

Chapter 17

Ecometrics: A Trait-Based Approach to Paleoclimate and Paleoenvironmental Reconstruction

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Abstract Ecometrics is a trait-based approach to study ecosystem variability through time. An ecometric value is derived from describing the distribution of functional traits at the community level, which may arise by environmental filtering, extinction, or convergence. An ecometric relationship describes the correspondence between spatially explicit ecometric values and corresponding environmental variation. Transfer functions and maximum likelihood approaches have been developed with modern trait-environment relationships to reconstruct paleotemperature, paleoprecipitation, and paleovegetation cover given the distribution of functional traits within a community. Because the focus for this approach is on the traits and not on species, it is transferable through space and time and can be used to compare novel communities. In this paper we review the concepts and history of ecometric analysis and then describe practical methods for implementing an ecometric study.

Keywords Functional morphology • Paleoecology
Maximum likelihood • Geographic distribution • Taxon-free

Summary

One of the factors that sort species geographically into communities is the filtering of species by their functional morphologies along climate and environmental gradients (e.g., mammalian herbivores with higher molars eat more gritty and abrasive vegetation and therefore more species with