolving into total randomness. Propensities are the *tendencies* that certain processes or events may occur within a given context, being a combination of mechanism and chance at the macroscopic level. Popper (1990) relates propensities to conditional

<sup>&</sup>lt;sup>53</sup> According to Depew and Weber (1995), the Newtonian world-view is based on some strong assumptions defining Newtonian systems such as: *causally closed*, that is, only mechanical or material causes are legitimate and they always cooccur, being other forms of action proscribed, such as Aristotle's formal, or final (top-down) causality; *atomistic*, being strongly decomposable into stable small units, which can be built up and taken apart again – it is atomism combined with closure that give rise to the notion of causal reductionism, whereby only those agencies at the smallest scales are of importance; *reversible*, because laws governing behavior work equally in both temporal directions; *deterministic*, because given precise initial conditions, the future and the past states of a system can be specified with precision; governed by *universal* physical laws applicable always and everywhere (in combination with determinism, universality says that nothing occurs except in accordance to a fundamental physical law.
probabilities, however not claiming that the latter quantify propensities. The sense is that the use of conditional probabilities is not simply to cover the ignorance of the observer, but also pertains to a degree of indeterminacy inherent in the situation itself, and this is a shift *from the epistemic to the ontological*, which jeopardizes the *determinism* tenet of the Newtonian worldview. What is assumed, in this Popperian view, is that living systems are not fully constrained, i.e., they retain sufficient flexibility to adapt to the changing circumstances in an open world. The relevant issue, in the context of my analysis, is that there exists ontic chance or radical *contingency* and that nature, in its complexity, is rife with singular events (Ulanowicz, 2007). Most events do not upset prevailing regularities, but on some occasions one can carry a system into a wholly different mode of *emergent* behavior. Hence, propensities are an intermediate between determinism and stochasticity.

Propensities cannot exist divorced from their surroundings (Ulanowicz, 1995, 1997, 1998, 2005). An essential element of propensities is their *context*, which invariably includes other propensities. It is then possible to see how circularity is actually built into the definition of propensities. The outcome of random noise acting upon a feedback circuit is generally non-random (Ulanowicz, 2007). Such bias is especially characteristic of one particular form of feedback: autocatalysis, meant as any instance of positive feedback wherein the direct effect of every link on its downstream neighbor is positive. Unalowicz considers autocatalysis a very relevant process to understand the "agencies" that impart directionality to ecosystems. In looking for directionality in natural systems we must consider feedback within living systems, an issue that I refer to before (see 3.2.1 and annex 2). Feedback has a central role in the theory of self-organization, and central to control and directionality in cybernetic systems is the concept of the causal loop. The causal loop is any concatenation of causal connections whereby the last member of the pathway is a partial cause of the first. Primarily because of the ubiquity of material recycling in ecosystems, causal loops have long been recognized by ecologists (Ulanowicz 1997; Jørgensen, 2012; Jørgensen et al., 2020). Henceforth, autocatalysis will be considered any manifestation of a positive feedback loop whereby the direct effect of every link on its downstream neighbor is positive.

Without losing generality, I describe in annex 4 an example of circular conjunction of three processes A, B, C to elaborate the analysis of autocatalysis, assuming mutualism<sup>54</sup> as the involved bilateral interaction. I depict, in figure A.3, a three-component interaction ABC. It is assumed that the action of process A has a propensity to augment the occurrence of a second process B. It must be emphasized that propensity implies that the stimulation that A exerts upon B is *not* wholly obligatory or mechanical. Rather, when A increases, most (but not all) the time B will also increase. B tends to accelerate C in similar fashion, and C has the same effect upon A. I present in annex 4 an ecological example of autocatalysis concerning the aquatic plant *Utricularia* (figures A.4a,b). In general, autocatalysis in ecology is not considered a mechanism (Ulanowicz, 1995, 2000, 2005, 2007). Taken as a whole, autocatalytic systems exhibit properties that comprise a distinctly non-mechanical dynamic, transcending the overused metaphor of a heat engine or machine.

One first notes that, by definition, autocatalysis is *stability-maintaining*. Furthermore, autocatalysis exists as a relational or formal structure of kinetic elements (Ulanowicz, 1995, 2000, 2005, 2007), a perspective that is close to the proposal of a new relational and dynamic ontology proposed by Santos (2015). Of notable importance is also autocatalysis' capability of exerting *selection* pressure upon its ever-changing, malleable constituents (Ulanowicz, 2005, 2007). If one considers a small spontaneous change in B, where this change makes B either more sensitive to A or a

<sup>&</sup>lt;sup>54</sup> Mutualism describes the ecological interaction between two or more species where each species has a net benefit. It is a common type of ecological interaction. Mutualism can be contrasted with interspecific competition, in which each species experiences reduced fitness, or it can be contrasted to parasitism, in which one species benefits at the expense of the other.

more effective catalyst of C, the transition will receive enhanced stimulus from A. Conversely, if the change in B makes it either less sensitive to the effects of A or a weaker catalyst of C, that perturbation will likely receive diminished support from A. That is, there is a preferred direction inherent in autocatalysis – that of increasing autocatalytic participation. Autocatalytic configurations impart a definite sense (direction) to the behavior of systems in which they appear, and such asymmetric action violates the Newtonian assumption of *reversibility* (Ulanowicz, 1995, 2005, 2007). Furthermore, as components are drawn further into autocatalysis, or mutually adapt to the cycle, they may lose the capability of acting on their own. Should they become separated from the cycle and still survive, they would behave radically differently from how they would act as part of autocatalytic schemes. Thus, the full cycle manifests an organic nature that contravenes the Newtonian assumption of *atomism*, emphasizing that we must assume a relational ontology according to which the existence conditions, the identity and the causal behavior of any entity must always be conceived, and explained, as constructed and transformed by the interplay of its relational processes (Santos, 2015).

One also notes, in particular, that any change in B is likely to involve a change in the amounts of material and energy that are required to sustain B. Hence, whenever activity and resources are coupled, selection will act to reward and support those changes that bring ever more resources into B. The same applies to all the other member of the feedback loop. Any autocatalytic cycle becomes the center of a centripetal pattern of flows toward which as many resources as possible will converge (Ulanowicz, 1995, 2005, 2007), as I portray in figure A.5. It is noteworthy that an autocatalytic selection pressure driving centripetality is exerted in top-down fashion. It is the agency proper to the macroscopic ensemble that actively influences its constituent elements. Not only does such mode of action directly contradict the Newtonian assumption of *closure*, but it also reveals that the effective agency behind the "creation" of new objects is not another object but a configuration of processes (Ulanowicz, 2007). Thus, emergent properties are the systemic properties that are generated by the qualitatively transformative interactions between system's components and, consequently, by the new relational properties that the components exhibit in such networks of co-dependency.

To be sure, autocatalytic systems are contingent upon their material constituents and usually also depend at any given instant upon a complement of embodied mechanisms (Ulanowicz, 2005). But such contingency is not, as in strict reductionism, entirely a one-way street. Autocatalysis, by its very nature, is prone to induce competition, not merely among different properties of components, as I have outlined above with selection, but among its very material and mechanical constituents themselves, prone to replacement by the active agency of the larger system (Ulanowicz, 1995). Let us suppose that, as in figure A.6a, some new element D appears that is more sensitive to catalysis by A and provides greater enhancement to the activity of C than does B (figure A.6b). Then D either will grow its activity to overshadow B's role in the loop, or will displace it altogether (figure A.6c). In the same manner one can argue that C could be replaced by some other component E (figure A.6d), and A by F, and thus the final configuration DEF contains none of the original elements despite retaining the same structure (figure A.6e). More generally, autocatalytic selection sometimes acts to stabilize, compartmentalize and regularize behaviors across the physical hierarchy. In my opinion, and contrary to the rigidity imposed by the Newtonian assumption of *universality*, under the ecological lens the consequences of an event or behavior at any point or time will rarely propagate up and down the hierarchy without attenuation, as Ulanowicz (2007) argues.

It is important to notice that the characteristic persistence time of the larger autocatalytic form is longer than that of its constituents. The appearance of centripetality and the persistence of form beyond constituents are decidedly non-Newtonian behaviors, and make it particularly difficult to maintain any hope that a strict reductionist and analytical approach to describe an ecosystem will in the end succeed (Ulanowicz, 1997, 2000, 2005). Although the system requires material and mechanical elements, it is evident that some behaviors, especially those on a longer time scale, are, to a degree, autonomous of lower level events. Thus, attempts to reduce the workings of an ecosystem to the properties of its composite elements will remain somewhat futile, in my perspective.

The foregoing considerations make clear that autocatalysis can be characterized as *emergent*, in the sense that some of the foregoing properties might be missed if one were to observe only part of the cycle. By considering only a fragment of an autocatalytic cycle one might mistakenly be led to identify an input as an autonomous initial cause and an output as a determined terminal effect. As soon as one increases the scope of observation so as to encompass all the members of the loop, however, the interdependence of such causes and effects becomes apparent, and the foregoing attributes begin to emerge (Ulanowicz, 1998, 2005), as I depict in figure A.7.

As to the overall effects that the combined autocatalytic properties have upon the development of a flow network, it may be said that they change both its extensive and intensive natures (Ulanowicz, 1998). Extensive properties are those that depend upon the size of the system, and the growthenhancing nature of autocatalysis acts like a ratchet to push the activity level of the cycle ever higher. Meanwhile, selection and associated properties change the qualitative (intensive) character of the network by "pruning" away, or diminishing, those elements of the network that are less engaged in autocatalytic activities. This net effect of indirect mutualism is depicted in figure A.8.

As I have argued above, in order to quantify the constraints operating in an ecosystem it is important to reconsider causality. Autocatalysis is thus seen to behave in ways quite uncharacteristic of machines. It is also important to note that the causal agency of autocatalysis appears in a form that is foreign to conventional mechanistic analysis. In particular, the selection pressure that arises from autocatalysis acts from higher scales *downwards*, something that I have already referred in section 1.2, because an holistic approach allows that both the higher levels ("downward causation") and the lower ones ("upward causation") participate in determining the properties of specific levels. The conventional reductionist perspective, however, allows only influences originating at lower realms to exert their effects at larger scales. This perspective is a legacy of the Newtonian worldview and the ensuing Enlightenment (Ulanowicz, 1995, 1997, 2005). Before Newton, however, the prevailing view on natural causality had been formulated by Aristotle, who explicitly recognized the existence of downward causation, crucial for understanding the nature of the emergent properties of a system.

Aristotle's image of causality was more complex than the one subsequently defended during the Enlightenment. Aristotle identified four categories of cause: material, efficient (or mechanical), formal and final. The thinkers of Enlightenment acted decisively to excise formal and final causalities from all scientific description (Ulanowicz, 1995, 1997, 2005). In my opinion, we have to reconsider whether these discarded categories might not serve the interpretation of complex phenomena, and if Aristotle's scheme provides a more satisfactory description of ecodynamics. I think that efficient, formal and final causes are hierarchically ordered, in accordance with the theory of integrative levels. It becomes apparent that autocatalytic loops of constraints are acting as a kind of formal agency, selecting for changes among participating ecosystem components. That is, formal cause should act most frequently at what is called the "focal" level of observation (Ulanowicz, 1995). Efficient causes tend to exert their influence over only a small subfield, although their effects can be propagated up the scale of action, while the entire phenomena lives under constraints set by some kind of final agency in a heuristic sense, as I have referred to in section 3.1. It is normally (not universally) assumed that events at any hierarchical level are contingent upon (not necessarily determined by) material elements at lower levels (Ulanowicz, 1995, 1997). Therefore, in my opinion, the issue concerning Newtonian

dynamics is that it cannot in general accommodate true chance or indeterminacy. I agree with Ulanowicz (2005), when he argues that Aristotelian causal theory is far more accommodating of chance. Any spontaneous efficient agency at any hierarchical level would be subject to selection pressures from *formal* autocatalytic configurations above. These configurations in turn experience selection from still larger configurations in the guise of a *final* cause.

After these considerations regarding contingency, autocatalysis and causality, let me now explain how one can quantify the *overall degree of constraint* in an ecosystem as manifested by its network of material and energy flows. Ulanowicz (1986, 1995, 1997, 1998, 2000, 2005, 2007) developed mathematically a scaled measure of constraint using information theory in the case of ecosystems, called *ascendency* (the development is described in annex 5 and presented in equation A5.6.<sup>55</sup> Ascendency was initially formulated as a phenomenological index that encapsulates several of the criteria that Odum (1969) had identified as characteristics of ecosystems in the later phases of ecosystem succession. His list of 24 criteria can be grouped in terms of four tendencies: ecosystems tend to increase in species richness, species interactions specificity, containment and recycling (Ulanowicz, 1998, 2005). All other things being equal, a rise in any of these four attributes also serves to increase the system' ascendency. It follows as a phenomenological principle that "in the absence of major perturbations, ecosystems have a propensity to increase in ascendency" (Ulanowicz, 2005, pp. 314). The hypothesis in question is that augmented autocatalytic selection and centripetality are the agencies behind increasing self-organization. Thus, quantifying the degree of constraint in an ecosystem must reflect these changes in both the magnitude and intensity of autocatalytic activities.

Ascendency measures both the size and the organizational status of the network of exchanges that occur in an ecosystem, that is, the degree to which ecosystem' activity is organized by its internal constraints (Ulanowicz, 1998, 2000). Ascendency is expressed by a variable called *average mutual information* (or average mutual constraint), which "measures the average amount of constraints exerted upon an arbitrary quantity of energy and materials in passing from any one compartment to the next" (where compartments refer to the individual organisms or populations making up a trophic level in the food web of an ecosystem, Ulanowicz, 1997, pp.73). Ascendency is then defined as the product of average mutual information and the total system throughput (Ulanowicz, 1997, 1998, 2000), as I describe in annex 5.

Ascendency thus seems to provide an appropriate goal function<sup>56</sup> by means of which to describe ecosystem development (Ulanowicz, 1997, 1998, 2005). However, two issues immediately arise (Ulanowicz, 1998). First, ascendency tells only one part of the story of ecosystem development. If ecosystems were fully constrained, without any degree of freedom, a mechanistic explanation would have been sufficient understand its behavior. But organic behavior requires a certain degree of freedom from total constraint. Nonetheless, it is possible to quantify this freedom, in this perspective, using an expression for residual freedom ( $\phi$ ), as I present in equation A5.7. This quantity  $\phi$  is

<sup>&</sup>lt;sup>55</sup>. Ulanowicz (1997, 2000) invokes information theory to quantify the indeterminacy associated with a highly indeterminate collection of matter and energy exchanges between ecological components, defined as species populations. Ulanowicz defines information as anything that causes a change in probability assignment, essentially equating information to constraint. Information theory is the field of mathematics that quantifies such changes in probabilities. The author uses the term indeterminacy to emphasize the potential for causal openness in developing systems, such as ecosystems, and the term information, which hinges more upon the agency behind a change in probability than upon any subjective perception of that change. Thus, information refers to the effects of that which imparts order and pattern to a system. Accordingly, information theory allows quantifying constraint in ecosystems. See annex 5.

<sup>&</sup>lt;sup>56</sup> Ecosystems show a propensity to move in a specific direction indicated by ecological orientors (ecosystem variables that describe the range of directions in which ecosystems have a propensity to develop), which can be described in ecological models by goal functions. In a model, the description of the development of the state variables of the model has to be rigorously indicated, which implies that goals are made explicit.

complementary to the ascendency and is termed the system *overhead* (Ulanowicz, 1997, 1998, 2000, 2005): it can be decomposed into four components representing the indeterminacies in the inputs, exports, dissipations, and internal connections. Overhead is complementary to ascendency and captures how much flexibility the ecosystem retains. The ascendency and the overhead together quantify the *structured complexity* of the ecosystem (Ulanowicz, 1998). Introducing these two concepts, one is then able to measure ecosystem flux networks as well as changes in such networks, i.e., the organizational changes of ecosystems (Yin and Herfel, 2011).

The second warning is that ascendency, in spite of being a surrogate for constraint and efficiency, is itself a non-mechanical attribute (Ulanowicz, 1998). It is based upon a probabilistic rather than a mechanistic depiction of reality. Any directed change, such as the tendency for ecosystems' increase in ascendency, should not be likened to a mechanical goal function. Probabilistic functions do not drive the ecosystem toward a fixed, pre-determined point, as in the common, Newtonian, deterministic notion of a goal function. Rather, probability operators behave as orientors, which merely guide the system along a vague direction. Therefore, ascendency must be regarded as an ecological orientor and, in my opinion, should not be criticized for reintroducing teleology in ecology, because it is heuristically defensible, in a manner analogous to that I have defended in section 3.1.

Therefore, I would argue that the focus in ecosystem dynamics should be shifted from the normal (symmetrical) equations of Newtonian physics and should be directed instead towards the origins of asymmetry in any system, that is, their boundary constraints. I have outlined how biotic entities serve as the origins of such constraints upon other elements of the biota, so that the core of ecodynamics is revealed to be the mutual, self-entailing constraints that occur within the ecosystem itself, forming a relational ontological structure. Then, using Ulanowicz development, a palpable and measurable entity (the network of material and energy exchanges) was identified upon which the innumerous (mostly hidden) constraints could exert their influence. Finally, a calculus was developed that could quantify the effects of all the hidden constraints, which will be an instrumental element for the moderate approach. As a result, by following changes in the ascendency and overhead of an ecosystem flow network, I believe that one is focusing upon the elements making ecodynamics fundamentally different from classical dynamics. However, I recognize that, in spite of the problems with the Newtonian assumptions sketched above, many ecologists continue to operate under the mechanistic umbrella of the Newtonian tenets, somehow exhibiting envy towards physics as a science.

An issue developed according to the systems research, which can constitute a limitation on ascendency, is the effort made to take the spatiotemporal details of ecosystems into account, termed as "organodynamics", that is, the dynamics that emerge from strictly biological properties of relationships between the organisms inhabiting the ecosystem, especially their spatiotemporal aspects (Yin and Herfel, 2011).<sup>57</sup> As already stressed several times, ecologists often ignore the biological characteristics of organisms when they are building their models. Such characteristics are averaged out and hence have no dynamic effect in models of ecosystem dynamics. Some ecologists have tried to rectify this problem, as Pahl-Wostl (1995), investigating ecosystems spatiotemporal patterns. Using far-from-equilibrium thermodynamics and complex adaptive system theories, they have investigated how organisms' existential activities influence ecosystems' organization and dynamical properties.

<sup>&</sup>lt;sup>57</sup> These properties and relationships include, but are not limited to, coevolution, body and habitat size, hunting or foraging range, as well as life span, reproductive cycle, and other spatio-temporal characteristics in organisms' life histories, such environmental heterogeneity as fractal properties in living surface or space, as well as spatial and temporal variation in light intensity, humidity, temperature, and nutrient supplies.

Pahl-Wostl (1995), adopting a complex systems approach to model ecosystem organization and dynamics, develops the flux pathway networks of energy and matter in ecosystems using Ulanowicz's concept of ascendency and his mathematics. However, while in Ulanowicz's model the flux network of energy and matter is mostly imposed by an autocatalytic process that is relatively independent of its constituent organisms, Pahl-Wostl argues that these flux networks partially selforganize, making an explicit effort to distinguish the imposed organization from self-organization. I believe this is an important point. According to Pahl-Wostl, self-organization: is endogenously generated; has distributed control; is realized through a flexible network of interactions that has little potential to adapt and change; and is predictable.

Pahl-Wostl (1995) does not eschew Ulanowicz' concept of ascendency; on the contrary, the author extends it incorporating organisms' properties and environmental heterogeneity into models and explaining the detailed mechanisms of how such pathway network organization *emerges*. While Ulanowicz (1986, 1997) claims that organisms' characteristics can be safely ignored when modeling ecosystem organization and dynamics, Pahl-Wostl (1995) argues that the diversity in the biological properties<sup>58</sup> of the constituent organisms, and in the heterogeneity of their environment, are essential for the *emergence* of the flow networks in ecosystems. However, in spite of this attention to organismal properties, Pahl-Wostl is not a reductionist ecologist because the author does not assume atomism; the core of her analysis are the relations in the ecosystem, the dynamic characteristics included in the referred biological properties. I think that this perspective is coherent with the dynamical and relational ontology that I defend, according to Santos (2015, 2020), because each part of the ecosystem is continuously conditioned, in terms of its qualitative properties, causal powers and interactions which it may possess and exercise, by the structured network of all of its direct and indirect relations within that system. This view converges with Santos (2020), and one can make sense of the idea that an ecosystem, formed from a structured network of interactions between its parts, can preserve an emergent ontological status vis-à-vis the collection of its proper parts.

Thus, in Pahl-Wostl perspective, spatiotemporal organization of flux networks is constructed under two sets of constraints. Firstly, because ecological organization emerges from the ongoing activities conducted by the constituent individual organisms, they are constrained by the dynamic characteristics of the constituent organism. Secondly, the organisms' existential activities are constrained by the dynamic properties of their immediate environment.<sup>59</sup> In the author's words, spatiotemporal organization "is the internal network structure that organizes itself at any moment in space and time to fill the envelope determined by these constraints in combination with the boundaries imposed by the physical environment" (Pahl-Wostl, 1995, pp. 139-140).

While it may be accepted that these putative new sources of ecological organization and dynamics bring about new ways to approach the traditional issues of ecosystem stability, complexity and succession, I think that they also raise some new interesting issues. I recognize that maybe these issues are inaccessible within the Odumian and Ulanowicz's framework, due to the "black-boxing" of constituent organisms into trophic levels or components, then constituting a limitation to the theoretical tool that I will use in the moderate approach: Ulanowicz' ascendency. This strategy of using "black-boxes" is evident in Ulanowicz's work, when the author, even acknowledging the self-

<sup>&</sup>lt;sup>58</sup> Pahl-Wostl (1995) terms them as *dynamic characteristics*, including body weight, foraging range, living space or surface, dietary habit, mating habit, active time (hunting or nutrient absorbing) during the circadian or annual cycle, reproductive cycle, and life span, as well as environmental characteristics including spatial and temporal properties, temperature, water and nutrient supplies in the environment.

<sup>&</sup>lt;sup>59</sup> These environmental properties include climate conditions, seasonal cycles, nutrient availability, light intensity, temperature range and rainfall range, the spatial distribution of food, nutrients, and water, etc., as well as other individual organisms that either share the physical environment or interact with them via symbiosis, competition or predation.

organizing nature of the flux network, takes this approach when he conceptualizes the structure of the network, describing the autocatalytic processes that impose structure to ecosystems using blackboxes.<sup>60</sup> However, I think that related to this limitation is the disadvantage of the complex calculation of ascendency as an index of directionality if one introduces a large amount of data, as would happen using data about organismal properties and respective dynamics. This it will become conspicuous when I illustrate the empirical example, in section 4.1, where data is "black-boxed" to species populations and larger taxonomical groups when needed. However, in the same example, I will show that directionality can be quantified in this way by the ascendency of the system, as an increase in this informational theoretic measure, and that this directionality opposes the tendency of the second law of thermodynamics, which is the increase of disorder in a natural system, such as an ecosystem.

In retrospect, I think that ELT (and eco-exergy), ascendency and the maximum power principle are different angles in the description of ecosystem's growth and development. Eco-exergy covers the storage, maximum power covers the flow and ascendency covers the ecological network, and all three concepts contribute to comprehend the process of moving away from thermodynamic equilibrium. The three concepts are also well rooted in theoretical soil. However, calculations of eco-exergy, maximum power and ascendency can become unfeasible due to the enormous complexity of ecosystems (Jørgensen *et al.*, 2020).<sup>61</sup> Thus, the three concepts may have a solid theoretical basis, but their applications in practice will have weaknesses that are rooted in the complexity of the ecosystems.

I concur with Ulanowicz (1997) when he argues that two dialectics emerge out of the thermodynamic traditions. The first one is between those authors, such as Jørgensen, who claim that ecosystems behave conservatively by minimizing their activity and retaining resources and those, on the other hand, who see ecosystems as more expansive and dissipative, e.g., Lotka, Odum and their followers. Ulanowicz (1997) states that enfolding both the emphasis on conservation and expansion into a single, overarching and quantitative framework was the first motivation to formulate the concept of system ascendency.<sup>62</sup>

The second dialectic occurs between those who emphasize contents and those who emphasize transformations, i.e., stocks or flows (Ulanowicz, 1997). Classical thermodynamics dwells upon state variables, those attributes that describe a system at equilibrium. Conceivably, transformations can take place in a system at equilibrium; such flows, however, are always balanced, and their associated dissipations are negligible. For these reasons, flows remain in the background of classical thermodynamic descriptions, which focus by default upon the contents of a system. Should a system undergo some transformation and return to its original configuration, the change in each of its state variables would be zero by definition. The amount of activity (flow) associated with the excursion is not unique but rather depends upon the exact nature (pathway) of the processes that comprise the

<sup>&</sup>lt;sup>60</sup> Such problems include niche construction and differentiation, the roles played by individual organisms' existential activities in constructing flow pathway networks of energy and materials, ecosystem resilience, individual organisms' biological diversity and environmental heterogeneity and their roles in ecosystem organization and dynamics.

 $<sup>^{61}</sup>$  Eco-exergy storage is the simplest of the three concepts, but clearly the assessment of the  $\beta$  values (see annex 3) has some shortcomings. Measuring power is more difficult because it is related to the amount of flow. Most ecological observations are based in concentrations and not on flows, making it harder to validate the flow values resulting from ecological models. Calculations of ascendency have the same complexities as calculations of power.

<sup>&</sup>lt;sup>62</sup> A tension between these opposing trends has been built into the ascendency. When external conditions become extreme, it is possible that one of the conflicting trends will prevail. For example, whenever external resources become quite abundant, the activities of those elements that can appropriate (and dissipate) them as quickly as possible dominate the system. The rise in ascendency during flush conditions is due almost entirely to increasing total system throughput. At the other extreme, when external resources are meager, those taxa persist that can, in cooperation with like-behaving species, sequester resources with a minimum of dissipative overhead. Under sparse conditions, which usually prevail later in the course of system development, a rise in ascendency almost always is due to an increment in the mutual information of the flow structure.

cycle. Once again, one should note how the conventional outlook emphasizes conservative state variables, such as pressure, temperature, or chemical composition, over non-conservative process variables, such as heat flow, dissipation or material throughput. As I have referred above, exergy sought to deal with this bias, by extending the notion of a state variable as far as possible to non-equilibrium situations, connoting the energy that potentially could appear as work: thus, exergy measures content or stock. Therefore, the contrast between Jørgensen' principle of maximal exergy storage and the ascendency hypothesis consists in the dialectic between the description of component stocks and a narrative of flows between distinct compartments. I would argue that some connection must exist between state descriptions and flow narratives and that an ecosystem might likely increase in both exergy content and ascendency in its development. As said above, it is easier to obtain data on stocks than to measure flows. However, as also referred, estimating the exergy of living organisms (since it depends on a primary estimate of entropy) can be problematic. In comparison, nonetheless, obtaining the ascendency of a trophic exchange network is conceptually straightforward, albeit laborious. Thus, I contend that ecologists should integrate the concepts, expanding the hypothesis based in eco-exergy and ELT, and complementing it with ascendency and the power principle.

To conclude, I would argue that the merits of the post-classical perspective, and its chief contribution for a moderate approach, is the need to emphasize that the ecosystem, as a whole, has its own set of properties and laws which are different from those relating to its parts, and that the whole can also *affect* each of its parts. As I have described above, the exergy of an ecosystem is a relative measure of the work capacity (relative to the ecosystem at thermodynamic equilibrium), that is, the available energy in the ecosystem. This constitutes a property of the whole affecting individual organisms and populations, because they depend on the work capacity of the ecosystem. Also, the ascendency and the overhead of an ecosystem, together quantifying the structured complexity of the ecosystem, are properties of the whole ecosystem. As referred above, with these two concepts, one is able to measure ecosystem flux networks as well as changes in such networks, i.e., the organizational changes of ecosystems, to study the constraints and degrees of freedom in their development. Consequently, these are the constraints and degrees of freedom affecting individual organisms and populations, as ecosystems' components. That is the reason why eco-exergy and ascendency will be crucial for a moderate approach. However, a potential limit to interpret the whole as a *previous* and self-sufficient entity - ontologically independent of its parts and somehow imposed on them -, might be highlighted. The whole would thus be presented as a somehow mysterious entity, as a "coarse" unit. We know what the whole does by observing it, but we cannot find the causes of its behavior: we cannot explain but only describe. I would argue that a dynamical relational ontology, to which I have already referred to in section 2.2.3, in accordance with Santos (2015, 2020), can in some way aid to tackle this problem. In this perspective, there is no priority of the parts over the wholes - there are parts and wholes, but they are construed by, and can only be explained through, their *relations*. Thus, in an integrated system, such as an ecosystem, each part will manifest properties and behaviors by virtue of the specific structure of relations of that very system – properties and behaviors that will not manifest outside of that whole. Since every entity is both a whole of its parts and a part of another whole, any system will have its own relations with its environment. I would argue that *relationalism*, following Santos (2015, 2020), can be seen as overcoming the antithesis between reductionism and holism and as a crucial conceptual basis for a moderate approach in ecology that I will finally articulate in the next section.

## 4. The Moderate Approach in Ecology

As related in section 2.2, the Clementsian superorganismal approach to communities has been progressively abandoned in favor of reductionist approaches. Yet, not all holistic elements of Clements's view have disappeared from ecology. Some present-day prominent ecologists endorse a moderate position and this ensuing hybrid position can be called either *moderately holistic* or, just as well, moderately reductionist. This moderate position recognizes communities and ecosystems as real and objective ontological entities with their emergent properties, which are not completely determined by the properties and activities of individual organisms, thus arguing that these complex entities are conceived as wholes composed of parts, whereby these wholes depend heavily on the activities of their parts and on the interrelations between them. By choosing an appropriate research target, the ecologist can identify the boundaries of the physical system under study, and unpack it in terms of the identification of trophic levels, thus allowing an analysis of the energetic ecosystems framework and the flux of energy and chemical elements going through the ecosystem. This framework constitutes the holistic element of the moderate position. Concomitantly, moderate ecologists recognize the need to decompose these wholes, to explain them in terms of their component parts. Accordingly, communities and ecosystems are considered well-delineated aggregates of individual organisms, whose composition and structure is determined by the random factors of migration and environmental fluctuation. Their properties must be explained through the analysis of populations and the dynamics of populations' interactions, which are ostensibly studied first, as if they were components, providing the reductionist element of the moderate position. As a consequence, organismal and population phenomena help to the understanding of the emergent properties of higher level ecological phenomena. This approach is also middle-way because the explanations are not entirely sought by identifying the ecological adaptations of species but also and particularly centering on the analysis of interspecific interactions.

The extreme complexity of ecological systems, imbued in its characteristic self-regulation – which has long daunted ecologists –, was seen as requiring, during the 1940s and 1950s, systems analysis. As a consequence, as I have described in section 3.2.1, there was an earlier accommodation of the reductionist and holistic positions in classical ecosystems ecology, an inchoate moderate approach, within the framework of the theoretical conception of the ecosystem concept coined by Tansley (1935). This was a more "nuanced" ecosystem approach contrasting a more "radical" holistic position. Even if these approaches explicitly see themselves as holistic, and even though they are holistic in the sense that they take the whole ecological system as a given and see the parts as existing in a functional relationship to the latter, they are nonetheless relatively reductionist in the sense that they approach organic wholes within an analytical frame. Rather than focusing on communities described as combinations of particular species, their object of study, instead, typically consists of populations, viewed in the same way as other components of the ecosystem, like the abiotic ones.

These holistic ecological approaches stemming from the second half of the twentieth century, of which the Odumian perspective can be considered as the starting point, have this systemic theoretical character. This is because they try to decompose the units of ecological research. It is this decomposition requirement that distinguishes them fundamentally from the old organicist holism, according to which there is no need to decompose wholes. A significant element of this view is that the endogenous development of an ecosystem leads to a predictable increase in biomass, diversity and stability in the course of succession. To a certain extent, such theories involve reformulating the holistic-organicist conception of wholeness within the framework of systems thinking, abandoning a tacit teleological perspective, in the heuristic sense referred to in section 3.1.

The old organicist holism attempted to describe the workings of the system constituted by the entire range of organisms occupying a specific space as a higher-order organism or at least to identify "superorganisms" among the more or less close associations of individual organisms. It basically sought, at a higher level, those objects in nature whose model of functioning is aimed at selfmaintenance. Ecosystem theory, by contrast, demarcates certain systems, largely for instrumental reasons, either of technical or theoretical nature. Some level of arbitrariness characterizes this moderate approach in identifying relevant ecosystems, depending on research interests. The same problem applies to the identification of the relevant communities in the individualistic approach. Ecosystems therefore can be considered in a sense artifacts. However, they can be considered "superorganisms" too, as in the old holistic tradition. According to this moderate position, the purpose of ascribing value to certain ecological organizations becomes different: the characteristics and behaviors of ecosystems that are "good" for the ecosystems themselves are those that make it possible for them to fulfill the functions defined by us and by our interests. The structure of "superorganisms" is reflexive: the parts are self-generating, a process that is mediated by the whole and that is the function of both parts and whole; "superorganisms" decide for themselves what is "good" for them. With ecosystems, however, we set an end point to what, in principle, is an endless cycle of functional utility, as utility is interpreted from the pragmatic standpoint of ecologists. By contrast, a "superorganism", like an organism, is an end in itself.

Despite all this, the more moderate ecosystem theory uses the old organicist rhetoric of self-regulation and self-preservation, even though the meaning of the terms is not the same. One thus refers to processes that contribute towards maintaining a state that is useful for the purpose *defined by us*. A great deal of ecological research may be considered to belong to this moderate approach (Looijen, 2000): analyses of food chains and food webs in ecosystems, analyses of the structure and assembly of communities, investigations into the mechanisms of coexistence of species and mechanisms of succession and, of course, all the theoretical and empirical research concerning interactions between species that play a role in these processes. My empirical example, as I shall illustrate in section 4.1, is also an instance of this moderate approach.

The classical ecosystems ecology, which I have developed in section 3.2.1, was thus an earlier attempt, originating with Odum and others, to build a consistent moderate approach to ecology, a middle way between the holistic and reductionist approaches. Even though emergentist ontology is a cornerstone of this position in ecology, it is also true that an energetic ecosystems framework ideally demands a complete analysis of all components involved, at all levels. I think that this balanced perspective is the most robust and promising to explain ecological phenomena, a stance that I shall henceforth advocate. In section 2, I have presented the possible limitations of the reductionist approaches to ecology and argued why one needs to involve a sense of *wholeness* in the study of complex entities that are in a meaningful sense objective and real such as communities and ecosystems. However, as I have argued, there are some critical elements of this kind of approaches that can be relevant to explain ecological phenomena.

In section 1.2, I started to argue that the various levels of ecological organization are characterized by new and specific properties – emergent properties –, which increase the degree of complexity of a given level compared with the various levels of which it is composed. By contrast, reductionism denies the existence of emergent properties; in fact, the existence of these emergent properties, it might be argued, invalidates any strict reductionist demonstration, no matter how apparently convincing. Nonetheless, as I have referred to in section 2.2, within the mechanistic account some advocates have found appropriate to describe some emergent phenomena as instances of

mechanistic emergence, which can either be conceived in only epistemological terms or also in ontological terms.

Coherently conceived, micro-reductionism is a doctrine according to which the system's macroproperties are reducible to a certain composition relation between some parts' intrinsic properties, i.e., properties which the lower-level entities instantiate independently of being interrelated parts of such wholes (Santos, 2020). This kind of micro-reductionism is grounded in micro-determinism, a position according to which the qualitative and causal identity of every entity is completely determined by its own intrinsic attributes; thus, the qualitative and causal identity of any entity must be completely independent from its exogenous relations with other entities, including in the context of higher-level systems' relational structures. I would argue that it is difficult to accept this intrinsicness-principle of identity, borrowing the expression of Santos (2020), in ecology. As I have outlined in section 2.1, the characterized anti-emergentist position was endorsed, for instance, by Gleason (1917, 1926), according to whom, for example, interactions such as predation, parasitism or competition were not crucial. According to this reductionist perspective, any ecological system, as a mereological complex, is completely determined by, and thus reducible to, some composition, arrangement or configuration of the intrinsic attributes instantiated by their historically or constitutively associated lower-level entities, the individual organisms. Therefore, the ecology of single individual organisms would be sufficient to explain the ecological phenomena of focus in community ecology and, accordingly, the community would become a whole that is entirely the sum of the parts. Following micro-determinism, any whole or higher-level organization is supposed to be micro-determined and, therefore, microexplainable, by the lower-level organization of its proper parts. Micro-determinism must thus exclude any mutual determination between parts and wholes (Santos, 2020).

In my opinion, when it is assumed that the higher-level properties of ecological systems are mere aggregates of their components' properties considered in isolation, as advocated by Schoener (1986) and Vellend (2010), simplification errors and biases in results might ensue. In this respect, Schoener erroneously thinks of defending Nagelian theory reduction in ecology when, in fact, he is defending a kind of micro-explanatory reduction: explaining the ecology of a community through the ecology of individual organisms, as if they were isolated components (see section 2.2.1).

From micro-determinism follows that no system's property can ever be emergent, since it can always be represented as a mere combinatorial product of intrinsic micro-properties, as well as respective micro-relations,<sup>63</sup> of that system's parts (Santos, 2020). This claim, as I have showed in section 2.2.1 (pp. 24), through the analysis of Holling's studies (1959), cannot be true. If it were true, one would in effect be assuming that any higher-level system property (e.g., predation in a community or ecosystem) was a micro-based property, in the sense of being completely decomposable into, or micro-reducible in terms of, a configuration of the intrinsically determined micro-constituents (individual organisms or their populations). Thus, one can argue that a system is emergent from the set of its lower-level entities, if and only if at least one of its attributes is not produced, or determined, by some relation between the attributes that the lower-level entities instantiate independently of the relation in which they are involved, as interacting parts, or correlated *relata* of that very system (Santos, 2020). This is the reason why I think that epistemic emergence is not sufficient to explain some emergent properties of ecosystems. Ontological emergence is thus needed, where, according to a genuine relational perspective, parts and wholes are correlative terms. Hence, parts and wholes come together; no one has ontological or chronological priority over the other. Every entity is, either a whole

<sup>&</sup>lt;sup>63</sup> Micro-relations thus refer to the local relations between the parts of a system, confronting the parts of a system and the system taken as a whole; in this case between the individual organisms (the parts) within an ecosystem (the whole).

constituted by some parts in relation, and at the same time a part of some relational context, or a whole. In sum, from an ontological point of view, parts, wholes and relations are on equal ontological footing. From an epistemological point of view, instead, relations are the key concept or the primary object of research (Santos, 2015).

If it is true that there are important problems in treating ecological systems as micro-determined aggregates, as I have related above, nonetheless I think that aggregation is not futile. Aggregation is an effective method to make complex mechanistic or reductionist models simpler, more mathematically or analytically tractable, constituting an important element for a moderate approach. And, as I have already said, the chief advantage of this endeavor is that it allows a theoretical understanding of how variation in individual-ecological properties (for instance those of behavior and physiological ecology) affects population and community structure. However, it should be emphasized that this kind of approach may entail an extraordinary degree of complexity when many species interactions are involved and, furthermore, a lack of realism if the abstractions and approximations are not correctly implemented. First, any particular model, if it is to incorporate enough behavioral or physiological variation, may have to be so complex as to be analytically opaque; second, even if individual based models are manageable, too many models, each with a very narrow application, may inflate the entire theory as to render ecology extremely complex. Thus, it is not that the mechanistic approach is in principle unable to handle phenomena involving numerous population- or community- level variables; it is rather that, in practice, this may become an overwhelming task. Here my position converges with the analysis provided by Grimm (1999).

However, I think that the main criticism that can be advanced against reductionist mechanistic approaches in ecology is its difficulty, or even impossibility, to explain the emergent properties of a higher ecological system. An ecologist must be able to distinguish the properties that an organism only has or manifests within some ecosystem, from the properties that an organism has or manifests independently of the ecosystem of which it is a part (i.e., the so-called intrinsic properties). Organismal behavior in case of predation belongs to the former case, for instance. The system-dependent relational properties of an entity are the properties which an entity only acquires or manifests by virtue of the specific set of relations that constitute a particular system (Santos, 2020). For example, by virtue of the interaction with the predator or even other preys, a qualitative change in the behavior of the organisms might result. The same happens with micro-predicting all the properties of an ecological system from the properties that its lower-level entities instantiate, independently of being interacting parts of that system.

Following Santos (2020), a property of an ecological system cannot be micro-reducible or micro-determined when some of the components' micro-properties (e.g., individual organisms' properties) contributing to its production are themselves instantiated by virtue of the parts' integration within that very ecological system; and a property of an ecological system cannot be micro-explainable when some of the parts' micro-properties (e.g., individual organisms' properties) to which such an explanation needs to appeal to are only, in turn, explainable by the parts' integration within that very ecological system. Therefore, there is no unilateral or asymmetric reduction of an ecological system to its parts, such as individual organisms or populations, nor vice versa but, rather, a reciprocal determination between lower and higher levels in ecology.

I consider the latter point about *reciprocal determination* as the most important point of my analysis so far as it captures the spirit of a moderate position, which I endorse. I am not assuming classical holism, according to which the wholes are seen as primitive or self-imposed entities that structure, but are not structured by, their parts, a position that is close to Clementsian organicism (see

section 3.1). I am also not assuming a fully coherent and strict micro-reductionism, in which ecological system's properties are reducible to a certain composition relation between some parts' intrinsic properties, a position that is close to the individualistic concept of Gleason (see section 2.1).

The moderate position corresponds to the modern holistic ecosystem approach in ecology that I have articulated in section 3.2.2. This ecological approach overlaps and extensively matches the dynamical relational view proposed by Santos (2015), according to which the qualitative and causal identity of any entity, as well as its very existence and persistence conditions, must be ultimately explained as constructed and transformable by the interplay of its endogenous and exogenous relations, including those instantiated in the context of higher-level relational structures such as an ecosystem. The moderate position must therefore be underpinned by a relational emergentist ontology. However, it is also true, as I have argued above, that an energetic ecosystems framework ideally demands a complete analysis of all components involved, at all levels. The mechanistic explanation of an emergent system's activity (such as an ecosystem) must always proceed by the decomposition and localization of the system's components and activities, by the recomposition of the global combination of such components and, finally, by situating the system as a whole within its environment. The "classical" mechanicism is sustained by atomist metaphysics, and does thus not allow emergent properties. In contrast, NMP (see section 2.2.3), allows a somewhat relational emergentist ontology. NMP gives a notion of organization that allows a mechanistic form of emergence, even though not comprehending an ontological kind of emergence, according to some authors (Craver et al., 2019).

Hence, a mechanistic notion of reduction, within this moderate approach, is necessary, but is in itself insufficient for the explanation of ecological phenomena. As I have related in section 2.2.3, reductionist ecologists extrapolate from the organismal level to the population level and often speak about *species populations*, or functional groups, as being the *relevant components* for explanation, making an aggregation for convenience. In the example of modern holistic ecosystems approach that I shall illustrate below, ecologists use species populations, but also some higher taxonomic groups (e.g. mollusks or crustaceans), as the components of interest, aggregating sometimes at an upper level of abstraction, in accordance to the focus of the study.

To surmount the insufficiency of the mechanistic account it is required an interlevel integrative and systemic account, which I have developed in section 3.2.2. In fact, as I have outlined there, and I shall exemplify in the next section, eco-exergy and ascendency are holistic and systemic properties, furthermore emergent in accordance to a relational emergentist ontology. The empirical example will further substantiate the need of postulating genuine ontological emergence. Epistemic emergence – which considers emergent features to be a result of the limited abilities of ecologists to predict, to calculate, to observe, and to explain –, and mechanistic emergence – due to a specific organization of the components of the ecosystem –, are not sufficient to understand emergent features of nature, being the result of a reciprocal determination between the parts and the whole, while their emergent status should be independent of human knowledge.

Concerning eco-exergy, one can calculate the contributions from the dominant biological components in an ecosystem, for instance, using a model or measurements that covers the most essential components for a focal problem, considering the amount of information (which also contains first-class energy able to do work) that the components have embodied due to a flow of energy through the ecosystem. Eco-exergy depends on the probability distribution of the components of interest that depends on the interdependencies between them, which, on their turn, are generated because the components are localized in the ecosystem according to a specific spatial arrangement.

This explicates why eco-exergy is a systemic property irreducible to the properties of lower-level components. It is this reciprocal co-determination between the ecosystem and the components that imply its ontologically emergent status.

Concerning ascendency, as I have related in section 3.2.2, the way to measure the constraints inherent in the entire network of ecosystems flows is to perform calculations, using information theory on the inputs and outputs concerning each component, weighting the result for each component by the throughflow of that node, and average over the ensemble. Thus, we have a calculation that is inclusive of all constraints at work in the ecosystem. Thus, ascendency is a systemic property that is generated by the qualitatively transformative interactions between system's components and, consequently, by the new relational properties that the components exhibit in such networks of co-dependency, henceforth emergent also in accordance with Santos' proposal (2015, 2020). This is evident in autocatalysis, as I have shown, and in predation, for example. In the latter case, if there is a change in the behavior of prey (an intrinsic property), derived from a change in the constraints of the ecosystem (its relation with a predator), one will have a transformative interaction that implies a co-determination between that part (prey) and the whole (ecosystem). This is the reason why ascendency is irreducible to the properties of components of the ecosystem. Although the ecosystem requires material and mechanical elements, it is evident that some behaviors, especially those on a longer time scale, are, to a degree, autonomous of lower level events.

I will now substantiate the moderate approach with an empirical example in modern ecosystems ecology, wherein the authors use eco-exergy and ascendency to explain a complex ecological phenomenon in Portugal.

#### 4.1. An empirical example in modern ecosystems ecology

I will now describe the application of eco-exergy (Marques *et al.*, 1997; Jørgensen *et al.*, 2002) and ascendency (Patrício *et al.*, 2004), as ecological indicators,<sup>64</sup> to the Mondego estuary. This estuary, located in the western coast of Portugal (see figure A6.1), has been studied by integrating different sources of information derived from different ecological indicators (eco-exergy, specific eco-exergy, and ascendency), as I illustrate with more specificity in annex 6. The ecological situation of interest is the occurrence of seasonal intertidal macro-algae blooms, mainly of the *Enteromorpha* species and, as a consequence, the drastic reduction of *Zostera noltii* beds (a common species of eelgrass). The latter represent the richest habitat with regard to productivity<sup>65</sup> and biodiversity, outcompeted by *Enteromorpha*. This is an example of benthic eutrophication (nutrients enrichment in the benthic<sup>66</sup> zone), showing how environmental factors often give origin to ecosystem qualitative alterations (e.g., in terms of species composition, biodiversity).

Jørgensen *et al.* (2002) attempt to use exergy as an ecological orientor (a variable indicating the range of directions towards which ecosystems have a propensity to develop) to describe adaptation and changes in species composition. The authors developed two models, one for the *Enteromorpha*-dominant community and another for the *Zostera*-dominant community in order to compare eco-exergy under several conditions. The results show that the highest exergy in the first case is found with rich nutrient (eutrophication) and high salinity conditions. In the second case, the highest exergy is

<sup>&</sup>lt;sup>64</sup>Ecological indicators are variables indicating the present ecosystem's condition or health.

<sup>&</sup>lt;sup>65</sup>Productivity refers to the rate of generation of biomass in an ecosystem, usually expressed in units of mass per volume (unit surface) per unit of time, such as grams per square meter per day (g  $m^{-2} d^{-1}$ ).

<sup>&</sup>lt;sup>66</sup>Benthic zone is the ecological region at the lowest level of a body of water such as an ocean, lake, or stream, including the sediment surface and some sub-surface layers.

found under low nutrient and low salinity conditions. The models show that if the freshwater with high concentration of nutrients is discharged during the last part of the year, *Enteromorpha* will be dominant (see Table A6.1 and figure A6.2). One can also observe that the *Zostera* community has the highest exergy when the freshwater is discharged in the first part of the year, at which time it has a low nutrient concentration.

The authors thus conclude that the ecological management of the freshwater discharge is a key factor causing the prevalence of one of the two communities. Consequently, freshwater should be discharged early during the year and with as low a nutrient concentration as possible in order to ensure the dominance of the *Zostera* community. The authors think that the application of the maximum exergy principle to model which community would be dominant under which conditions has great environmental management interest. It is also important to be able to determine under which conditions a shift from one less desirable to a more desirable ecosystem structure would take place.

Marques *et al.* (1997) analyze the spatial and temporal variation of eco-exergy, specific ecoexergy, species richness and heterogeneity<sup>67</sup> in order to examine to what extent these ecological indicators would capture changes in benthic communities along the gradient of eutrophication in the same estuary. These authors, in their approach, try to understand the relationships between exergy and other more conventional ecological indicators, such as biodiversity. In practice, they try to estimate exergy values and make this indicator operational as a goal function. The objective of this analysis is to verify if the exergy estimated values are capable of elucidating the state of development of this ecosystem. Thus, the benthic communities in the estuary were monitored during a yearly cycle and samples were taken in three different sites following an estuarine gradient of eutrophication.

After identifying the major contributions to the exergy of the estuary in terms of taxonomic groups (see table A6.2), the authors analyze the variation of exergy and specific exergy in comparison with species richness and heterogeneity along the eutrophication gradient, as presented in figure A6.3.

The results show that the hypothesis that exergy and biodiversity would follow the same trends in space and time was validated with regard to species richness, but not to heterogeneity. Actually, exergy, specific exergy and species richness responded as hypothesized, decreasing from non-eutrophicated to eutrophicated areas (see figure A6.3b), but heterogeneity responded in the opposite way, showing the lowest values in the non eutrophicated area (see figure A6.3a). On the other hand, both exergy and species richness were able to grade situations presenting relative subtle differences, while specific exergy and heterogeneity did appear to be less sensitive. Moreover, as an ecological indicator, heterogeneity (measured using the Shannon- Wiener's index, see equation A6.3) appeared to be of more difficult interpretation.

Thus, I think that, although biodiversity may be considered as an important property of ecosystem structure, the relative subjectivity of its measurements and their interpretation constitutes an obvious problem, due to the use of two indicators that can present some difficult methodologies: heterogeneity (evenness) and species richness. Exergy and specific exergy appeared to be capable of elucidating the state of the ecosystem (benthic communities) along the gradient of eutrophication – therefore constituting suitable system-oriented characteristics and good indicators of ecosystem integrity. The fact that, as was observed, specific exergy may shift very drastically as a function of the system yearly dynamics, providing a spatial and temporal picture different from exergy, makes advisable to use both complementarily (see equation A6.1). However, the authors recognize that the

<sup>&</sup>lt;sup>67</sup> Heterogeneity is related to species evenness – the apportionment of individuals among species, i.e., the number of individuals corresponding to each species, which can be much different.

need arises of improving the accuracy in determining the weighing factors (see equation A3.20) in order to estimate exergy from organisms' biomass.

If biodiversity can be characterized as the full range of biological diversity from intraspecific genetic variation to species richness, connectivity and spatial arrangement of entire ecosystems at a landscape level (Marques *et al.* (1997), then, in my opinion, exergy, as a system oriented characteristic and as an ecological indicator of ecosystem integrity, may encompass biodiversity. As Marques *et al.* (1997, pp. 166, italic added) emphasize, " (...) exergy estimations, as described above, really imply to transport information through scales, from the genetic to the ecosystem level, accounting not only for the biological diversity, but also for the evolutionary complexity of organisms, and ecosystem *emergent properties* arising from self-organization processes". As I have said in section 4, these self-organizing processes arise from reciprocal co-determination between the ecosystem and the components (species populations, taxonomical groups and abiotic factors), impeding a reduction of the ecosystem' properties, such as eco-exergy, to their component properties, and this transport of information (energy) through the ecological levels implies an emergent relational ontology following Santos (2015, 2020).

Patrício *et al.* (2004) also attempt to define quantitatively the process of eutrophication, using an index that combines the attributes of system activity level and community structure. According to these authors, eutrophication can be described in terms of network attributes as any increase in system ascendency (due to nutrient enrichment), causing a rise in the total system throughput that more than compensates for a concomitant fall in the average mutual information.<sup>68</sup> As they argue, this particular combination of changes in variables allows one to distinguish between instances of simple enrichment and cases of undesirable eutrophication. The aim of the study was to test whether the network formulation of eutrophication properly tracks changes in community structure along a known gradient of eutrophic, of the intermediate eutrophic, and of the strongly eutrophic areas – were chosen. Estuarine food webs were reconstructed at the three sites and these quantified food webs were examined using network analysis. The authors then characterized the trophic status of the three estuarine systems, as presented in table A6.3.

The results show that, although nutrients tend to stimulate an ecosystem's growth, the organization of the system, reflected in the values of ascendency, is degraded, despite its augmented activity. The long-term study in the Mondego estuary indicated that years of low precipitation tended to be associated with reductions in turnover rates and increases in water column stability, temperature, salinity and light penetration. These changes in habitat conditions encouraged blooms of macroalgae that gradually replaced the resident macrophytes. In the intermediate and strongly eutrophic areas, primary production is largely the result of these macro-algal blooms. Production appears as a strong pulse during this specific time, but remains at very low levels during the rest of the year. This limited temporal interval of primary production results in a significantly lower figure of cumulative annual primary production and total system throughput in these areas as compared with the corresponding measures in the *Zostera* beds. Comparing the average mutual information values (calculated as in equation A5.5) of the flow structure for the three areas, it is possible to discern a very small decrease in the measure among the three zones, suggesting that, in regard to trophic structure, these areas are indeed different. The three zones appear nevertheless much more distinct by eye than what is illustrated by the average mutual information values.

<sup>&</sup>lt;sup>68</sup>As I have described in annex 5, ascendency is the product between average mutual information (or average mutual constraint) and the total system throughput. See equations A5.5 and A5.6.

In the light of these results, Patrício *et al.* (2004) argue that the network definition of eutrophication appears to be inappropriate for the Mondego estuarine ecosystem. It would be more accurate to describe the enrichment processes occurring in this ecosystem as "pulse eutrophication". Accordingly, this process must be characterized as a disturbance to system ascendency in the form of an intermittent supply of excess nutrients that, when coupled with a combination of physical factors (e.g. salinity, precipitation, temperature, etc.), causes both a decrease in system activity and a drop in the mutual information of the flow structure. Even though a significant rise in the total system throughput does occur during the algal bloom period and, moreover, even though at that time does give rise to a strong increase of the system ascendency, the annual picture nevertheless suggests that the other components of the intermediate and strongly eutrophic communities were unable to accommodate the pulse in production. The overall result was a decrease in the annual value of the total system throughput and, as a consequence, of the annual ascendency as well.

I think that this study of the Mondego estuarine ecosystem provides an example of how the measures coming out of network analysis, such as ascendency and other indices, can lead to an improved understanding of the eutrophication process. The need ensues of integrating diverse data over a significant spatial area for great intervals of time in order to account for both the seasonal and inter-annual variability of physico-chemical and biological factors. However, I would argue that network analysis might provide a systematic approach to understand what is happening at a wholesystem level. In fact, as I have outlined in section 4, with ascendency and overhead, we have a calculation that is inclusive of all constraints and degrees of freedom at work in the ecosystem. Thus, in this way it is possible to capture systemic properties that are generated by the qualitatively transformative interactions between the ecosystem's components (species populations, taxonomical groups and the abiotic factors) and, consequently, by the new relational properties that the components exhibit in such networks of co-dependency, which are emergent also in accordance with Santos (2015, 2020). As becomes evident with this example, during a process of eutrophication the changes in the total system throughput or average mutual information (properties of the whole) imply changes in energy budgets and information indexes in the components of the ecosystem (properties of the parts), and vice-versa, in a reciprocal determination. Then, ascendency, as the product between the total system throughput and the average mutual information cannot be micro-determined by the lower-level properties, being an emergent property correlated with the ecosystem growth and development.

## 5. Conclusion

I think I have demonstrated, with the above empirical example, that eco-exergy and ascendency are ontologically emergent properties of the ecosystems, which also proved to be promising ecological orientors and indicators. The use of these two systemic properties, despite the discussed limitations, lends support to, and encourages, a moderate approach in ecology with both holistic and reductionist elements. Considering the reciprocal determination between lower and higher ecological levels allows surmounting the insufficiency of the reductionist mechanistic approach in the explanation of emergence, the phenomenon that has driven great part of the discussion for my thesis. However, this approach undeniably provides the analytical frame that is crucial for a robust moderate approach in ecology. The straightforward conclusion is that an ecosystem has at its disposal properties that cannot be reduced to those of the lower levels. These properties arise from the interactions between parts, between the whole and the parts and between the parts and the whole, in accordance to the conceptualization provided by a relational emergentist ontology. The properties of ecosystems cannot be explained in a comprehensive way by considering those of their components alone, because they

are much more than the sum of the components' properties. Ecosystems have unique and emerging holistic properties that explain their behavior, most importantly growth and development. I would argue that we really have to understand much better the emergent properties in ecosystems in order to manage the environment.

I have hopefully provided sufficient insight on the issue that, when we are dealing with complex natural processes such as the workings of an ecosystem, their dynamics are inevitably somehow elusive. In ecology, we are within the realm of non-conserved quantities, thus, we should use non-conservative and non-Newtonian terms of analysis. It is thus appropriate to use exergy, not the total energy, because it is a more informative concept in the examination of dissipative structures such as ecosystems. The most important idea from thermodynamics that was applied in systems ecology is the idea of irreversibility, related to the seminal concept of entropy. The point is that if entropy is being created through dissipative processes, as in ecosystems, one is dealing with systems that are not at thermodynamic equilibrium. When these processes occur they generate entropy, as do all natural processes. However, there were some problems with the early formulation of irreversible thermodynamics because it was couched in the language of reversible mechanics. This is the chief problem, in my opinion, of reductionist mechanistic ecology, which tries to build a description of irreversible systems in Newtonian terms. Reductionists are fixated on the assumption that natural processes are not inherently changing. This is the reason why we need a relational emergentist ontology: because the ecosystems and its components are changing in a permanent process of reciprocal determination. I have thus offered an understanding of how much free energy it costs to maintain the ecosystem away from thermodynamic equilibrium. If the exergy flow exceeds the needed free energy for maintenance, it is even possible for the ecosystem to move further away from thermodynamic equilibrium. The distance from thermodynamic equilibrium is determined by the ecoexergy. Ecosystems thus use some growth forms to move away from thermodynamic equilibrium: such growth is realized in terms of biomass, of boundaries, of information and of the complexity of ecological network. The moderate approach, a modern holistic ecosystems approach, is thus able to present, in a realistic way, holistic and systemic properties, such as eco-exergy and ascendency, which facilitate the understanding of how ecosystems use these forms of growth and development, as illustrated by the empirical example.

The goal of the thesis was to contribute towards the articulation of a common framework of reference for further development of a more profound and comprehensive ecosystem theory than the one that most ecologists endorse today. I maintain that, as in the modern holistic ecosystem approach that I advocate, the future core pattern of ecology should concern a systemic view of life, and reveal how interactions, conceptualized from the perspective of a relational emergent ontology, lead to complex organization and dynamics. Understanding, measuring and tracking these dynamical patterns is of paramount importance and various ecological orientors and indicators have been developed in order to do so. Taken together, we can use this systems-oriented thermodynamic and informational approach to formulate a limited number of hypotheses in order to explain a very large number of ecological observations. The moderate approach stems from the convergence of holism and reductionism and not from the point of view that they are incommensurable worldviews. Therefore, they can complement and enrich each other, and these recent developments in systems ecology represent a profound paradigm shift that mirrors the approximation between the two positions. The paradigm that is now receding has dominated our scientific culture for several hundred years, as I have related, viewing the universe as a mechanical system composed of elementary building blocks. The new paradigm is based on a holistic and emergentist worldview. The natural world must be seen as an integrated whole, recognizing the fundamental interdependence of all phenomena.

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# **Glossary**

Abiotic factors –in ecology, abiotic components or abiotic factors are non-living chemical and physical parts of the environment that affect living organisms and the functioning of ecosystems. Abiotic factors and the phenomena associated with them underpin ecology as a whole. Abiotic components include physical conditions and non-living resources that affect living organisms in terms of growth, maintenance, and reproduction. Resources are distinguished as substances or objects in the environment required by one organism and consumed or otherwise made unavailable for use by other organisms. Abiotic factors can include water, light, radiation, temperature, humidity, atmosphere, acidity, and soil.

Acclimation – (or acclimatization, or acclimatation) is the process in which an individual organism adjusts to a change in its environment (such as a change in altitude, temperature, humidity, photoperiod, or pH), allowing it to maintain performance across a range of environmental conditions.

*Allometry* – in allometries and scaling relationships, body size or mass is used as an independent variable of different dependent variables representing anatomical, physiological, morphological, behavioral, social, ecological or paleo-ecological traits.

Anabolism – is the set of metabolic pathways that construct molecules from smaller units, and usually these reactions require energy. Anabolism is the building-up aspect of metabolism.

Ascendency – is a measure of the information and flows embodied in the ecological network.

Autotrophs – see primary producers.

*Behavioral ecology* – is the study of the evolutionary basis for animal behavior due to ecological pressures.

*Benthic zone* –is the ecological region at the lowest level of a body of water such as an ocean, lake, or stream, including the sediment surface and some sub-surface layers. The benthic boundary layer, which includes the bottom layer of water and the uppermost layer of sediment directly influenced by the overlying water, is an integral part of the benthic zone, as it greatly influences the biological activity that takes place there.

Bioma – is a collection of organisms that have common characteristics for the environment they exist in. They can be found over a range of continents. Biomes are distinct biological communities that have formed in response to a shared physical climate. Biome is a broader term than habitat; any biome can comprise a variety of habitats.

*Biotic factors* – biotic components, or biotic factors, can be described as any living component that affects another organism or shapes the ecosystem. This includes both organisms that consume other organisms within their ecosystem, and the organisms that are being consumed.

*Carrying capacity* – the carrying capacity of an environment is the maximum population size of a biological species that can be sustained by that specific environment, given the food, habitat, water, and other resources available. The carrying capacity is defined as the environment's maximal load, which in population ecology corresponds to the population equilibrium, when the number of deaths in a population equals the number of births.

Catabolism – is the set of metabolic pathways that breaks down molecules into smaller units that are either oxidized to release energy or used in other anabolic reactions. Catabolism breaks down large molecules (such as polysaccharides, lipids, nucleic acids, and proteins) into smaller units (such as monosaccharides, fatty acids, nucleotides, and amino acids, respectively).

Climax – in the holistic approach, and just like in the case of an individual organism, the community develops according to internal rules of development through different "stages" to reach a state of maturity: the climax.

Community -is a collection of populations of different species in a given area.

*Competition* –is an interaction between organisms or species in which either the organisms or species are harmed. Limited supply of at least one resource (such as food, water, and territory) used by both can be a factor engendering competition. Competition both within and between species is an important topic in ecology, especially community ecology. Competition is one of many interacting biotic and abiotic factors that affect community structure. Competition among members of the same species is known as intraspecific competition, while competition between individuals of different species is known as interspecific competition. Competition is not always straightforward, and can occur in both a direct and indirect fashion.

*Compositionality* – the notion that captures the ontological relationship between a set of lower-level entities constituting an entity of the hierarchical level above.

Constraint – is a parameter that a system must obey to be functional. In systems ecology, and using theory information, I refer to the concept as the biochemical and thermodynamic parameters, in terms of material and energy flows, that the ecosystem must obey to distance itself from the thermodynamic equilibrium.

*Consumers* – otherwise known as heterotrophs, depend upon producers (and occasionally other consumers) for food.

*Decomposers* – otherwise known as detritivores, break down chemical compounds from dead bodies of producers and consumers into simpler forms that can be reused.

Detritivores - see decomposers.

*Ecological goal function* –ecosystems do not have defined goals, but their propensity to move in a specific direction indicated by ecological orientors can be described in ecological models by goal functions. In a model, the description of the development of the state variables of the model has to be rigorously indicated, which implies that goals are made explicit.

*Ecological indicators* – ecosystem variables that indicate the present ecosystem condition or health. Many different indicators have been used such as specific species, specific contaminants and indices giving the composition of groups of organisms.

Ecological orientors - ecosystem variables that describe the range of directions in which ecosystems have a propensity to develop.

Ecomorphology – is the study of the relationship between the ecological role of an individual organism and its morphological adaptations.

Ecophysiology – is a biological discipline that studies the response of an organism's physiology to environmental conditions.

*Ecosystem* –is a collection of communities and their physical environment (abiotic factors), thus, a unit of biological organization made up of all of the organisms in a given area interacting with the physical environment.

Ectotherm – is an organism in which internal physiological sources of heat are of relatively small or of quite negligible importance in controlling body temperature. Such organisms (for example frogs) rely on environmental heat sources, which permit them to operate at very economical metabolic rates.

*Edaphic* – related to or caused by particular soil conditions, such as of texture or drainage, rather than by physiographic or climatic factors.

Emergy – is the amount of energy that was consumed in direct and indirect transformations to make a product or service. Emergy is a measure of quality differences between different forms of energy and is an expression of all the energy used in the work processes that generate a product or service in units of one type of energy. Emergy is measured in units of *emjoules*, which refers to the available energy consumed in transformations. In systems ecology, emergy attempts to account for the energy required in the formation of organisms at different trophic levels and is determined by the biogeochemical energy flow into an ecosystem component, measured in solar energy equivalents.

Enthalpy – is a property of a thermodynamic system, defined as the sum of the system's internal energy and the product of its pressure and volume, H = U + pV. It is a convenient state function standardly used in many measurements in chemical, biological, and physical systems at a constant pressure. The pressure-volume term expresses the work required to establish the system's physical dimensions, i.e. to make room for it by displacing its surroundings. As a state function, enthalpy depends only on the final configuration of internal energy, pressure, and volume, not on the path taken to achieve it. The unit of measurement for enthalpy is the *joule*. The total enthalpy of a system cannot be measured directly because the internal energy contains components that are unknown, not easily accessible, or not of interest in thermodynamics. In practice, a change in enthalpy ( $\Delta H$ ) is the preferred expression for measurements at constant pressure, because it simplifies the description of energy transfer. When matter transfer into or out of the system is also prevented, the enthalpy change equals the energy exchanged with the environment by heat.

*Entropy* –is a scientific concept, as well as a measurable physical property that is most commonly associated with a state of disorder, randomness, or uncertainty. Entropy predicts that certain processes are irreversible or impossible, aside from the requirement of not violating the conservation of energy, the latter being expressed in the first law of thermodynamics. Entropy is central to the second law of thermodynamics, which states that the entropy of isolated systems left to spontaneous evolution cannot decrease with time, as they always arrive at a state of thermodynamic equilibrium, where the entropy is highest. Boltzmann explained entropy as the measure of the number of possible microscopic arrangements or states of individual atoms and molecules of a system that comply with the macroscopic condition of the system. He thereby introduced the concept of statistical disorder and probability distributions into a new field of thermodynamics, which fluctuate about an average configuration, to the macroscopically observable behavior, in form of a simple logarithmic law, with a proportionality constant, the Boltzmann

constant. The concept of entropy is described by two principal approaches: the macroscopic perspective of classical thermodynamics and the microscopic description central to statistical mechanics. The classical approach defines entropy in terms of macroscopically measurable physical properties, such as bulk mass, volume, pressure and temperature. The statistical definition of entropy defines it in terms of the statistics of the motions of the microscopic constituents of a system – modeled at first classically, e.g. Newtonian particles constituting a gas, and later quantum-mechanically (photons, phonons, spins, etc.). The two approaches form a consistent, unified view of the same phenomenon as expressed in the second law of thermodynamics, which has found universal applicability to physical, chemical and ecological processes.

*Eutrophication* – is a limnological (the study of limnology includes aspects of the biological, chemical, physical, and geological characteristics and functions of inland waters) term for the process by which a body of water becomes progressively enriched with minerals and nutrients. Water bodies with very low nutrient levels are termed oligotrophic and those with moderate nutrient levels are termed mesotrophic. Eutrophication is a process of increasing biomass generation in a water-body caused by increasing concentrations of plant nutrients, most commonly phosphorus compounds and nitrate, or other nitrogen compounds. Increasing nutrient concentrations leads to increasing fecundity of plants, both macrophytes and in the plankton. As more plant material becomes available as a food resource, there are matching increases in the number of herbivorous animals and also carnivorous animals feeding on them. As the process continues, the bio-mass of the water body increases but biological diversity decreases. In the more severe eutrophication the bacterial degradation of the excess biomass results in oxygen consumption, which can create a state of hypoxia throughout the water body. Hypoxic zones are commonly found in deep water lakes in the summer season due to stratification into the cold oxygen poor hypolimnion (the dense, bottom layer of water in a thermally-stratified lake) and the warm oxygen rich epilimnion (is the top-most layer in a thermally stratified lake, occurring above the deeper hypolimnion). Strongly eutrophic freshwaters can become hypoxic (with low concentration of oxygen) throughout their depth following severe algal blooms or macrophyte overgrowths.

Evapotranspiration – is the sum of water evaporation and transpiration from a surface area to the atmosphere. Evaporation accounts for the movement of water to the air from sources such as the soil, canopy interception, and water bodies. Transpiration accounts for the movement of water within a plant and the subsequent exit of water as vapor through stomata in its leaves. Evapotranspiration is an important part of the water cycle.

Exergy – in thermodynamics, the exergy of a system is the maximum useful work possible during a process that brings the system into equilibrium with a heat reservoir, reaching maximum entropy. When the surroundings are the reservoir, exergy is the potential of a system to cause a change as it achieves equilibrium with its environment. Exergy is then the energy that is available to be used, being a measure of the useful work that can be performed by the system. In the case of ecosystems it includes the energetic content of the biomass, but also its organizational state.

*Feedback* – feedback occurs when outputs of a system are routed back as inputs as part of a chain of cause-and-effect that forms a circuit or loop.

*Free Energy* – in thermodynamics, the Gibbs free energy (or Gibbs energy) is a thermodynamic potential that can be used to calculate the maximum reversible work that may be performed by a thermodynamic system at a constant temperature and pressure. The Gibbs free energy ( $\Delta G = \Delta H$ -

 $T\Delta S$ , measured in joules in SI) is the maximum amount of non-expansion work that can be extracted from a thermodynamically closed system (where the latter can exchange heat and work with its surroundings, but not matter). This maximum can be attained only in a completely reversible process. When a system transforms reversibly from an initial state to a final state, the decrease in Gibbs free energy equals the work done by the system to its surroundings, minus the work of the pressure forces. The Gibbs energy (G) is also the thermodynamic potential that is minimized when a system reaches chemical equilibrium at constant pressure and temperature. Its derivative with respect to the reaction coordinate of the system vanishes at the equilibrium point. As such, a reduction in G is necessary for a reaction to be spontaneous at constant pressure and temperature.

Habitat – in ecology, the term habitat summarizes the array of resources, physical and biotic factors that are present in an area, such as to support the survival and reproduction of a particular species. A species habitat can be seen as the physical manifestation of its ecological niche.

*Herbivore* – is an organism that principally eats autotrophs such as plants, algae and photosynthesizing bacteria. More generally, organisms that feed on autotrophs in general are known as primary consumers.

*Homeostasis* –is the state of steady internal, physical, and chemical conditions maintained by living systems. This is the condition of optimal functioning for the organism (and ecosystem, in holistic approaches) and includes many variables, being kept within certain pre-set limits (homeostatic range). Each of these variables is controlled by one or more regulators or homeostatic mechanisms, which together maintain life.

Information - in systems ecology, in the calculations of eco-exergy, one way to measure the complexity of organization in an ecosystem is the information content of the material, which can be the complexity at the genetic, organismal, or ecosystem level: it can be estimated using Kullbach's measure of information (an information index) based on the genetic complexity of the organism, and in this way, eco-exergy complies with the information in the genomes of the individuals, as storage of information. In another way, ascendency expresses the amount of information embodied in the ecosystem networks, related to the interactions that are involved and respective constraints: information theory is invoked to quantify the indeterminacy associated with a highly indeterminate collection of matter and energy exchanges between ecological components. Accordingly, information is defined as anything that causes a change in probability assignment, essentially equating information to constraint; the term indeterminacy is introduced to emphasize the potential for causal openness in developing systems, such as ecosystems, and the term information, which hinges more upon the agency behind a change in probability than upon any subjective perception of that change. Thus, information refers to the effects of that which imparts order and pattern to a system. Accordingly, information theory allows quantifying constraint in ecosystems, being the field of mathematics that quantifies the changes in the referred probabilities.

*Macrophyte* – are plants that have adapted to living in aquatic environments (saltwater or freshwater). They are also referred to as hydrophytes or macrophytes to distinguish them from algae and other microphytes. A macrophyte is a plant that grows in or near water and is emergent, submergent, or floating. In lakes and rivers macrophytes provide cover for fish, substrate for aquatic invertebrates, produce oxygen, and act as food for some fish and wildlife. Macrophytes are primary producers and are the basis of the food web for many organisms. They have a significant effect on soil chemistry and light levels, as they slow down the flow of water and capture

pollutants and trap sediments. Excess sediment will settle into the benthos aided by the reduction of flow rates caused by the presence of plant stems, leaves and roots. Some plants have the capability of absorbing pollutants into their tissue. Seaweeds are multicellular marine algae and, although their ecological impact is similar to other larger water plants, they are not typically referred to as macrophytes.

*Mass specific rate of metabolism* – is the rate at which organisms consume energy per unit of body weight.

*Mutualism* – describes the ecological interaction between two or more species where each species has a net benefit. It is a common type of ecological interaction. Mutualism can be contrasted with interspecific competition, in which each species experiences reduced fitness, and exploitation, or parasitism, in which one species benefits at the expense of the other.

*Niche* – in ecology, a niche is the match of a species to a specific environmental condition. It describes how an organism or population responds to the distribution of resources and competitors (for example, by growing when resources are abundant or when predators, parasites and pathogens are scarce) and how it in turn alters those same factors (for example, limiting access to resources by other organisms, acting as a food source for predators and a consumer of prey).

*Plankton* – are the diverse collection of organisms found in water (or air) that are unable to propel themselves against a current (or wind). The individual organisms constituting plankton are called plankters. In the ocean, they provide a crucial source of food to many small and large aquatic organisms, such as bivalves, fish and whales. Marine plankton includes bacteria, archaea, algae, protozoa and drifting or floating animals that inhabit the saltwater of oceans and the brackish waters of estuaries. Freshwater plankton is similar to marine plankton, but is found in the freshwaters of lakes and rivers.

*Pleiotropy* – pleiotropy occurs when one gene influences two or more seemingly unrelated phenotypic traits. Such a gene that exhibits multiple phenotypic expressions is called a pleiotropic gene.

Population -is a collection of individual organisms of the same species in a given area.

Predation – is a biological interaction where one organism, the predator, kills and eats another organism, its prey.

*Predator* – is an organism that uses predation for feeding.

Primary consumers - see herbivores.

*Primary producers* – otherwise known as autotrophs, are organisms that convert energy (through the process of photosynthesis) into food.

*Production* – is the synthesis of organic compounds, performed by autotrophs, from atmospheric or aqueous carbon dioxide. It principally occurs through the process of photosynthesis, which uses light as its source of energy, but it also occurs through chemosynthesis, which uses the oxidation or reduction of inorganic chemical compounds as its source of energy.

Proxy – in statistics, a proxy or proxy variable is a variable that is not in itself directly relevant, but that serves in place of an unobservable or immeasurable variable. In order for a variable to be a good proxy, it must have a close correlation, not necessarily linear, with the variable of interest. This correlation might be either positive or negative.

*Regression* – in statistical modeling, regression analysis is a set of statistical techniques for estimating the relationships between a dependent variable and one or more independent variables. Regression analysis is primarily used for two conceptually distinct purposes. First, regression analysis is widely used for prediction and forecasting. Second, in some situations regression analysis can be used to infer causal relationships between the independent and dependent variables. Importantly, regressions by themselves only reveal relationships between a dependent variable and a collection of independent variables in a fixed dataset. To use regressions for prediction or to infer causal relationships, respectively, a researcher must carefully justify why existing relationships have predictive power in a new context or why a relationship between two variables has a causal interpretation. The latter is especially important when researchers hope to estimate causal relationships using observational data.

*Respiration* – the two main processes that contribute to ecosystem respiration are photosynthesis and cellular respiration. Photosynthesis uses carbon-dioxide and water, in the presence of sunlight to produce glucose and oxygen, whereas cellular respiration uses glucose and oxygen to produce carbon-dioxide, water, and energy. The coordination of inputs and outputs of these two processes creates a completely interconnected system, constituting the underlying functioning of the ecosystems overall respiration. Cellular respiration depends on the overall relationship between autotrophs and heterotrophs in an ecosystem.

*Scaling* – in scaling relationships, body size or mass is used as an independent variable of different dependent variables representing anatomical, physiological, morphological, behavioral, social, ecological or paleoecological traits.

*State function* – in the thermodynamics of equilibrium, a state function, function of state, or point function is a function defined for a system relating several state variables or state quantities, which depends only on the current equilibrium thermodynamic state of the system (e.g. gas, liquid, solid, crystal, or emulsion), rather than the path which the system took to reach its present state. A state function describes the equilibrium state of a system, thus also describing the type of system. Internal energy, enthalpy and entropy are examples of state quantities because they quantitatively describe an equilibrium state of a thermodynamic system, regardless of how the system reached that state. In contrast, mechanical work and heat are process quantities or path functions because their values depend on the specific "transition" (or "path") between two equilibrium states.

*State variable* – is one of the sets of variables that are used to describe the mathematical "state" of a dynamical system. The state of a system describes enough about the system to determine its future behavior in the absence of any external forces affecting the system. Models that consist of coupled first-order differential equations are said to be in state-variable form.

*Steady state* – in systems theory, a system (or a process) is in steady state if the variables, the state variables, which define the behavior of the system (or the process), are unchanging in time.

*Stochastic* – refers to the property of being well described by a random probability distribution. Although stochasticity and randomness are at times distinguished in that the former refers to a modeling approach and the latter captures an ontological property of natural phenomena, these two terms are often used synonymously. Furthermore, in probability theory, the formal concept of a stochastic process is also referred to as a random process.

*Stoichiometry* – in ecology, refers to the quantities, proportions or ratios of chemical elements in different entities, such as organisms or their environments.

*Succession* – ecological succession is the process of change in the species structure of an ecological community over time. It is a phenomenon or process by which an ecological community undergoes more or less orderly and predictable changes following a disturbance or the initial colonization of a new habitat.

Supervenience – is a notion in analytical philosophy that states that a set of properties A supervenes upon another set B just in case no two things can differ with respect to A-properties without also differing with respect to their B-properties. Thus there cannot be an A-difference without a B-difference.

*Symbiosis* – is any type of close and long-term biological interaction between two different biological organisms, be it mutualistic (a relationship where both organisms benefit), commensalistic (a relationship between two organisms where one benefits and the other is not significantly harmed or helped), or parasitic (the parasite benefits while the host is harmed). Symbiosis can be obligatory, which means that one or more of the symbionts entirely depend on each other for survival, or facultative (optional) when they can generally live independently.

Taxa – in biology, taxonomy is the scientific study of naming, defining and classifying groups of biological organisms based on shared characteristics. Organisms are grouped into taxa (singular: taxon) and these groups are given a taxonomic rank; groups of a given rank can be aggregated to form a more inclusive group of higher rank, thus creating a taxonomic hierarchy

*Thermodynamic equilibrium* – in accordance with classic thermodynamics, all isolated systems will move toward thermodynamic equilibrium, a state of equal distribution of components and maximum probability. This means that all the gradients have been eliminated, i.e., there are no differences in any energy potentials such as concentration of chemicals or temperature differences, and structures in the system will have ceased to exist: a homogenous dead system will be the result. This is expressed thermodynamically as follows: entropy will always increase in an isolated system. As work capacity is a result of gradients in certain intensive variables such as temperature, pressure, and chemical potential, etc. a system at thermodynamic equilibrium can do no work.

*Trophic level* – the trophic level of an organism is the position it occupies in a food chain, i.e., a succession of organisms that eat other organisms and may, in turn, be eaten themselves. The trophic level of an organism is the number of steps it is situated from the start of the chain. The path along the chain can form either a one-way flow or a food "web". A food web starts at trophic level 1 with primary producers such as plants, can move to herbivores at level 2, carnivores at level 3 or higher, and typically finish with apex predators at level 4 or 5. Ecological communities with higher biodiversity form more complex trophic paths.

Work – in physics, work is the energy transferred to or from an object via the application of force along a displacement. In its simplest form, it is often represented as the product of force and

displacement. A force is said to do positive work if (when applied) it has a component in the direction of the displacement of the point of application. A force does negative work if it has a component opposite to the direction of the displacement at the point of application of the force.

### <u>Annex 1 – Mathematical structure of Metabolic Theory of Ecology</u>

Allometries and scaling relationships can be represented as regression equations or power equations, in which one variable changes as a power of another. According to MTE, all characteristics of organisms vary predictably with body size, thus one has the so-called allometric equations:

$$(eq.A1.1) Y = aM^b$$

Y is the dependent variable, M the body mass, a is the normalization constant and b the allometric constant. In allometries and scaling relationships, body size or weight is treated as an independent variable of different anatomical, physiological, morphological, behavioral, social, ecological, and paleoecological dependent variables.

Depending on the value of their scaling exponents, allometries and scaling relationships are called either allometric ( $b \neq 1$ ) or isometric (b = 1). Scaling exponents can take both negative and positive values. In general, the larger the value of b, the faster Y increases (if b is positive in value) or decreases (if b is negative in value) with increasing M. If the scaling exponent, b, is less than unity, Y increases (or decreases if negative in value) more slowly than M does. On double log axes, the values of Y and M yield straight lines, and a gives the intercept or elevation of the regression line and b gives its slope.

There is a plenitude of biological traits that correlate with body mass, M, and can be represented as dependent variables, Y (Raerinne, 2011, 2013), such as:

- Fasting endurance scales as  $aM^{0.44}$  for mammals and between  $aM^{0.40}$  and  $aM^{0.60}$  in birds
- The size of the home range of birds and mammals varies positively with body size,  $aM^1$
- The inverse scaling rule: the maximum density, D, of herbivorous mammals declines as their body size increases,  $D = aM^{-0.75}$
- Kleiber's rule: basal metabolism, an estimate of the energy required by an organism for the basic processes of living, varies as aM<sup>0.75</sup>
- An Individual's total energy consumption varies as aM<sup>0.75</sup>
- In most mammal groups gut volume is isometric to M, aM<sup>1</sup>
- Heart rate varies as aM<sup>-0.25</sup>
- In mammals within species sociality increases with body size
- Group behavior increases with body size in mammals

In statistics, the coefficient of determination, denoted as  $r^2$ , is the proportion of the variance in the dependent variable that is predictable from the independent variable(s). It is a statistical measure used in the context of statistical models whose main purpose is either the prediction of future outcomes or the testing of hypotheses, on the basis of other related information. It provides a measure of how well observed outcomes are replicated by the model, based on the proportion of total variation of outcomes explained by the model. Thus, in the literature that explores this kind of correlation between body mass as an independent variable and other traits as dependent variables, it captures how the correlation is dependent on the indices of fit, usually the value of  $r^2$ .

Kleiber, in 1932, showed that the individual metabolic rate, I, scale as (Brown et al., 2004):

$$(eq.A1.2) I = i_0 M^{3/4}$$

The element  $i_0$  is the normalizing constant independent of body size.

It has been known that biochemical reactions rates, metabolic rates and nearly all other rates of biological activity increase exponentially with temperature. This kinetics is described by the Boltzmann factor or Van't Hoff-Arrhenius relation (Brown *et al.*, 2004):

$$(eq. A1.3) e^{-E/kT}$$

E is the activation energy, k is the Boltzmann constant and T is the absolute temperature. This equation specifies how temperature affects the rate of reaction by changing the proportion of molecules with sufficient kinetic energy. This relationship holds over the temperature range of normal activity, which is  $0-40^{\circ}$ C for most organisms.

Gillooly, in 2001, developed a model for the scaling of metabolic rate that combines the effects of body size and temperature, which leads to a single equation for individual metabolic rate, I (Brown *et al.*, 2004; Allen *et al.*, 2004):

$$(eq.A1.4) I = i_0 M^{3/4} e^{-E/kT}$$

This simple analytical expression yields quantitative predictions on metabolic rate that are supported by empirical data for a broad assortment of taxonomical groups. As a result, its explanatory power has been claimed to be substantial (Brown *et al.*, 2004; Allen *et al.*, 2004).

Characteristics of organisms vary with their body size, temperature and chemical composition or stoichiometry. In ecology, stoichiometry refers to the quantities, proportions or ratios of chemical elements in different entities, such as organisms or their environments. All organisms have internal chemical compositions that differ from those in their environments; therefore, they must expend energy to maintain concentration gradients across their boundaries, to acquire necessary elements and to excrete waste products. Fundamental stoichiometric relations dictate the quantities of elements that are transformed in the reactions of metabolism. Biochemistry and physiology specify the quantitative relation between the metabolic rate and the flows of elements through an organism. The metabolic rate dictates the rates at which material resources are taken up from the environment, used for biological structure and function, and excreted as waste back to the environment. The chemical equations of metabolism specify not only the molecular ratios of elements, but also the energy yield or the demand of each reaction. Ecological stoichiometry is concerned with the causes and consequences of variation in elements' composition among organisms and between the organisms and their environment; indeed, there is great variation within and among organisms, and especially between different taxonomic or functional groups. The concentrations of elements in ecosystems are therefore directly linked to the flows and turnover rates of elements in the constituent organisms (West et al., 1997; Enquist et al., 2003; Brown et al., 2004; Allen et al., 2004). On the one hand, environmental concentrations can limit metabolic rates, and thereby growth rates, reproductive rates and quantities of organisms; on the other hand, the size of stock of elements and rates of turnover in organisms can regulate environmental concentrations of elements and compounds. The equation (A4) gives, as referred above, the combined effect of body size and temperature on individual metabolic rate, I. Because the mass specific rate of metabolism, B, is simply I/M, it follows that B scales as:

$$(eq. A1.5) B \propto M^{-1/4} e^{-E/kT}$$
The advantage of this concise mathematical expression is that it combines the effect of size and temperature in a single quantitative expression. This makes precise comparisons between organisms and different functional and taxonomical groups differing substantially in these variables to be possible (Brown *et al.*, 2004). When such comparisons are made, the commonalities of life and their ecological manifestations are revealed. Brown *et al.* (2004) present empirical data plotting rates of T-corrected individual production against body mass for a wide variety of organisms, showing that Metabolic Theory predicts that equation (A5) should account for much of the variation in some characteristics of individual performance and life history, such as individual biomass production, ontogenetic growth, survival and mortality, and stoichiometry.

The MTE extends this framework to population and community levels of ecological organization, claiming that many features of population dynamics and community organization are due to effects of body size, temperature and stoichiometry on the performance of individual organisms. The maximal rate of exponential increase in a population,  $r_{max}$ , is predicted to scale according to equation (A5) (Brown *et al.*, 2004); this inference follows from the fact that reproduction is fueled by metabolism, and that mass-specific production rates and mortality rates follow the same equation. Advocates of this metabolic ecological approach contend that it is possible to explain the equilibrium number of individuals or carrying capacity, K, predicted to vary as:

## $(eq. A1.6) K \propto [R] M^{-3/4} e^{-E/kT}$

Therefore, K varies linearly with the supply rate or concentration of the limiting resource [R], as a power function of body mass and exponentially with temperature. Thus, if [R] increases, there will be more organisms of decreased size. However, if the temperature increases, the carrying capacity is reduced because the same supply of energy supports a smaller number of organisms, each fluxing energy and materials at a higher rate. Brown *et al.* (2004) present empirical evidence for an inverse Boltzmann relationship between equilibrium abundance and environmental temperature.

### <u>Annex 2 – Ecosystems as Cybernetic Systems</u>

Cybernetic systems are systems with feedback. They are a special class of cause-and-effect (inputoutput) systems in which input is determined, at least in part, by output. The portion of output that is returned to input is the feedback, and this may become the basis for feedback control. Very small feedbacks may exert very large effects. Figure 1a illustrates a basic input-output system. Energy, matter, or information coming from the environment causes the system to respond; this reaction is transmitted as energy, matter, or information output back to the environment. Figure A.1b shows a feedback system consisting of two component subsystems.<sup>69</sup> This system is determinate because its behavior is governed only by past causes. Its feedback structure may passively or emergently make its behavior stable, regular, or otherwise predictable, and may enable it to damp disturbance. Figure A.1c illustrates a feedback control system in which the feedback subsystem is a controller through which information about desired output can be introduced. Actual output information is fed back to the controller, and the deviation of actual from desired becomes the basis for corrective action. This system is teleological because its behavior is guided by future or desired goals. The behavior is stable, regular, and purposeful since the feedback organization has been designed to actively achieve such characteristics. Feedback control systems may be man-made or natural, and may have living or nonliving components. Both determinate and teleological feedback systems are cybernetic because they contain feedback.

Engelberg and Boyarsky (1979) claim that ecosystems are not cybernetic systems. This view goes against the tenet in ecosystem theory stating that ecosystems are regulated through feedback processes. A great part of the goal-oriented processes (according to a heuristic interpretation) is represented by *homeostasis*: those processes through which the material and energetic situation of an ecosystem is maintained constant. These regulations are supposedly governed, to a wide extent, by feedback mechanisms (Bertalanffy, 1950).

Engelberg and Boyarsky (1979) start by arguing that cybernetic systems are characterized by the existence of an information network within them. The essence of cybernetic systems lies in the existence of a communication network connecting all parts of the system of the integrated whole so that the functions of this global network steer or regulate the entire system, determining also how matter flows through space. In contrast, they say, noncybernetic systems are not organized around informational linkages. These authors contend that information networks are characterized by mapping and amplification; in mapping, information is transcribed in one-to-one correspondence from one physical entity to another; in amplification, low energy causes give rise to high energy effects. Beyond information, Engelberg and Boyarsky (1979) also assume that cybernetic systems are characterized by networks, feedback loops and stability. The elements of a cybernetic system are organized to operate together, where this becomes possible only when they are all in communication with one another. The action of any element of the system ultimately exerts an influence upon every other element, and this influence ultimately returns to the element which first caused it. It follows that there exist many feedback pathways in a cybernetic system. Feedback is the basis of goal direction, regulation and stability. These authors also claim that negative feedback loops are goal-directed and stabilize the cybernetic system. When the system is perturbed, the feedbacks reduce the effect; this leads to regulation in which certain variables are held constant, and such systems are said to possess the property of stability. However, Engelberg and Boyarsky (1979) argue that ecosystems do not appear to be connected by an information network, although some of their living components interact by

<sup>&</sup>lt;sup>69</sup> Figure adapted from Patten and Odum (1982).

informational means. Consequently, the absence of an information network means absence of information-mediated feedback cycles. In ecosystems there are no low energy (informational) causes producing high energy effects; by contrast, in ecosystems the dominant interaction is that of high-energy phenomena giving rise to other high-energy one. They also argue that, in cybernetic systems, cycles denote causal closure and lead to regulation, whereas in ecosystems the term cycle means only the movement of energy or matter from compartment to compartment and that, ultimately, the cycle of the ecosystem is the history of a piece of matter or energy.

Accordingly, Engelberg and Boyarsky argue that there is a forced "cybernation" of ecosystems. Ecosystems do damp environmental perturbations, but this is based on physical or chemical rather than cybernetic principles. They also contain information, but this is a property of their constituents and the information is not linked to form an integrated whole. Ecosystems may contain cybernetic subsystems, but this is not sufficient to make the entire system cybernetic. Similarly, the existence of feedback loops - as in predator-prey interactions and element cycles - is insufficient to characterize the whole ecosystem as cybernetic. According to these authors, genuine examples of cybernetic systems are the cells or a multicellular organism. One interpretation of this critical conclusion is that, more than to contrast the noncybernetic or cybernetic character of ecosystems, the basic problem is how to conceptualize ecosystems and how to place them within the scheme of known things. Cybernation, continue Engelberg and Boyarsky, is analogizing the ecosystem to an (super) organism, that is, as I have argued above, the first challenge that ecosystem theory must confront.

Some authors, such as Patten and Odum (1982), reject this argumentation, arguing that it is clear that in their analysis, Engelberg and Boyarsky (1979) equate cybernetic systems with teleological systems (see figure A.1c). That is, they would expect of a cybernetic system: to be actively goal directed, presumably with an identifiable centralized goal setter; to possess a distinct, information based, communication network; that this network span all constituents in global feedback closures; and that the source of stability and purposeful regulation reside in the feedback organization and is not concomitant of noncybernetic principles establishing the background conditions for existence. Therefore, according to Patten and Odum (1982), Engelberg and Boyarsky (1979) require that an ecosystem must be a superorganism and, because it is not, they deny their obvious cybernetic character. In contrast, according to Patten and Odum (1982) ecosystems are cybernetic. However, they are not thinking about an ecosystem as a teleological system. These authors argue that the cybernetic attributes emerge passively out of large and complex, decentralized system organization, and that the interplay of material cycles and energy flows, under informational control, generates self-organizing feedbacks, with no discrete controller required (see figure A.1b). If goals are needed in order to qualify an ecosystem as cybernetic, the suggestion is that in the case of every ecosystem can be found a set of variables that are relatively time invariant or that change in repeatable temporal patterns (e.g., total system production, total biomass, ambient nutrient concentration, population size, etc.). These variables can be regarded as components of an objective function in the ecosystem that is to be maximized or minimized, subject to a set of constraints. The constraints would be the applicable physical, chemical and biological laws conditioning and limiting the variables' dynamic behaviors, just as they constrained and guided the development of a set point.<sup>70</sup> If it is useful to regard ecosystems as purposeful, we can discover analogues of goals in some ecosystems. However, I think that these are only teleological metaphors, which, by being insightful metaphors might generate new knowledge, as I have argued in section 3.1. I nonetheless tend to agree with Patten and Odum (1982) when they argue

<sup>&</sup>lt;sup>70</sup> Homeostasis typically involves negative feedback loops that counteract changes of various properties from their target values, known as set points.

that a non-teleological model (fig A.1b) fits better the behavior of ecosystems and, concomitantly, with the somewhat mechanistic view which is, in my opinion, necessary for articulating what I called the moderate position.

The principal function of an ecosystem is to make possible the orderly cycle of life. This means cleaning up the residues from past cycles and converting them to forms that can initiate and support new cycles. Consequently, the primary network in ecosystems is the system of conservative (non-informational) energy-matter flows resulting from a variety of materialistic transformation and exchange processes (Odum, 1968; Patten and Odum, 1982). They are conservative because they follow the first law of thermodynamics (see note <sup>38</sup>). These processes are mainly trophic, so the food web is the most fundamental element of the conservative network. Other constitutive processes, rather than feeding, include primary production, decomposition and nutrient cycling, growth and development as well as the transport of productive and reproductive products, secretions, excretions and dead bodies. Coordinated movement and transformation of organic and inorganic energy-matter are the functions of the primary network in ecosystems. However, to achieve orderliness, a secondary informational network is needed, superimposed upon the primary one (Patten and Odum, 1982). Without such a network to regulate the conservative processes, nature would be chaotic and imbalanced. All the factors, processes and interactions that serve to mediate the movement or transformation of energy and matter constitute this secondary network.<sup>71</sup> It is probably because ecologists mainly focus on components individually that these elements of the informational network are often not represented as part of a more encompassing system. In a sense, I surmise that the issue of the cybernetic versus noncybernetic nature of ecosystems reduces to the philosophical acceptance or rejection, respectively, of a systemic point of view.

The concept of a secondary information network superimposed on a primary energy-matter one fits the non-teleological interpretation of ecosystem (described in fig. A.1b). In this kind of feedback dynamics, conservative storages are connected by conservative flows, while each of the latter is regulated by a set of control factors operating in the informational sense that is not dependent on their energy or matter contribution to the interaction. They catalyze, rate limit and otherwise control the conservative transfers. And the energy flows are modulated through the information feedbacks. The ecologist clearly distinguishes conservative from informational processes.

Engelberg and Boyarsky (1979) require of a cybernetic system that its information network forms a closed cycle and, furthermore, that this closure is global, i.e., encompassing the entire system. Patten and Odum (1982) recognize that we cannot demonstrate this property for ecosystems; the constituents of the secondary network are too diversified and located at the different levels of organization in order to connect up merely between themselves. However, these authors emphasize that global feedback can be demonstrated for the primary conservative network *which the information network controls*. Matter cycles in ecosystems and the conservative closures provided by biogeochemical cycling are rich in information mappings: they can trigger microbial blooms or new cycles of plants growth, for instance.

 $<sup>^{71}</sup>$  The informational network encompasses all the non-conservative uses by organisms of the abiotic factors (air, water, soil) and of the surfaces, gradients, and objects (including other organisms) dispersed in the environment; it also includes the sights, sounds, tastes, odors, touches, pressures, magnetic fields, and other possible sensory cues provided by physical, chemical, and biological signals available in the environment that contribute to the orderly flux of conservative substances. The laws defining the conditions of existence (gravity, conservation, dissipation, limiting factors, etc.) are all part of the information network. The time of the year, the height of the sun above the zenith, the position of the moon, temperature – all these are part of it.

Finally, that in cybernetic systems the information networks with feedback are the source of stability is another claim challenged by Engelberg and Boyarsky (1979). Negative feedback damps perturbations and leads to the homeostatic regulation of certain variables. These authors acknowledge this ability of ecosystems, but they hold that these properties are derived from physical, not cybernetic principles. I would argue that underlying general laws are part of the information network; physical or chemical stability principles are expressions of broader cybernetic imperatives at these lower levels of organization. Therefore, the contribution of such laws to ecosystem stability and regulation is consistent with their cybernetic nature, because they are informational processes.

In short, although I do not agree with all these criticisms advanced by Engelberg and Boyarsky (1979), I think they are right when they assert that the crucial issue is that more than to contrast the noncybernetic or cybernetic character of ecosystems, the basic problem is how to conceptualize ecosystems and place them within the scheme of known things. The illustrated criticisms raise an important issue concerning the nature of ecological networks. If one focuses on components or individual organisms as some ecologists tend to do, one will have a different systems perspective than if one focuses on the flows of matter, energy and information directly. The former ecologists prefer not to think about systems at all: ecology can be understood by merely focusing on individual organisms and their populations. I do not agree with this position and believe that we must ask how it is that it looks that the environment is "ready" for the organism: in order to understand the functional role of an individual organism in nature, the ecologist must understand the environment in which the organism is embedded as well, where the latter is not chaotic and unfathomable. In brief, the ecologist must approach the environment as an ecosystem, the level of organization concerned with the orderly, not chaotic, and processing of energy and matter in nature. I would argue that, even though they are not superorganisms, this is the goal of ecosystems. Borrowing the expression from Patten and Odum (1982, pp. 894): "the balance of nature calls for a conjugate action-reaction kind of organization that creates order where there could be chaos as a matter of implicit design that simply evolved over geological time". The relevant notion of design is represented by the non-teleological model, in which a diffused, decentralized and indistinct informational subsystem regulates the primary energy-matter subsystem in order to achieve order. Systemic models tend to be established so that components or set of components are linked together in a network. While, admittedly, the analysis of information in ecology can be greatly complex, I believe the crucial question is, rather, how the control of ecosystem dynamics is mediated in this non-teleological model.



Figure A. 1 Analysis of basic input-output systems and feedback controlled systems.

## Annex 3 – Laws of Thermodynamics and Ecology

In order to understand the development of the Ecological Law of Thermodynamics (ELT), it is important to understand the conservation laws and some core thermodynamic functions, especially free energy covering the work capacity of a system. In this annex I will explain briefly how thermodynamic laws are applied in ecology.

The first law of thermodynamics expresses that energy is conserved. Energy cannot be destroyed or created. The law is often expressed mathematically by the following equation (Jørgensen, 2012; Jørgensen *et al.*, 2020):

$$(eq. A3.1)\Delta U = \Delta Q + \Delta W$$

Where U is the energy and  $\Delta U$  is the increase of energy,  $\Delta Q$  is the amount of heat received from the environment, and  $\Delta W$  is the amount of work received from the environment. The equation expresses just a bookkeeping of the energy considering the two forms of energy: heat and the energy that can do work. The gain in energy is just a matter of how much energy the system receives from the environment either as heat or as work.

Helmholtz showed that, when a gas expands, the internal energy of the gas decreases in proportion to the amount of work performed. These observations led to the first law of thermodynamics: energy can neither be created nor destroyed. Introducing the concept of internal energy, dU:

$$(eq.A3.2)dU = dQ - dW$$

where dQ is the thermal energy added to the system, dU is the increase in internal energy of the system, and dW is the work done by the system on its environment. Work done by the environment on the system would of course contribute positively to the energy of the system, as expressed in eq.A3.1. This important law is often formulated in several different versions. The difference between the two formulations in equations A3.1 and A3.2 is not only that  $\Delta$  is used in A3.1 and d in A3.2, but that the work in A3.2 is the work done by the system, while in A3.1  $\Delta$ W is the work done on the system. Both versions are used in ecology.

Work can take various forms. Presuming that the work is carried out as an increase in volume,  $\Delta V$ , under constant atmospheric pressure, p, for the system, we have:

$$(eq.A3.3)\Delta U = Q - p\Delta V$$

This equation is applied to define a new function, enthalpy (or heat content), H (Jørgensen, 2012):

$$(eq. A3.4)H = U + pV$$
$$(eq. A3.5)\Delta H = \Delta U + \Delta(pV)$$

If we assume that the ideal gas law is valid, we have that  $\Delta H = \Delta U + \Delta (nRT)$ .<sup>72</sup> The interesting point concerns the enthalpy change when the process occurs in the system at a fixed external pressure, for instance, 1 atm, as it is the case with many biochemical and ecological processes. Under these circumstances, the work done by the change of the volume (e.g. by generation of a gas) cannot be

<sup>&</sup>lt;sup>72</sup> Ideal Gas Law states that pV = nRT; n is the amount of the gas, R the gas constant and T the absolute temperature.

utilized, and therefore the change in enthalpy becomes as relevant as the change in energy of the considered system.

Classical thermodynamics has introduced two more energy-based functions: the work function, A, and free energy, G. They have been introduced because it is desirable to obtain criteria for thermodynamic equilibrium under practical conditions, which means that the temperature is approximately constant in addition to either constant volume. The two functions are defined according to the following equations (Jørgensen, 2012):

$$(eq. A3.6)A = U - TS$$
$$(eq. A3.7)G = U + pV - TS$$

Or, by differentiating:

(eq.A3.8)dG = dU + pdV + Vdp - TdS - SdT

And since dU = TdS - pdV, we obtain that:

$$(eq.A3.8)dG = Vdp - SdT$$

For a change at constant temperature and volume:

$$(eq. A3.9)\Delta A = \Delta U - T\Delta S$$
$$(eq. A3.10)\Delta G = \Delta H - T\Delta S = \Delta U - p\Delta V - T\Delta S$$

Where S is the function named entropy defined by dS = dQ/T. The introduction of entropy is often associated with the second law of thermodynamics, which I will explain below. Most chemical processes in laboratories or in organisms are carried out at constant temperature and pressure. This implies that dG = -dW. We are often presuming constant temperature and pressure when we study processes in ecosystems. At thermodynamic equilibrium, all gradients are eliminated according to the definition. This means that no work can be performed. This implies, given constant temperature and pressure, that dG = 0, which is an important consequence of the energy conservation law. A general dynamic equilibrium, but not a thermodynamic one, is possible when process rates in opposite directions balance each other to ensure that steady state is maintained.

One can distinguish among different forms of energy. All forms can be described as a quantitative (extensive) variable times a qualitative (intensive) variable. For example, in expansion, the volume is the extensive variable and the pressure the intensive one. Work can be performed when the extensive variable is changed from one level of the intensive variable to another, and the work equals the extensive variable times the difference of the intensive variable between the two levels. As energy is conserved, work implies that one energy form is transferred to another energy form.

The organic matter accumulated in the biomass of an ecosystem may be defined as the ecopotential, E, equal to the free energy difference, which can be released by the process,  $\Delta G$ , per unit of carbon, C (Jørgensen, 2012). Thus, the ecopotential is a function of the concentration of biomass and organic matter. The product of ecopotential and ecoflux,<sup>73</sup> dC/dt, has the dimension of power:

<sup>&</sup>lt;sup>73</sup> Jørgensen (2012) defines ecoflux in analogy with electrical current: J (a flow rate) is J=L\*X, where L means the conductivity between two points See pp. 30.

$$(eq. A3.11)Power = E * J = \sum \Delta G * dC/(C * dt)$$

Where C is the concentration of biomass measured as carbon. Power is the increase in biomass concentration per unit of time converted to free energy. It is noteworthy that the maximum power principle focuses on a rate – in equation A3.11 indicated as dC/dt, i.e., the ecoflow – multiplied by the fraction that is able to do useful work, i.e.,  $\Delta G/C$ . Maximum power of an ecosystem becomes thereby equal to the sum of flow rates of useful energy in the system. Odum (1983) defines the maximum power principle as a maximization of useful power. This implies that equation A3.11 is applied to the ecosystem level by summing up all the contributions to the total power that are useful. This means that non-useful power is not included in the summation. The difference between useful and non-useful power will be further discussed below, because the emphasis on useful power is perhaps the key to understanding Odum's principle and utilizing it to interpret ecosystem properties.

The concept of embodied energy, or emergy, was introduced by Odum (1983) in order to account for the energy required for the formation of organisms at different trophic levels. The idea is to correct energy flows for their quality. Energies of different types are converted into equivalents, of the same type, by multiplying by the energy transformation ratio. For example, fish, zooplankton, and phytoplankton can be compared by multiplying their actual energy content by their solar energy transformation ratios. The more transformation steps there are between two kinds of energy, the greater the quality and the greater the solar energy required to produce a unit of energy (Joule) of that type. When one calculates the energy of one type, that generates a flow of another; this is sometimes referred to as the embodied energy of that type.

The difference between embodied energy flows and power simply seems to be a conversion to solar energy equivalents of the free energy. The increase in biomass, in equation A3.11, is a conversion to the free energy flow, and the definition of embodied energy is a further conversion to solar energy equivalents. Embodied energy is determined by the biogeochemical energy flow into an ecosystem component, measured in solar energy equivalents. The stored emergy, Em, per unit of area or volume to be distinguished from the emergy flows can be found from (Jørgensen, 2012):

$$(eq.A3.12)Em = \sum_{i=1}^{i=n} \Omega_i C_i$$

Where  $\Omega_i$  is the quality factor = transformity (seJoule/Joule), which is the conversion to solar equivalents, and  $C_i$  is the concentration expressed per unit of area or volume.

The calculations allowed by equation A3.12 reduce the difference between stored emergy (embodied energy) and stored exergy, another thermodynamic concept, which I will describe below; the latter can also be found with good approximations as the sum of concentration times, a quality factor, to a difference in the definition of the quality factor. The quality factor for eco-exergy, another concept that I will explain below, accounts for the information embodied in the various components in the system. On the other hand, the quality factor for emergy accounts for how much solar energy it costs to form the various components. Emergy thereby accounts for how much solar energy (which is our ultimate energy resource) it costs to obtain one unit of biomass for various organisms, while eco-exergy accounts for how much "first class" energy (defined as energy that can do work, see below) the organisms have, as a result of their complex interactions in an ecosystem. Both concepts attempt to account for the quality of the energy: emergy by looking into the energy flows in the ecological network to express the energy costs in solar equivalents; and eco-exergy by considering the amount of

information (which also contains first-class energy able to do work) that the components have embodied. Both concepts can be used to understand ecosystems better and to reveal the energetic consequences of the ecological processes. Emergy calculations of products are also made and are used to assess how effectively various productions are able to utilize the ultimate energy source, i.e., sunlight.

In summary, these are the differences between exergy and emergy (Jørgensen, 2012):

1. Emergy has no clear reference state, which is not needed, as it is a measure of energy flows, while exergy is defined relative to the environment;

2. The quality factor of exergy is based on the content of information (see below), while the quality factor for emergy is based on the cost in solar equivalents;

3. Exergy is anchored in thermodynamics (but not classical thermodynamics) and has a wider theoretical basis;

4. The quality factor,  $\Omega$ , may be different from ecosystem to ecosystem, and in principle, it is necessary to assess in each case the quality factor based on an energy flow analysis.

I have previously used the term work capacity to express the ability of a part of the total energy to perform work in contrast to heat energy at the temperature of the environment, that is, without work capacity. The classical thermodynamics uses the G-function (free energy of Gibbs) to cover the work capacity, but when one is dealing with very far from equilibrium thermodynamic systems, one can no longer use state variables that are independent of the pathway. Furthermore, one needs in different situations different reference states. Therefore, one has to define a work capacity that can also be used very far from thermodynamic equilibrium systems, such as ecosystems. Exergy is defined as the amount of work (entropy-free energy) a system can perform when it is brought into thermodynamic equilibrium with its environment (Jørgensen, 2012; Jørgensen *et al.*, 2020). I will not delve into the details of constructing the complex mathematical formulation of exergy, but it will suffice to define the exergy of a system as characterized by the extensive variables of entropy (S), energy (U), volume (V), and the moles of the various chemical compounds involved (N<sub>i</sub>); and the intensive state variables such as temperature (T), pressure (p), and the chemical potential of that compounds ( $\mu_i$ ). The expression for exergy is (Jørgensen, 2012):

$$(eq. A3.13) Ex = S(T-T_0) - V(p-p_0) + \sum_{c} (\mu_c - \mu_{co}) N_i$$

Exergy is dependent on the state of the environment, as the exergy of the system is dependent on the intensive state variables of the system. Furthermore, exergy is not conserved, unless entropyfree energy is transferred, which would imply that the transfer is reversible. All natural processes are, however, irreversible, which means that exergy is lost (and entropy is produced). I will mention below in more detail the production of entropy when I present the second law of thermodynamics.

Energy is conserved by all processes according to the first law of thermodynamics, as I have related above. It is therefore meaningless to discuss the energy efficiency of an energy transfer because it will always be 100%. Instead, the exergy efficiency is of interest because it will express the ratio of useful energy (work energy) to total energy, which is always less than 100% for natural processes. All transfers of energy imply that exergy is lost because energy is transformed to heat at the temperature of the environment. Thus, it is of interest to estimate for all environmental systems, in addition to an energy balance, an exergy balance (Jørgensen *et al.*, 2020). The loss of exergy is relevant because that means loss of work capacity, or "first class energy", which can do work and is

lost as "second class energy" (heat at the temperature of environment), which cannot do work. So, the particular properties of heat, including that temperature is a measure of the movement of molecules, limit nature possibilities to utilize this energy form to do work.

Exergy seems more useful to apply than entropy to describe the irreversibility of real processes, as it has the same unit as energy and is an energy form, while the definition of entropy is more difficult to relate to concepts associated with our usual description of reality (Jørgensen, 2012). In addition, entropy is not clearly defined for "far from thermodynamic equilibrium systems," particularly for living systems. Moreover, it should be mentioned that the self-organizing abilities of systems are strongly dependent on temperature (Jørgensen *et al.*, 1999). Exergy takes the temperature into consideration as the definition shows, while entropy does not. Exergy becomes a good measure of "ecosystem' creativity", which increases proportionally with the temperature. Furthermore, exergy facilitates the understanding of the difference between low-entropy energy and high-entropy energy, as exergy is entropy-free energy.

Jørgensen (2012) argues that information contains exergy, following Boltzmann's idea that the free energy of the information that one possesses (in contrast to the information we need in order to describe the system) is  $k^T \ln I$ , where I is the information we have about the state of the system, for instance, that the configuration is 1 out of W possibilities (i.e., W = I)<sup>74</sup> and k is Boltzmann's constant =  $1.3803 \times 10^{-23}$  (J/molecules\*deg). Transformation of information from one system to another is often almost an entropy-free energy transfer. If the two systems have different temperatures, the entropy lost by one system is not equal to the entropy gained by the other system, while the exergy lost by the first system is equal to the exergy transferred and equal to the exergy gained by the other system, provided that the transformation is not accompanied by any loss of exergy, which it always occurs in nature. In this case, it is obviously more convenient to apply exergy than entropy.

The exergy of the system measures a contrast: it refers to the difference in free energy in case there is no difference in pressure and temperature, as may be assumed for an ecosystem or an environmental system and its environment—against the surrounding environment. If the system is in equilibrium with the surrounding environment, exergy is zero. The only way to move systems away from equilibrium is to perform work on them. Therefore, it is reasonable to use the available work, i.e., the exergy, as a measure of the distance from thermodynamic equilibrium. Exergy in the case of ecosystems presumes reference to the same system (ecosystem) but at thermodynamic equilibrium, which means the assumption that all the components would be inorganic at the highest possible oxidation state (less reactive) and homogeneously distributed in the system (no gradients), which is not the case.

As the chemical energy embodied in the organic components and the biological structure contributes far more to the exergy content of the system, there seems to be no reason to assume a (minor) temperature and pressure difference between the system and the reference environment. Under these circumstances we can calculate the exergy, labeled eco-exergy, as coming entirely from the chemical energy (Jørgensen, 2012; Jørgensen *et al.*, 2020). Equation A3.13 becomes:

# (eq. A3.14) $Ex = \sum_{c} (\mu_{c} - \mu_{co}) N_{i}$

This represents the non-flow chemical exergy. It is determined by the difference in chemical potential  $(\mu_c - \mu_{co})$  between the ecosystem and the same system at thermodynamic equilibrium. This difference is determined by the concentrations of the considered components in the system and in the reference

<sup>&</sup>lt;sup>74</sup> W measures the total number of ways that a particular macrostate in a system can be microscopically constituted.

state (thermodynamic equilibrium), as is the case for all chemical processes. One can measure the concentrations in the ecosystem, but the concentrations in the reference state (thermodynamic equilibrium) can be based on the usual use of chemical equilibrium constants.



Figure A. 2 Calculation of exergy of an ecosystem, relative to a reference environment of the same ecosystem at thermodynamic equilibrium.

Eco-exergy is a concept seemingly close to Gibbs free energy but somewhat opposite to it because, first, eco-exergy has a different reference state from case to case (from ecosystem to ecosystem), and it can furthermore be used far from thermodynamic equilibrium; conversely, Gibbs free energy, in accordance to its exact thermodynamic definition, is only a state function close to thermodynamic equilibrium.

We find by these calculations the eco-exergy of the system compared with the same system at the same temperature and pressure, but in the form of an inorganic soup without any life, biological structure, information, or organic molecules. As  $(\mu_c - \mu_{co})$  can be found from the definition of the chemical potential replacing activities by concentrations, we get the following expression for the eco-exergy (Jørgensen, 2012; Jørgensen *et al.*, 2020):

$$(eq. A3.15) Ex=RT\sum_{i=0}^{i=n} C_i \ln C_i/C_{i,o}$$

Where R is the gas constant (8.317 J/K moles = 0.08207 L.atm/K moles), T is the temperature of the system, and  $C_i$  is the concentration of the i-th component expressed in a suitable unit (for a lake  $C_i$  could be expressed as mg/L or as mg/L of a focal nutrient, for example).  $C_{i,0}$  is the concentration of the i-th component at thermodynamic equilibrium and n is the number of components.  $C_{i,o}$  is, of course, a very small concentration (except for i = 0, which is considered to cover inorganic compounds), corresponding to a very low probability of forming complex organic compounds spontaneously in an inorganic soup at thermodynamic equilibrium.

By using this particular exergy based on the same system at thermodynamic equilibrium as reference, the eco-exergy becomes dependent only on the chemical potential of the numerous biochemical components that are characteristic of life: this is consistent with Boltzmann's statement that life is a struggle for free energy (Jørgensen, 2012). It is important to notice that the definition of eco-exergy is, however, a difference in free energy between the system and the same system at thermodynamic equilibrium. The reference system used is different for every ecosystem according to the definition of eco-exergy. Furthermore, free energy is not a state function far from thermodynamic equilibrium.

Biological structures maintain and reproduce themselves by transforming energy and information from one form to another. An important feature of life is that the information laid down in the genetic material is developed and transferred from one generation to the next. The information content increases in the course of ecological development because an ecosystem integrates all the modifications that are imposed by the environment. Thus, it is against the background of genetic information that systems develop which allow interaction of information with the environment. Herein lays the importance in the feedback organism-environment that means that an organism can only evolve in an evolving environment, which in itself is modifying.

The conservation laws of energy and matter set limits to the further development of "pure" energy and matter, while information may be amplified (almost) without limit. Limitation by matter is known from the concept of the limiting factor: growth continues until the element that is the least abundant relatively to the needs of the organisms is used up. Very often in developed ecosystems (for instance an old forest) the limiting elements are found entirely in organic compounds in the living organisms, while there is no or very little inorganic forms left in the abiotic part of the ecosystem. The energy input to ecosystems is determined by the solar radiation and many ecosystems capture about 75%-80% of the solar radiation, which is their upper physical limit. Unlike energy capture which has an upper limit, the information content may continue to increase in terms of both structural information (i.e., the network) and also genetic information.

Information has some properties that are very different from mass and energy (Jørgensen *et al.*, 2020):

- 1. Information, unlike matter and energy, is not conserved, and it can disappear without a trace. When an organism dies, the enormous information content of the living organism may still be there microseconds after the death in form of the right amino acid sequences but the information is useless and after a few days the organic polymer molecules have decomposed. In contrast, the living organism is able to multiply information by copying already achieved successful information. The information is able to provide a pattern of biochemical processes that ensure survival of the organisms as they interact with the physico-chemical environment and the other organisms present in the ecosystem. Organisms copy the information embodied in the genomes as they grow and reproduce. Growth and reproduction require input of energy in terms of environmental food resources. The food has energy content, but it also has information content, which like the dead organism, no longer has the capacity to act upon.
- 2. The disappearance and copying of information, that are characteristic processes for living systems, are irreversible processes. A made copy cannot be taken back and death is an irreversible process. Although information can be expressed as eco-exergy in energy units, it is not possible to recover chemical energy from information on the molecular level as known from the genomes. Similarly, the conversion of energy to information that is characteristic for many biological processes cannot be reversed directly in most cases. The transformation matter/energy/molecular information, which can be copied at low cost, is possible on earth, but these transformation processes are irreversible.

3. Information exchange is communication, which brings about the self-organization of life. Life is an immense communication process that happens over several hierarchical levels. Information exchange is possible with a very tiny consumption of energy, while information storage requires that it is linked to material substances. For instance, genetic information is stored in the genomes and it is transferred to the amino acid sequence.

It is therefore important to understand information in thermodynamic terms, trying to relate eco-exergy and information in an ecosystem.

In statistical mechanics, entropy is related to probability. A system can be characterized by averaging ensembles of microscopic states to yield the macrostate. If W is the number of microstates that will yield one particular macrostate, the probability P that this particular macrostate will occur as opposed to all other possible macrostates is proportional to W. It can further be shown that (Jørgensen, 2012; Jørgensen *et al.*, 2020):

## (eq. A3.16) S=K\* ln W

Where k is Boltzmann's constant,  $1.3803.10^{-23}$  J/(molecules.K). The entropy (S) is a logarithmic function of W, and thus measures the total number of ways that a particular macrostate can be constituted microscopically. K Av = R, where Av is Avogadro's number.

It is noteworthy that entropy measures the information we need to describe the system. S may be called thermodynamic information, meaning the amount of information needed to describe the system, which must not be interpreted as the information that one actually possesses. The information that one has becomes equal to negentropy (–S), which from a strict thermodynamic point of view does not exist. According to the third law of thermodynamics, entropy cannot be negative, and it would be more correct to use the phrase "the free energy (or exergy) of the information we have" = kT ln W (Boltzmann also used the expression the free energy of information). The more microstates there are and the more disordered they are, the more information is required and the more difficult it will be to give a complete description of the system—and the higher is the entropy. This means that entropy + information = constant. When we gain information, entropy decreases, and when we lose information, entropy increases. The constant expresses the total information needed to know all details of a considered system. When we have the full information about the considered system, information = constant and entropy = 0. When we have no knowledge about the system, the entropy = constant and information = 0.

It is possible to distinguish between the contribution to the exergy of information and of biomass (Jørgensen, 2012; Jørgensen *et al.*, 2020). P<sub>i</sub> being defined as C<sub>i</sub>/B, where  $B = \sum_{i=1}^{n} C_{i}$  is the total amount of matter in the system. Introducing it as a new variable in equation A3.15, one has:

# (eq. A3.17) $Ex=BRT\sum_{i=1}^{n} p_i \ln p_i/p_{i,o} + B \ln B/B_0$

As the biomass is the same for the system and the reference system,  $B\approx B_0$ , exergy becomes a product of the total biomass of the system (multiplied by RT) and Kullback measure (K) (Jørgensen, 2012; Jørgensen *et al.*, 2020):

(eq. A3.18) 
$$K = \sum_{i=1}^{n} p_i \ln p_i / p_{i,o}$$

Where  $p_i$  and  $p_{i,o}$  are probability distributions, a posteriori and a priori to an observation of the molecular detail of the system. This means that K expresses the amount of information that is gained as a result of the observations.

Therefore, exergy density can be found as biomass times RTK (Jørgensen, 2012):

Where B is the biomass, R the gas constant, T the absolute temperature, and K the Kullback measure of information. In this manner, the information that the organism carries is the basis for the organism's eco-exergy (Jørgensen *et al.*, 2020):

(eq. A3.20) 
$$Ex_i = \beta_i C_i$$

Where  $Ex_i$  is the exergy of the i-th species,  $\beta_i$  is a weighting factor that considers the information the ith species is carrying in  $C_i$ .  $\beta_i$  has different values for different organisms. They express the free energy of the information stored in their (amino acid) constitution.

Due to the incoming free energy of solar radiation, an ecosystem is able to move away from the thermodynamic equilibrium; i.e., the system evolves, obtains more information and organization. The ecosystem must produce entropy for maintenance, but the low-entropy energy flowing through the system may be able to more than cover this production of disorder, resulting from maintenance of the order and structure.

As I have referred above, Boltzmann emphasized that competition in nature is a struggle for free energy and that information embodies free energy. By the use of chemical statistics Boltzmann expresses entropy as  $S = R \ln W$ , and free energy as  $-RT \ln W$ , where W is the number of microstates (that are presumed unknown). If we presume that we know the present (a posteriori) probability,  $p_i = 1.0$ , while  $p_{i,o}$  (a priori) has a probability corresponding to W, it is possible to understand that eco-exergy = Biomass \* RTK is close to what Boltzmann considered free energy. The difference is that free energy is not a state function for far from equilibrium systems such as ecosystems, while one has accepted that eco-exergy is not a state function, and that it is a relative measure of the work capacity (relative to the ecosystem at thermodynamic equilibrium). Thus, the important point is that:

$$(eq. A3.21)$$
 Eco-exergy =  $-TS = kT \ln W$ 

It is relevant to notice that S measures the information one needs to get, while Ex measures the work capacity of the information that we do have.

I will now introduce the second and third law of thermodynamics. Ecosystems are open systems: they have to receive an inflow of free energy – energy that can do work – to be able to maintain their complex structure (Jørgensen, 2012; Jørgensen *et al.*, 2020). However, in accordance to the second law of thermodynamics, all dynamic systems will inevitably produce entropy, lose order and free energy. As ecosystems have to receive energy to combat these consequences of the second law, I will briefly describe the laws and its consequences for ecosystems.

Ecosystems are open systems in the sense that they are open for mass and energy transfers. Ecosystems receive energy from solar radiation and receive water from precipitation, dry deposition from the atmosphere, inputs by wind, and inflows and outflows of various types, plus emigration or immigration of species. A system that is closed for inputs and outputs of energy and mass is called an isolated system, while a system that is closed to inputs and outputs of mass, but open to energy transfers, is denoted a closed system. A non-isolated system is a closed or open system. If an ecosystem were isolated, it would inevitably move toward thermodynamic equilibrium and become a dead system with no gradients to do work.

This is the consequence of the second law of thermodynamics, which states that all systems will lose order and gain disorder, that is, all systems will gain entropy, lose energy that can do work to energy that cannot do work, i.e., all systems will lose exergy. As I have illustrated above, the thermodynamic equilibrium will correspond to dG = 0 and dS = 0 at a maximum S value and a minimum value of free energy.

Openness explains why an ecosystem can maintain life and stay far from thermodynamic equilibrium, because maintenance of life requires input of energy (or rather, free energy, i.e., energy that can do work), which of course is only possible if an ecosystem is at least non-isolated. As there is exchange of matter between the environment and the ecosystems, the latter must be open (Jørgensen, 2012; Jørgensen *et al.*, 2020). The use of the second law of thermodynamics for open systems is crucial. At first glance, it looks like ecosystems violate the first law of thermodynamics because they are moving away from thermodynamic equilibrium by formation of a biological structure, implying that they gain chemical energy. Ecosystems receive, however, energy as solar radiation, which delivers the energy for the formation of the biological structure and also the energy needed for maintenance of the system far from thermodynamic equilibrium. Before moving to the application of the second law, I will describe some basic implications of the openness of ecosystems.

Concerning physical openness, one can write an energy balance for an ecosystem in accordance with the principle of energy conservation (Jørgensen, 2012):

# (eq. A3.22) $E_{cap} = Q_{evap} + Q_{resp} + \dots + \Delta E_{bio}$

Where  $E_{cap}$  is the external energy captured per unit of time and  $\Delta E_{bio}$  is the difference between anabolism (formation of biological compounds) and catabolism (their decomposition), which in ecosystem steady state is in approximate balance. That is, in energy terms,  $\Delta E_{bio}\approx 0$  and  $E_{cap} = Q_{evap}+Q_{resp}+...$  The energy captured per unit of time is, accordingly, used to pay the cost of maintenance per unit of time =  $Q_{evap}+Q_{resp}+...$  The overall results of these processes require that  $E_{cap}>0$ , which entails openness: energy and matter openness is needed. Energy inflows to ecosystems are of high-quality energy (i.e., with high contents of work and information) and low entropy, suitable to raise the organizational states of matter far from equilibrium. The outflows are, in contrast, sinks for energy and matter and have lower work capacity, are higher in entropy, and closer to equilibrium (Jørgensen, 2012; Jørgensen *et al.*, 2020).

Concerning ontic openness, Jørgensen *et al.* (2012, 2020) assumes that the world is ontically open = nondeterministic. The sense is, according to the author, the use of propensities and conditional probabilities to describe the phenomena, and not simply to cover the ignorance of the observer. This openness pertains to a degree of indeterminacy inherent in the situation itself.

Moreover, after very theoretical considerations, the author concludes that we shall never be able to obtain a sufficient number of observations to describe even one ecosystem in detail<sup>75</sup>. Due to the enormous complexity of ecosystems one cannot, as already stress, know all their details. When one cannot know all the details, one is not able to describe fully the initial stage and the processes that determine the development of the ecosystems—as expressed above, ecosystems are therefore

<sup>&</sup>lt;sup>75</sup> Jørgensen (2012, pp. 62-64) formulates some practical uncertainty relations in ecology in order to articulate these theoretical considerations, comparing them with the theoretical developments in quantum mechanics.

irreducible and non-deterministic, also in an epistemic sense. Ecosystems are non-deterministic because we cannot provide all the observations that are needed to give a full deterministic description.

Thus, being open, in an ontic and epistemic sense, they are irreducible, and due to their enormous complexity, which prohibits one to know all details, one will only be able to indicate the propensities and directions of their development. Nevertheless, the more one knows about ecosystems, the better one can describe their possible development as a consequence of different impacts on the ecosystems.

Now we can move to application of the second law of thermodynamics on physical and ontic open systems such as ecosystems.

If ecosystems were isolated, no energy or matter could be exchanged across their boundaries. The systems would spontaneously degrade their initially contained exergy (loss of work energy to heat energy at the temperature of the environment), increase their entropy (i.e., lose order and organization) and increase in the randomness of their constituents and microstates. This dissipation process would cease at equilibrium, where no further motion or change would be possible. All gradients of all kinds would be eliminated, and the system would be frozen in time in a stable, fixed configuration. The high-energy chemical compounds of biological systems, faced suddenly with isolation, would decompose spontaneously to compounds with high-entropy contents. The process would be progressive, to higher and higher entropy, and given the presence of oxygen, end with a mixture of inorganic residues at high oxidation state—carbon dioxide and water, nitrates, phosphates, sulfates, etc. These simpler compounds could only, with an extremely low probability, be reconfigured into the complex molecules necessary to carry on life processes without the input of new low-entropy energy to be employed in biosynthesis. An isolated ecosystem could therefore, in the best case, sustain life for only a limited period of time, less than that required from the onset of isolation to reach thermodynamic equilibrium.

The change in entropy for an open system,  $dS_{system}$ , consists of an external contribution from the environment,  $d_eS = S_{in}-S_{out}$ , and an internal contribution due to the system state,  $d_iS$ , which must always be positive, by the second law of thermodynamics (Jørgensen, 2012; Jørgensen *et al.*, 2020). Hence, there are possibilities for the entropy balance:

 $(eq. A3.23) dS_{system}/dt = d_eS/dt + d_iS/dt > 0$  $(eq. A3.24) dS_{system}/dt = d_eS/dt + d_iS/dt < 0$  $(eq. A3.25) dS_{system}/dt = 0$ 

Thus, the system loses order in the first case. In the second case, it is only possible to gain order if  $-d_eS > d_iS > 0$ , and this means that if order is to be created in a system,  $d_eS$  must be <0, and therefore  $S_{in} < S_{out}$ . Consequently, creation of order in a system must be associated with a greater flux of entropy out of the system than into the system. This implies that the system must be open or at least non-isolated.

In the third case, one has a stationary situation, and using the following equations for the energy U and the entropy S balance (Jørgensen, 2012):

$$(eq. A3.26) dU/dt = 0 \text{ or } d_e U/dt = -diU/dt = 0$$

#### $(eq. A3.27) dS_{system}/dt = 0 \text{ or } d_eS/dt = -d_iS/dt = 0$

Using free energy, and admitting that thermodynamic processes occur at constant temperature and pressure, we have that  $d_eG/dt = T d_iS/dt > 0$ . This means that a status quo situation for an ecosystem requires input of free energy to compensate for the loss of free energy and corresponding formation of heat due to maintenance processes, i.e., respiration and evapotranspiration. If the system is not receiving a sufficient amount of free energy, the entropy will increase. If the entropy of the system continues to increase, the system will approach thermodynamic equilibrium: the system will die.

Hence, life without the input of free energy or energy that can do work is not possible. The entropy produced by life processes can be exported by three processes (Jørgensen, 2012; Jørgensen *et al.*, 2020): transfer of heat to the environment, exchange of material with the environment, and biochemical processes in the system. The first process is of particular importance.

As ecosystems are not isolated, they are able to maintain a certain concentration of lowentropy compounds against the second-law dissipation gradient. Ecosystems receive a continuous supply of free energy from outside to compensate for the positive entropy produced internally as a consequence of the second law of thermodynamics. On earth, solar radiation is the main source of this input of free energy, or low-entropy energy. The incoming energy has low entropy, while the outgoing energy has higher entropy.

All ordered structures require low entropy for maintenance, and therefore for a system to maintain structure or increase its internal order it must receive input of low-entropy energy from external sources. Structure, in this context, is a spatial or temporal order describable in terms of information theory (Jørgensen, 2012; Jørgensen *et al.*, 2020). The term dissipative structure can be used to denote self-organizing systems, thereby indicating that such systems dissipate energy (produce entropy) for the maintenance of their organization (order). Hence, all systems, because they are subject to the second law of thermodynamics, are inherently dissipative structures. To offset the dissipative processes they require inputs of low-entropy energy to maintain or produce a more internally organized structure, measurable in terms of information content. Thus, all natural systems must be open, or at least non-isolated.

Ecosystems, in common with all natural systems, have a global attractor state, the thermodynamic equilibrium (Jørgensen *et al.*, 2020). Through their openness they avoid reaching this state by importing low entropy energy and matter from their surroundings. This anabolism combats and compensates for the catabolic deterioration of structure; the two processes operate against each other. It is important to stress that the equilibrium attractor represents a resting state, one that is passively devolved to if system openness or non-isolation is compromised (Jørgensen *et al.*, 1999).

The first law of thermodynamics is often applied to ecosystems, first of all when energy balances of ecosystems are made. Also, the second law of thermodynamics is applied to ecosystems when we consider the entropy production of ecosystems as a consequence of the maintenance of the system far from thermodynamic equilibrium. I will now briefly describe the application of the third law of thermodynamics on ecosystems, which has a more indirect or theoretical application.

The third law of thermodynamics states that the entropies of pure chemical compounds, S<sup>0</sup>, are zero, and that entropy production,  $\Delta S^0$ , by chemical reactions between pure crystalline compounds is zero at absolute temperature, 0K (Jørgensen, 2012; Jørgensen *et al.*, 2020). In this context, temperature is a measure of how fast atoms are moving, where 0K corresponds to no movement at all. The third

law implies, since both  $S^0 = 0$  (absolute order) and  $\Delta S^0 = 0$  (no disorder generation), that disorder does not exist and cannot be created at absolute zero temperature.

However, at temperatures of >0 K disorder can exist ( $S_{system}$ >0) and be generated ( $\Delta S_{system}$ >0). The third law defines the relation between entropy production,  $\Delta S_{system}$ , and the Kelvin temperature, T:

$$(eq. A3.28) \Delta S_{system} = \int_0^T \Delta C_p dln \ T + \Delta S_0$$

Where  $\Delta C_p$  is the increase in heat capacity by the chemical reaction. Since order is absolute at absolute zero, its further creation is precluded there.

At higher temperatures, nonetheless, order can be created and maintained. As I have mentioned above, it is necessary for an ecosystem to transfer the generated heat (entropy) to the environment and to receive low-entropy energy (solar radiation) from the environment for formation of a dissipative structure. And, as a matter of fact, it has been shown, using simple model systems and basic thermodynamics, that an energy source and sink are sufficient to initiate the formation of a dissipative structure (Jørgensen, 2012). It also has been shown that open systems that are exposed to an energy throughflow exhibit coherent self-organization behavior and are known as dissipative structures. The formation of complex organic compounds from inorganic matter is a typical example of self-organization. Such systems can remain in their organized state by exporting entropy outside the system, but are dependent on outside free energy fluxes to maintain their organization, as was already mentioned and emphasized above. The organization is inexorably torn down according to the second law of thermodynamics. Only a flow of free energy can compensate for this decomposition of the organization, since, according to the second law, all systems have loss of exergy or work capacity, especially as lost of heat energy at the temperature of the environment, as I have related above.

The dissipative structure of an ecosystem can be interpreted using the concept of eco-exergy (Jørgensen, 2012; Jørgensen *et al.*, 2020). As an ecosystem is non-isolated, the entropy changes during a time interval, dt, can be decomposed into the entropy flux due to exchanges with the environment and the entropy production due to the irreversible processes inside the system, such as diffusion, heat conduction and chemical reactions. The entropy equation A3.23 can be expressed by the use of exergy:

(eq. A3.29) 
$$Ex/dt = d_e Ex/dt + d_i Ex/dt$$

Where  $d_eEx/dt$  represents the exergy input to the system and  $d_iEx/dt$  is the exergy consumed (is negative) by the system for maintenance.

The equation A3.29 shows that systems can only maintain a non-equilibrium steady state by compensating the internal exergy consumption with a positive energy influx ( $d_eEx/dt>0$ ). If  $d_eEx>d_iEx$  (the exergy consumption in the system), the system has surplus energy input, which may be used to construct further order in the system: the dissipative structure.

#### <u>Annex 4 – Autocatalysis</u>

In this annex I will describe what happens when many propensities (propensities are the tendencies that certain processes or events may occur within a given context, being a combination of mechanism and chance at the macroscopic level) interact with which other, focusing in one type of bilateral interaction.

If unilateral effects can be characterized as being either positive (+), negative (-), or neutral (0), then the nature of bilateral interactions can be denoted by couples of unilateral interactions, i.e., predation (+,-), competition (-,-), neutralism (0,0), for example. Mutualism (+,+) exhibits singular characteristics that impart to its participants the advantage to persist, on the average, beyond the duration of components engaged in other types of interactions. Furthermore, it may be argued that ensembles of mutualistic interactions, or what in chemistry is called "autocatalytic configurations", exhibit behaviors that are decidedly organic in nature (Ulanowicz, 1998, 2000, 2005).

To illustrate the nature of autocatalysis I will consider a triad of processes, A, B, and C. It is assumed that the activity of A has a propensity to increase the activity of B. B, in turn, exerts a similar propensity upon C, which has the same effect upon A. Thus, the indirect effect of A upon itself is positive, giving rise to autocatalysis. It should be noted, however, that, unlike in chemistry, A, B, and C do not have to be mechanically linked. The activity of A does not have to stimulate that of B in every instance, just in most of them. A schematic of autocatalysis among three processes is presented in figure A.3:



Figure A. 3 Hypothetical three-component autocatalytic cycle

In keeping with the idea of an open and contingent universe, it is not required that A, B, and C should be linked together in an obligatory fashion. To achieve autocatalysis, it is only required that the propensities for positive influence must be stronger than cumulative decremental interferences (Ulanowicz, 1998, 2000, 2005).

An example of autocatalysis in ecology is the community that forms around that aquatic macrophyte *Utricularia* (Ulanowicz, 1995, 2007). All members of the genus *Utricularia* are carnivorous plants. Small bladders, called utricles, are scattered along its featherlike stems and leaves. Each utricle has a few hairlike triggers at its terminal end, which, when touched by a feeding zooplankter, opens the end of the bladder and the animal is sucked into the utricule by a negative osmotic pressure maintained inside the bladder. In nature the surface of *Utricularia* plants is always host to a film of algal growth known as periphyton. This periphyton serves, in turn, as food for any number of species of small zooplankton. The autocatalytic cycle is closed when the Utricularia captures and absorbs many of the zooplankton. In a more detailed way (Ulanowicz, 2005):



Utricularia, a carnivorous plant

a)

Utricularia system

Figure A. 4 Scheme for the Utricularia plant system and its cycle of rewards

Inhabiting freshwater lakes over much of the world, and especially in subtropical, nutrientpoor lakes and wetlands, these plants are sometimes anchored to the lake bottom, and they do not possess feeder roots that draw nutrients from the sediments (Ulanowicz, 1995). Rather, they absorb their source of sustenance directly from the surrounding water. One may identify the growth of the filamentous stems and leaves of Utricularia into the water column with process A in figure A.3.

Upon the leaves of the bladderworts invariably grows a film of bacteria, diatoms and bluegreen algae: the periphyton. If one identifies process B with the growth of the periphyton community, it is clear that bladderworts provide an areal substrate needed by the periphyton (not being well adapted to grow in the pelagic substratum, or free floating mode) to grow.

One can think of component C in the form of a community of small, almost microscopic motile animals, collectively known as the zoophytes, which feed upon the periphyton film. These zoophytes can be from any genera of cladocerae (water fleas), copepods (other microcrustacea), rotifers and ciliates (multicellular animals with hairlike cilia used in feeding). In the process of feeding upon the periphyton film, these small animals occasionally bump into hairs attached to one end of small bladders (the referred utricle). When moved, these trigger hairs open a hole in the end of the bladder, the inside of which is maintained by the plant at negative osmotic pressure with respect to the surrounding water. The result is that the animal is sucked into the bladder, and the opening quickly closes behind it. Although the animal is not digested inside the bladder, it does decompose, releasing nutrients that can be absorbed by the surrounding bladder walls. The cycle of the figure A.3 is now complete.

Autocatalysis traditionally has been viewed in rather mechanical terms, but in the face of environmental contingencies, autocatalytic activities behave in ways that transcend mechanism (Ulanowicz, 1995, 1997). For example, there is a selection pressure that the overall autocatalytic form exerts upon its components. If a random change should occur in the behavior of one member that either makes it more sensitive to catalysis by the preceding element or accelerates its catalytic influence upon the next compartment, then the effects of such alteration will return to the starting compartment as a reinforcement of the new behavior. The opposite is also true. Should a change in the behavior of an element either make it less sensitive to catalysis by its instigator or diminish the effect it has upon the next in line, and then even less stimulus will be returned via the loop.

Unlike Newtonian forces, which always act in equal and opposite directions, the selection pressure associated with autocatalysis is inherently asymmetric. Autocatalytic configurations give a definite direction to the behaviors of systems in which they appear. They tend to ratchet all participants toward ever greater levels of performance (Ulanowicz, 1995, 2000).

It is important to analyze the way transfers of material and energy between the components of autocatalytic systems and the environment. Figure A.3 does not portray such exchanges, which generally include the import of substances with higher exergy (available energy) and the export of degraded compounds and heat, as I explain in annex 3. The degradation of exergy is a spontaneous process mandated by the second law of thermodynamics, as I also refer in the same annex. However, it would be a mistake to assume that the autocatalytic loop is itself passive and merely driven by the gradient in exergy (Ulanowicz, 2000, 2005). For example, if one supposes that some arbitrary change happens to increase the rate at which materials and exergy are brought into a particular compartment, then this event would enhance the ability of that compartment to catalyze the downstream component, and the change eventually would occur. Conversely, any change decreasing the intake of exergy by a participant would ratchet down activity throughout the loop. The same argument applies to every member of the loop, so the overall effect is one of centripetality (Ulanowicz, 2000). The autocatalytic assemblage behaves as a focus upon which converge increasing amounts of exergy and material that the system draws into itself:



Figure A. 5 Autocatalytic cycle exhibiting centripetality

Autocatalytic systems are contingent upon their material constituents and usually also depend at any given instant upon a complement of embodied mechanisms. But such contingency is not, as often is in reductionism, entirely a one way route, where the components are usually the same. By its very nature autocatalysis is prone to induce competition, not merely among different properties of components; rather, its very material and mechanical constituents are themselves prone to replacement by the active agency of the larger system. Supposing, for instance, that A, B, and C are three sequential elements comprising as in figure A.6a (adapted from Ulanowicz, 2000), and that some new element D appears, is more sensitive to catalysis by A and provides greater enhancement to the activity of C than does B (figure A.6b). Then D either will grow to overshadow B's role in the loop, or will displace it altogether (figure A.6c). In the same manner one can argue that C could be replaced by some other component E (figure A.6d), and A by F, and thus the final configuration DEF contains none of the original elements (figure A.6e):



Figure A. 6 Successive replacement of components in an autocatalytic loop

It is important to notice that the characteristic existence time of the larger autocatalytic form is longer than that of its constituents.

The appearance of centripetality and the persistence of form beyond constituents are decidedly non-Newtonian behaviors (Ulanowicz, 1997, 2000, 2005). Although a living system requires material and mechanical elements, it is evident that some behaviors, especially those on a longer time scale, are, to a degree, autonomous of lower level events. I think that it becomes difficult to explain and predict the course of an autocatalytic configuration by ontological reduction to material constituents and the respective mechanical operation.

The autonomy of a system may not be apparent at all scales. If one's field of view does not include all the members of an autocatalytic loop, the system will appear linear in nature. Under such linear circumstances, an initial cause and a final result will always seem apparent (Ulanowicz, 2005):



Figure A. 7 The emergence of non-mechanical behavior as the scope of observation is enlarged.

The subsystem can appear wholly mechanical in its behavior. Once the observer expands the scale of observation enough to encompass all members of the loop, however, then autocatalytic behavior with its centripetality, persistence and autonomy emerges as a consequence of this wider vision. Thus, considering autocatalytic systems, agency can arise quite naturally at the very level of observation. This occurs via the relational form that processes bear to one another, and autocatalysis takes on the guise of a formal cause, in the Aristotelian sense (Ulanowicz, 2000).

Lastly, autocatalytic configurations, by definition, are growth enhancing. An increment in the activity of any member engenders greater activities in all other elements. The feedback configuration results in an increase in the aggregate activity of all members engaged in autocatalysis over what it would be if the compartments were decoupled.

Thus, autocatalytic systems can exhibit at least eight behaviors, which, taken together, mitigate against viewing them as mechanical systems that would yield to reductionist analysis (Ulanowicz, 1995, 1997, 2000, 2005). Autocatalysis induces: (1) growth and (2) selection. It exhibits an (3) asymmetry that can give rise to the (4) centripetal amassing of material and exergy. The presence of more than one single autocatalytic pathway in a system presents the potential for (5) competition. Autocatalytic behavior is (6) autonomous, to a degree, of its micro-constitution. Its attributes (7) emerge whenever the scale of observation becomes larger, usually in the guise of an Aristotelian (8) formal cause.

The overall effects of autocatalytic behavior are exhibited both extensively (as a function of system size) and intensively (independent of size). The former is expressed as an increase in total system activity, whereas the latter resembles a "pruning" of the processes that contribute less in autocatalytic activities. The combined result is depicted as (adapted from Ulanowicz, 2000):



Figure A. 8 Schematic representation of the major effects that autocatalysis exerts upon a system.

The first figure represents an inchoate network with ill-defined transfers among the components. After autocatalysis has increased the activity level of the system (indicated by the thicker arrows) and pruned away the autocatalytically less efficient links, the network comes to resemble more the second configuration.

#### <u>Annex 5 – Ascendency</u>

The extensive nature of an ecosystem' growth is rather easy to quantify. According to Ulanowicz (1997), there are four separate categories that need to be estimated in order to complete the inventory of material or energy exchanges in an ecosystem, as in figure A.9, adapted from Ulanowicz(1997): internal transfers, which shall be referred as  $T_{ij}$ , where the subscripts mean that the amount has been transferred from compartment or species i to component j (compartments are usually numbered 1,2,3,...n, so that i and j can be any integer from 1 to n); imports from the external world into compartment i; exports of energy and material from compartment i to another comparable system; dissipation of energy or conversion of material by component i into its base form.



Figure A. 9 The different types of exchanges to quantify ecosystem flows network.

One begins the analysis by defining the transfer of material or energy between component i and component j as  $T_{ij}$ , where i and j range over all members of a system with n elements (Ulanowicz, 1986, 1997, 2000, 2005). The total activity of the system can be measured simply as the sum of all system processes,  $T = \sum_{i,j} T_{ij}$ , or what is called the "total system throughput". The first aspect of autocatalysis can thus be represented as any increase in the total system throughput.<sup>76</sup>

Quantifying the intensive process of an ecosystem' development is somewhat more complicated. The object here is to quantify the transition from a very loosely coupled, highly indeterminate collection of exchanges to one in which exchanges are more constrained by autocatalysis to flow along the most efficient pathways (Ulanowicz, 1997, 2000). One begins, therefore, by invoking information theory to quantify the indeterminacy,  $h_j$ , of category j. Ulanowicz (1997, 2000) defines information as anything that causes a change in probability assignment, essentially equating information to constraint.

Information theory is the field of mathematics that quantifies such changes in probabilities, in much the same sense that differential calculus quantifies changes in algebraic quantities. Ulanowicz (1997) contends that there has been a shift in attitude regarding what exactly it is that probabilities measure. This change has been away from the idea that probabilities measure our ignorance about a deterministic situation, towards the notion that they reflect indeterminacy inherent in the process itself. That is, we are not working with "quantitative epistemology", but on the ontological character of

<sup>&</sup>lt;sup>76</sup> If reckoning the size of a system by its level of activity seems at first a bit strange, Ulanowicz (2000) recalls that such is common practice in economic theory, where the size of a country's economy is gauged by its gross domestic product.

events. However, Ulanowicz (1997) recognizes that the central concept in information theory remains "uncertainty" – a state of knowledge, not a state of nature. Nonetheless, the author prefers the term indeterminacy, which, accordingly, emphasizes the potential for causal openness in developing systems, such as ecosystems. He retains the term information, despite its heavy epistemic connotations, which hinges more upon the agency behind a change in probability than upon any subjective perception of that change. Thus, information refers to the effects of that which imparts order and pattern into a system.

Ulanowicz (1997) starts deriving a formula for the capacity of an ecosystem, for either information or indeterminacy. This capacity for either order or disorder he takes as a surrogate for the ecosystem's complexity, an otherwise ill-defined and controversial property of any system. The point is that the complexity of any system is generated by the number of combinations of possible "encounters", which in ecosystems theory translates into the possibility of pathways to material and energy flows.

Information theory, therefore, must contain clues as how to quantify constraint. It does not however, address information (constraint) directly. Rather, it uses as its starting point a measure of the rareness of an event, as defined by Boltzmann:

## $(eq. A5.1) h_j = -k \log p (B_j)$

Where  $p(B_j)$  is the marginal probability, a value between 0 and 1, that event  $B_j$  will happen, and k is a scalar constant that imparts dimensions to the measure. One notices that for rare events ( $p \approx 0$ ) this measure is very large, and for very common events ( $p\approx 1$ ), it is diminishing small. Roughly speaking,  $h_j$  is correlated with how surprised an observer will be when  $B_j$  occurs. The formula expresses that the potential for each configuration (as event  $B_j$ ) to contribute to the overall complexity is proportional to the negative logarithm of the probability that the configuration will occur.

Until this point, one is discussing how events can generate complexity in an ecosystem. The interest is to ask how to decide whether these events inform the system, i.e., contribute toward a particular ordered pattern, or whether they act to disrupt it by contributing to random, unpredictable behavior.

Constraint abrogates indeterminacy. That is, the indeterminacy of a system with constraints should be less than what it was in unconstrained circumstances. Supposing, for example, that an *a priori* event A<sub>i</sub> exerts some constraint upon whether or not B<sub>j</sub> subsequently occurs. The probability that B<sub>j</sub> will happen in the wake of A<sub>i</sub> is defined as the conditional probability p (B<sub>j</sub>|A<sub>i</sub>). Hence, the (presumably smaller) indeterminacy of B<sub>j</sub> under the influence of A<sub>i</sub> (call it h<sub>j</sub><sup>\*</sup>) will be measured by the Boltzmann formula as (Ulanowicz, 1998, 2000):

$$(eq. A5.2) h_j^* = -k \log p (B_j|A_i)$$

It follows that one may use the decrease in indeterminacy,  $(h_j-h_j^*)$ , as one measure of the intensity of the constraint that  $A_i$  exerts upon  $B_j$ . Whatever the mechanism, this change in probability assignment reduces the complexity of the system. Call this constant  $h_{ij}$ , where:

$$(eq. A5.3) h_{ij} = h_j \cdot h_j^* = [-k \log p(B_j)] \cdot [-k \log p(B_j|A_i)] = k \log [p(B_j|A_i)/p(B_j)]$$

One may use this measure of constraint between any arbitrary pair of events  $A_i$  and  $B_j$  to calculate the amount of constraint inherent in the system as a whole: one simply weights the mutual constraint of each pair of events by the associated joint probability, p ( $A_i$ ,  $B_j$ ), that the two will co-

occur, and then sums all over possible pairs. This yields the expression for the *average mutual constraint*, AMC, as (Ulanowicz, 1998, 2000):

$$(eq. A5.4) AMC = k \sum_{i,j} p(A_i, B_j) \log [(p(A_i, B_j))/((p(A_i)p(B_j)))]$$

We are seeking to quantify the factors that help to constrain flows along certain preferred pathways. In order to apply A to quantify constraint in ecosystems, it is required to estimate  $p(A_i, B_j)$  in terms of measurable quantities. To estimate the average constraint at work in the system as a whole, one weights each individual propensity by the joint probability of constrained flow from i to j and sums over all combinations:

$$p(A_i) \sim \sum_i T_{ij}/T$$
 and  $p(B_j) \sim \sum_i T_{ij}/T$ 

Thus, in terms of these measurable trophic exchanges, the estimated average mutual constraint (AMC) takes the following form (Ulanowicz, 1998, 2000):

$$(eq. A5.5) AMC = k \sum_{i,j} (T_{ij}/T) \log [T_{ij}T/(\sum_k T_{ik} \sum_l T_{lj})]$$

That is, the way to measure the constraints inherent in the entire network of ecosystems flows is to perform these calculations on the inputs and outputs around each compartment, weight the result for each compartment by the throughflow of that node, and average over the ensemble. Thus, we have a calculation that is inclusive of all constraints at work in the ecosystem.

One notes in the formula for AMC that the scalar constant, k, has been retained. Although autocatalysis is a unitary process, separate measures have been defined for its two attributes. One can easily rectify this disparity and combine the measures of both attributes simply by making the scalar constant k represent the level of system activity, T, that is, k is set equal to T, and the resulting product is called the system *ascendency*, A, where the dimensions of A will contain the units used to measure the exchanges. The ascendency expressed in terms of trophic exchanges becomes (Ulanowicz, 1998, 2000, 2005):

$$(eq. A5.6) A = \sum_{i,j} T_{ij} \log [T_{ij}T/(\sum_k T_{ik}\sum_l T_{lj})]$$

It measures both the size and the organizational status of the network of exchanges that occur in an ecosystem. Ulanowicz (2005) emphasizes that increasing ascendency in ecosystems is only half of the dynamic story. Ascendency accounts for how efficiently and coherently the system processes matter and energy. Using the same mathematics, one can compute as well an index called the system *overhead*,  $\phi$ , which is complementary to ascendency and quantifies the inefficiencies and incoherencies present in the system. It is expressed as:

$$(eq. A5.7) \phi = -\sum_{i,j} T_{ij} \log [T_{ij^2}/(\sum_k T_{ik} \sum_l T_{lj})]$$

The overhead,  $\phi$ , can be decomposed into four components representing the indeterminacies in the inputs, exports, dissipations, and internal connections (Ulanowicz, 2000).

The ascendency and the overhead together quantify the structured complexity of the system, X, which includes both organized and inchoate attributes (Ulanowicz, 1998):

# Annex 6 – Application of ecological indicators to the Mondego Estuary

In this annex, I will briefly describe the methods and results of the application of eco-exergy and ascendency as ecological indicators to the case of the Mondego estuary, in the coast of Portugal, as presented in the works of Marques *et al.* (1997), Jørgensen *et al.*, (2002), and Patrício *et al.* (2004).

The Mondego River drains a hydrological basin of approximately 6670 km<sup>2</sup>, on the western coast of Portugal. Urban wastewater is still discharged into the Mondego without treatment and the estuary supports industrial activities, desalination ponds, and aquaculture (Marques et al., 1997; Jørgensen et al., 2020). Additionally, the lower Mondego River valley has about 15,000 ha of farming fields (mainly rice paddies), with a significant loss of nutrients to the estuary. The Mondego estuary is located in a warm/temperate region with a basic Mediterranean temperate climate. It consists of two arms, north and south, as represented in figure A.10, borrowed from (Marques et al., 1997), and separated by an island. The two arms split in the estuarine upstream area about 7 km from the sea, and join again near the mouth. These two arms of the estuary present very different hydrographic characteristics (Marques et al., 1997; Patrício et al., 2004). The north arm is deeper (5-10 m during high tide, tidal range about 2-3 m), while the south arm (two to four m deep, during high tide) is almost filled with silt in the upstream areas, directing most of the freshwater through the north arm. The water circulation in the south arm is controlled by tidal circulation and the relatively small fresh water input from the tributary, the Pranto River, which is controlled by a sluice located 3 km from the confluence with the south arm of the estuary. Due to differences in depth, the tidal excursion is longer in the north arm, causing daily changes in salinity to be much stronger, whereas daily temperature changes are highest in the south arm (Marques et al., 1997, Jørgensen et al., 2020).



Figure A. 10 Representation of the Mondego estuary

Nutrient loading into the south arm of the estuary was estimated, assuming that the major discharge is through the Pranto River, from the Armazéns Channel (there is no freshwater discharge but, in each cycle, the tidal wave washes out the channel, where several industries discharge waste waters), and from the downstream communication of the south arm. The only way out of the system is the downstream communication (as can be seen in figure A.10). The nutrient inputs from the Pranto River and Armazéns Channel, and the exchanges (input vs. output) in the downstream communication of the south arm have been monitored from May 1993 to June 1994 (Jørgensen *et al.*, 2002). The

annual nitrogen loading to the south arm of the Mondego estuary was roughly estimated to 134 tons (126 tons of nitrate and 8 tons of nitrite), of which 14 tons are still in the system (18 tons of nitrate were imported and 4 tons of nitrite were exported) and 120 tons were transported to the sea. For phosphorus the loading was estimated to 14 tons (1 ton was imported to the system, while 15 tons were exported to the sea, which means that 14 tons were net released from the south arm of the estuary).

Seasonal intertidal macroalgae blooms (mainly of *Enteromorpha* species) have been reported in the south arm of the estuary for several years, and *Zostera noltii* (an macrophyte eelgrass) beds, which represent the richest habitat with regard to productivity and biodiversity, are being drastically reduced in the south arm of the Mondego estuary, presumably outcompeted by *Enteromorpha* (Marques *et al.*, 1997; Jørgensen *et al.*, 2002; Patrício *et al.*, 2004). In this estuary, the *Enteromorpha* dominant community, with the presence of *Cyathura carinata* (a common species of Isopoda in Portugal), mollusks and crustacean, shows often a crash at early summer due to oxygen depletion and is found where the salinity is not too low and the nutrient concentration is high. The *Zostera nolti* dominant community has the presence of oligochaeta and polychaeta (aquatic worms), mollusks and crustaceans, but mollusks are more abundant in this community than the other, and crustaceans are less abundant, and this ecosystem is found where the nutrient concentration is lower. From the ecological management point of view, the *Zostera noltii* dominant community is preferred, because the oxygen concentration is higher, because the water is clearer, and no crash due to anaerobic conditions (absence of oxygen) take place (Marques *et al.*, 1997; Patrício *et al.*, 2004).

This is an example of benthic eutrophication (nutrients enrichment in the benthic zone), showing how environmental factors often give origin to qualitative alterations in the ecosystems (e.g. species composition, biodiversity). Concerning the competition between macrophytes and macroalgae, nutrient enrichment tends apparently to favor the latter adaptive strategies (Marques *et al.*, 1997). This shift in primary producers may of course determine changes in species composition at other trophic levels, and through time such modifications may give origin to a selected new trophic structure (Marques *et al.*, 1997; Patrício *et al.*, 2004).

These authors did not use traditional models of aquatic ecosystems because they argue that they are not adequate to predict when qualitative changes, like shifts in species composition at various trophic levels, will take place. This is mostly due to the fact that measurements typically carried out to account for and to assess impacts over ecosystems (e.g. biomass and production measurements) are not able to capture the qualitative ongoing changes (Marques *et al.*, 1997). For instance, in aquatic ecosystems, the impact of eutrophication is not always expressed as an increase or decrease in production of biomass. Nonetheless, with structural dynamic models, it is possible to incorporate this type of changes. This new generation of models is able to include and describe changes in species composition and ecosystem trophic structure, and allows improving the existing models. This improvement not only concerns models' predictive capability, but their descriptive accuracy, yielding a better understanding of ecosystems behavior and, consequently, better environmental management (Jørgensen *et al.*, 2002).

Instead of using the most common modeling strategy - which consists in including more trophic levels and more types of organisms to represent each level -, the new models proposed by these authors use goal functions to represent/describe ecosystem's behavior and development, allowing in addition to save time and to bypass some of the problems by traditional models'

unmanageable complexity (Marques *et al.*, 1997; Jørgensen *et al.*, 2002).<sup>77</sup> The ecological goal functions used are mathematical algorithms that act as ecosystems quality indicators, constituting putative emergent properties arising from self-organization processes during their development. Marques *et al.* (1997) and Jørgensen *et al.* (2002) propose the exergy parameters as being one of the most promising approaches, showing a possible role in expressing shifts in species composition and trophic structure. Exergy is then assumed to become optimized during the development of ecosystems, which are supposed to self-organize towards a state of an optimal configuration of this property. Thus, exergy is used as an orientor to describe adaptation and changes in species composition.

Starting from the working hypothesis that it is the ecosystem structure with the highest exergy index among the possible ones that will prevail,<sup>78</sup> Jørgensen *et al.* (2002) develop two models, one for the *Enteromorpha* dominant community (ecosystem 1) and another one for the *Zostera* dominant community (ecosystem 2), using conceptual diagrams and STELLA software. The results are shown by means of two conceptual models, one for each community.<sup>79</sup> Ecosystem growth was described as a function of internal concentrations of nutrients, temperature, light and salinity. If the working hypothesis is correct, by comparing the models for the two types of ecosystems, the highest exergy under eutrophied and medium to high salinity conditions should be found for ecosystem (1), while the highest exergy should be found for ecosystem (2) under low nutrient and low salinity conditions.

The authors analyses the results of the calibration based upon the freshwater discharge and the oxygen depletion (for *Enteromorpha* only). The peak exergy value is approximately the same, namely about 11 300 g detritus equivalent/m<sup>2</sup> at maximum for the two models. The results are summarized in the figure A.11. Table A.1 gives the exergy and biomass peak results of the following simulations, being the respective figure and table adapted from (Jørgensen *et al.*, 2002):

A) The above mentioned calibration results with discharge of freshwater from day 213 to 365 with the peak at day 274. Phosphorus in the tide water is 670-700 mmol/ $m^3$  and in the freshwater 200 mmol/ $m^3$ .

B) The above mentioned calibration results with discharge of freshwater from day 0 to 152 with the peak at day 63. Phosphorus in the tide water is 670-700 mmol/ $m^3$  and in the freshwater 200 mmol/ $m^3$ .

C) The above mentioned calibration results with discharge of freshwater from day 0 to 152 with the peak at day. Phosphorus in the tide water is 670-700 mmol/ $m^3$  and in the freshwater 40 mmol/ $m^3$ .

D) The above mentioned calibration results with discharge of freshwater from day 0 to 365 with the peak at day 114. Totally, the annual discharge of freshwater is 3 times what it is in case A. Phosphorus in the tide water is  $670-700 \text{ mmol/m}^3$  and in the freshwater 40 mmol/m<sup>3</sup>.

<sup>&</sup>lt;sup>77</sup> In this case, the selection of other species and the selection of other food webs may be accounted by a change of model parameters according to an ecological goal function. This allows introducing in the models parameters that change as a function of changing forcing functions and conditions of state variables, optimizing by a stepwise approach the ability of the ecosystem to move away from thermodynamic equilibrium.
<sup>78</sup> As I have explained in section 3.2.2, exergy is utilized by an ecosystem to move further away from thermodynamic

<sup>&</sup>lt;sup>78</sup> As I have explained in section 3.2.2, exergy is utilized by an ecosystem to move further away from thermodynamic equilibrium, meaning that the ecosystem which gains a bigger surplus of eco-exergy will be able to use it for growth and development, in terms of increase in boundaries and biomass, network complexity and information storage. As a consequence, it will be the ecosystem structure that will prevail among the possible ones.

<sup>&</sup>lt;sup>79</sup> See the schemes in pp. 235-236.

E) The above mentioned calibration results with discharge of no freshwater. Phosphorus in the tide water is 670-700 mmol/m<sup>3</sup>.

Case	Description: µmol P/I	Exergy and plant biomass peak values				
		Discharge period	Zostera		Enteromorpha	
			Exergy	Pl. Bio.	Exergy	Pl. Bio.
A	200	213-365	11300	162	11300	318
B	200	0-152	11500	160	10500	248
С	40	0-152	11500	158	10300	233
D	40	0-365	11500	158	10300	235
E	No freshwater at all		11500	162	10200	318

<b>Table A.</b> I Exergy and plant blomass peak results for the different simulations in Mondego est
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b)

a)

(crmol),

(g detritus equivalents/m<sup>2</sup>)

crustacean

Figure A. 11 Density and exergy relative of the taxonomic groups for the different simulations in the Mondego estuary

The models show that if the fresh water with high concentration of nutrients (particularly nitrogen) is discharged during the last part of the year, as is often the case at present, Enteromorpha will be dominant. This bloom takes place because Enteromorpha grows faster, and it is too sensitive to low salinity and is dependent on the presence of phosphorous and nitrogen in the water column. If the freshwater with high concentration of nutrients (particularly nitrogen) is discharged during the last part of the year, as is often the case at present, Enteromorpha will be dominant. The eco-exergy

calculations show that the exergy is approximately the same for the two models, which may be interpreted as evidence that the initial value may be crucial for the final results. *Enteromorpha* has the highest initial concentration according to observations (Marques *et al.*, 1997) and the exergy is about the same. Therefore, the conditions corresponding to case A may lead to an *Enteromorpha* community. If we, however, shift the freshwater discharge to the beginning of the year, the exergy and the plant biomass of the *Zostera* community will hardly change (simulations B to D), while the exergy and biomass of the *Enteromorpha* will decrease significantly. The exergy and biomass of the *Enteromorpha* will decrease further if the phosphorus concentration in the freshwater is reduced, which could occur if a big amount of freshwater is discharged, since phosphorus is mainly produced in estuarine sediment (Jørgensen *et al.*, 2002). According to the models, a discharge of freshwater all year round does not change the exergy and biomass compared with the cases B to D significantly. The *Zostera* model is independent on the salinity and is not very dependent on the phosphorus concentration in the water column.

In summary, the results of the five simulations suggest that the ecological management of the freshwater discharge is a key factor for the prevailing of the two communities (*Enteromorpha*, *Zostera noltii*). From a management viewpoint, at least two possibilities can be considered: artificial control of the freshwater discharges through the use of sluices, increasing the discharge during the first part of the year; or reduction of the nutrient input from fresh water (and if possible also from tide water). The joint use of these two alternatives should give the *Zostera* dominated community better conditions.

Marques *et al.* (1997) analyze the spatial and temporal variation of eco-exergy, specific ecoexergy, species richness, and heterogeneity, in order to examine to what extent these ecological indicators would capture changes in benthic communities along the gradient of eutrophication. These authors, in their approach, try to understand the relationships between exergy and other more conventional ecological indicators, like biodiversity. And in practice, they try to estimate exergy values and make it operational as a goal function. The objective is to verify if the estimated exergy values are capable to elucidate the state of an ecosystem.

The benthic communities in the Mondego estuary were monitored during a yearly cycle, from February 1993 to February 1994. Samples of macrophytes, macroalgae, and associated macro-fauna were taken fortnightly at different sites, during low tide, along an estuarine gradient of eutrophication in the south arm of the estuary (see figure A.10), from a non eutrophicated zone, where the macrophytes community (Zostera noltii) is present, up to a heavily eutrophicated zone, in the inner areas of the estuary, from where the macrophytes disappeared while Enteromorpha blooms have been observed before. In this area, as a pattern, *Enteromorpha* biomass normally increases from early winter (February/March) up to July, when an algae crash usually occurs. A second but much less important algae biomass peak may normally be observed in September followed by a decrease up to the winter. Simultaneously, corresponding to each biological sample, the following environmental factors were determined: salinity (g l<sup>-1</sup>), temperature (°C), pH, oxygen dissolved, ammonia, silica, chlorophyll a, nitrites, nitrates, and phosphates (mg l<sup>-1</sup>), for the water, and organic matter contents (g m<sup>-2</sup> afdw), for the sediments. The organisms collected (macrophytes, macroalgae, and macroinvertebrates) were almost always identified to the species level, and their biomass determined (g  $m^{-2}$ afdw). The exergy was then estimated and an overview of the major taxonomic groups contributing to the exergy in this system is provided in table A.2, adapted from (Marques et al., 1997).

Marques *et al.* (1997) consider that, through time, the variation of exergy in an ecosystem may be considered as resulting from the variation in the biomass and of the information built in each unit of biomass.<sup>80</sup> If the total biomass in the system remains constant through time, then the variations of exergy will be only a function of the structural complexity of the biomass or, in other words, of the information embedded in the biomass. This parameter, was then called specific exergy (SpEx) by the authors, expresses as exergy by unit of biomass and, for each instant, specific exergy is given by:

$$(eq. A6.1)$$
 SpEx =  $Ex_{tot}/B_{tot}$ 

 $B_{tot}$  is the total biomass of the system and  $Ex_{tot}$  is the total exergy of the ecosystem.

Values of exergy and specific exergy were calculated from the biomass of the different organisms (g  $m^{-2}$  afdw) through the use of weighing factors enabling to discriminate different 'qualities' of biomass (as I have described in annex 3, see equation A3.20). For this purpose, taking into account the available set of weighing factors, data on organisms' biomass was pooled as a function of higher taxonomic levels (e.g. Phylum or Class).

 Table A. 2 Major contributors to the exergy in the Mondego estuary benthic communities along the gradient of eutrophication

Contributors	Non eutrophi- cated area	Intermediate eu- trophicated area	Eutrophicated area—before the algae crash	Eutrophicate area—after the algae crash
Enteromorpha	2.099	28.211	264.642	1.273
+ Ulva				
Other macroaal- gae	16.141	2.138	6.152	0.165
Z. nolti leafs	128.368	0.000	0.000	0.000
Z. nolti roots	87.975	0.000	0.000	0.000
Z. nolti-total	216.343	0.000	0.000	0.000
Anthozoa	0.003	0.000	0.000	0.000
Sipunculia	0.001	0.001	0.001	0.002
Nemertinea	0.005	0.003	0.005	0.001
Oligochaeta	0.128	0.031	0.010	0.002
Polychaeta	1.254	0.709	0.569	0.846
Mollusca	63.950	14.192	31.195	13.240
Crustacea	1.3720	1.088	14.945	3.419
Insecta	0.007	0.006	0.009	0.001
Echinodermata	0.000	0.000	0.000	0.000
Pisces	0.000	0.006	0.034	0.000

lajor contributors to the exergy i	n the Mondego estuary	benthic communities along th	e gradient of eutrophication
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For the non eutrophicated and intermediate eutrophicated areas, the average anual biomass (g m<sup>-2</sup>) of each is given. For the eutrophicated area, the average biomass (g m<sup>-2</sup>) of each group before and after the algae crash is given.

Regarding biodiversity, the authors took into consideration species richness and heterogeneity (species richness and evenness – the number of individuals for each species). For each date the measurements were effectuated taking into account data on the number of individuals (ind m<sup>-2</sup>) per species, and on species biomass (g m<sup>-2</sup> afdw). In both cases, only the macro-fauna was taken into consideration. Marques *et al.* (1997) considered the use of Margalef index (I) the most adequate to compute species richness, and the Shannon-Wienner's index (H'), based on information theory, the best to compute heterogeneity:

## $(eq. A6.2) I = (n-1)/log_e N$

Where n is the number of species found and N is the total number of individuals, and:

<sup>&</sup>lt;sup>80</sup> According to equations A3.19 and A3.20, exergy in an ecosystem depends on the total biomass and on the information that individual organisms carries in their organic constitution.

# (eq. A6.3) $H' = -\sum_{i=1}^{n} p_i \log p_i$

Where n is the number of species, and  $p_i$  is the proportion of the biomass of species i in a community where the species proportions are  $p_1, p_2, ..., p_i, ..., p_n$ .

The spatial and temporal variation of exergy, specific exergy, species richness and heterogeneity were then analyzed in order to test the hypothesis that these ecological indicators would capture changes in benthic communities along the gradient of eutrophication, providing a similar picture of the ecosystem.

With regard to eco-exergy, as hypothesized, values were consistently higher in the Zostera noltii community than in the eutrophicated areas. Also, eco-exergy values were higher in the most heavily eutrophicated area when compared with the intermediate eutrophicated area, especially during spring and early summer. This was related to the intensity of the *Enteromorpha* bloom, which gave rise to much higher values for total biomass in the most eutrophicated area. Specific eco-exergy was found to be consistently higher in the Zostera noltii community than in the eutrophicated areas until late spring when the picture changed completely and values became higher in the eutrophicated areas. This was due to a macroalgae crash in the eutrophicated areas, which determined not only a drastic reduction of the total biomass but also a change from a primary production-based situation toward a detritus-based food web. Therefore, since total biomass values after late spring consisted basically of animals (consumers), primary deposit feeders and detritus feeders (e.g., annelid worms and crustaceans), it is clear that the abrupt increase of specific eco-exergy in the eutrophicated areas after the algae crash do not reflect any augmentation of the structural complexity of the community, but simply the different quality of the biomass involved in the calculations.

Regarding the *Zostera* community (data from after July 6), accounting for the primary producers and the consumers, specific exergy is lower than in the eutrophicated areas. But if accounting only for the consumers, it is higher, following the same pattern from before the algae crash. Hence, specific eco-exergy may shift very drastically as a function of yearly dynamics, providing a spatial and temporal picture that may not be related with the long-term evolution and integrity of the system.

With regard to biodiversity, the variation of species richness and of heterogeneity (species richness + evenness) along the gradient of eutrophication provided quite a different picture. Through time, species richness was consistently higher in the *Zostera* community, decreasing along the gradient of eutrophication. On the contrary, heterogeneity was always higher in the eutrophicated areas, except for the decrease observed in the most heavily eutrophicated area after an algae crash. The observed spatial variation of heterogeneity is due to the fact that the Shannon-Wienner's index integrates two components, the number of species (species richness), and their relative abundance (evenness). Therefore, although species richness decreased as a function of increasing eutrophication, as the authors expected, the dominance of a few species (e.g., *Hydrobia ulvae*, a detritus feeder and epiphytic grazer gastropod, and *Cerastoderma edule*, a filter feeder bivalve) in the *Zostera* community, probably due to the abundance of nutritional resources, decreased species evenness and consequently heterogeneity values. In the latter case, the authors argue, lower values of heterogeneity must be interpreted as expressing higher biological activity (production of biomass), and not as a result of environmental stress.

Taking into account the yearly data series for each site along the eutrophication gradient (noneutrophicated, intermediate eutrophicated, eutrophicated), eco-exergy and specific eco-exergy were significantly correlated providing a similar picture of the ecosystem. Values were consistently higher and more stable in the non-eutrophicated area. The comparison of yearly data series showed that using eco-exergy values it was possible to distinguish between the three situations considered, even though differences between the intermediate and eutrophicated areas were not significant, which suggests that eco-exergy, an extensive function, might be more sensitive to detect subtle differences.

Species richness and eco-exergy were significantly correlated, following a similar pattern, both decreasing from non-eutrophicated areas (see figure A.12b). On the contrary, heterogeneity and eco-exergy appeared negatively correlated (although not significantly), providing a totally distinct picture of the benthic communities along the eutrophication gradient (see figure A.12a). For each situation, respectively, non-eutrophicated (ZC), intermediate eutrophicated (INT), and eutrophicated (EUT), we indicate the average values and the standard deviation, taking into account the entire yearly data set. The spatial variation of exergy and specific exergy was significantly correlated (r = 0.59; P <0.5). The spatial variation of heterogeneity was not significantly correlated with either exergy or specific exergy (r=0.48 and r = 0.38, respectively; P<0.5). The figure is from Marques *et al.* (1997):



Figure A. 12 Variation of exergy and specific exergy in comparison with heterogeneity and species richness along the gradient of eutrophication gradient in the Mondego estuary.

This obviously resulted from the properties of the heterogeneity measure, as explained above. Similar results were obtained comparing the patterns of variation of species richness, heterogeneity and

specific eco-exergy. Species richness and specific eco-exergy appeared clearly positively correlated (figure A.12b), while the patterns of variation of heterogeneity and specific eco-exergy showed to be distinct (figure A.12a). Moreover, from the comparison of yearly data series, heterogeneity values were not significantly different in the intermediately eutrophicated and eutrophicated areas and therefore did not permit to discriminate relatively subtle differences.

The hypothesis that eco-exergy and biodiversity would follow the same trends in space and time was then validated with regard to species richness, but not for heterogeneity. Actually, eco-exergy, specific eco-exergy, and species richness responded as hypothesized by the authors, decreasing from non-eutrophicated to eutrophicated areas, but heterogeneity responded in the opposite way, showing the lowest values in the non-eutrophicated area. Their range of variation (eco-exergy and specific eco-exergy) through time was smaller in the non-eutrophic area, expressing a more stable situation, while the magnitude of the variations was stronger in the other two areas, but especially in the intermediate eutrophic area. On the other hand, both ecoexergy and species richness were able to grade situations presenting relatively subtle differences, but specific ecoexergy and heterogeneity appeared to be less sensitive. Although biodiversity may be considered as an important property of ecosystem structure, the relative subjectivity of its measurements and their interpretation constitutes an obvious problem, according to the authors.

Patrício et al. (2004) also try to define quantitatively the process of eutrophication, using an index that combines the attributes of system activity level and community structure. According to these authors, eutrophication can be described in terms of network attributes as any increase in system ascendency (due to a nutrient enrichment), causing a rise in the total system throughput that more than compensates for a concomitant fall in the average mutual information.<sup>81</sup> As they argue, this particular combination of changes in variables allows one to distinguish between instances of simple enrichment and cases of undesirable eutrophication. The aim of the study was to test whether the network formulation of eutrophication properly tracks changes in community structure along a known gradient of eutrophication in the south arm of the Mondego estuary. Three sampling stations representative of the non-eutrophic, of the intermediate eutrophic and of the strongly eutrophic areas were chosen. Estuarine food webs were constructed at the three sites and these quantified food webs were examined using network analysis. The whole information indices were calculated as I described in annex 5, and the authors added redundancy (the degree to which pathways parallel each other in a network), the specific overhead of the system<sup>82</sup> (which measures the total flexibility of the system on a per-unitflow-basis), and the Finn cycling index (which reveals the proportion of the total system throughput devoted to the recycling of carbon). It was then possible to characterize the trophic status of the three estuarine systems (table from Patrício et al., 2004):

<sup>&</sup>lt;sup>81</sup> This compensation is due to the fact that ascendency is the resulting product between average mutual information (or average mutual constraint) and the total system throughput. See annex 5.
<sup>82</sup> That is, the authors obtained the specific overhead dividing the overhead of the ecosystem, which measures the total

<sup>&</sup>lt;sup>82</sup> That is, the authors obtained the specific overhead dividing the overhead of the ecosystem, which measures the total flexibility of the ecosystem (see equation A5.7), by the total system throughput (TST), obtaining a measure of this flexibility on a per-unit-flow-basis.
Table A. 3 Network analysis ecosystems indices for the three different areas of eutrophication in the Mondego estuary

Information indices	Non-eutrophic area	Intermediate eutrophic area	Strongly eutrophic area
Total system throughput (g AFDW $m^{-2} y^{-1}$ )	10852	1155	2612
Development capacity (g AFDW $m^{-2} y^{-1}$ ; bits)	39 126	5695	10831
Ascendency (%)	42.3	30.4	36.7
Overhead on imports (%)	12.3	8.2	6.2
Overhead on exports (%)	1.3	1.5	2.5
Dissipative overhead (%)	17.7	22.1	19.9
Redundancy (%)	26.4	37.8	34.6
Average mutual information (bits)	1.52	1.50	1.52
$\Phi/\mathrm{TST}$	2.08	3.43	2.62
Connectance indices			
Overall connectance	1.67	2.43	2.1
Intercompartmental connectance	2.41	3.57	2.63
Finn cycling index	5.75E-02	0.2045	0.1946
Total number of cycles	74 517	15009	9164

Although the three habitats are clearly distinct in physical appearance, network analyses revealed both differences and similarities among their trophic structures that had not been apparent at first glance. It was possible to observe that the *Zostera*-dominated community had the highest total system throughput (TST), followed (unexpectedly) by the strongly eutrophic system, and finally by the intermediate eutrophic area. The development capacity was highest in the *Zostera* beds and lowest in the intermediately eutrophic area. This index differed significantly among the three areas. Due to the logarithmic nature of this index, small differences can represent appreciable disparities in structure. The average mutual information (AMI) was slightly higher in the non-eutrophic area, followed closely by the eutrophic area, and was lowest in the intermediate eutrophic area.

Concerning ascendency, it increased in order from the intermediate eutrophic to the heavily eutrophic zone to the *Zostera* beds, while redundancy increases in the opposite direction. The long-term study of the Mondego estuary indicated that years of low precipitation tended to be associated with reductions in turnover rates and increases in water column stability, temperature, salinity and light penetration. These changes in habitat conditions encouraged blooms of macroalgae that gradually replaced the resident macrophytes (Marques *et al.*, 1997). In the intermediate and strongly eutrophic areas, primary production is largely the result of these macro-algal blooms. Production appears as a strong pulse during this specific time, but remains at very low levels during the rest of the year. This limited temporal interval of primary production results in a significantly lower figure for the cumulative annual primary production and TST in these areas as compared with the corresponding measures in the *Zostera* beds. Comparing the AMI values of the flow structure for the three areas, it is possible to discern a very small decrease in the measure among the three zones, suggesting that, as trophic structure is concerned, these areas are indeed different. The three zones appear nevertheless much more distinct by eye than is illustrated by the AMI values.

In light of these results, the network definition of eutrophication appears to be inappropriate for the Mondego estuarine ecosystem. It would be more accurate to describe the enrichment processes occurring in this ecosystem as "pulse eutrophication." This process could be characterized as a disturbance to system ascendency in the form of an intermittent supply of excess nutrients that, when coupled with a combination of physical factors (e.g., salinity, precipitation, temperature, etc.), causes both a decrease in system activity and a drop in the average mutual information of the flow structure. Even though a significant rise in the TST occurs during the period of the algal bloom and at that time there is a strong increase of the system ascendency, the annual picture nevertheless suggests that the other components of the intermediate and strongly eutrophic communities were unable to accommodate the pulse in production. The overall result was a decrease in the annual value of the TST and, as a consequence, of the annual ascendency as well. Regarding the results of the trophic analysis, the *Zostera* community has one more trophic level than those counted in the strongly eutrophic chain, implying that this community possesses a more complex web with additional top consumers. At the same time, the *Zostera* community exhibits lower transfer efficiency at the first trophic level, probably because the production of *Zostera* meadows usually cannot be eaten directly, but needs to be decomposed first, the authors argue. Concerning the analysis of cycled materials, the overall percentage of cycled matter increases as the degree of eutrophication rises, which is indicated by the Finn cycling index.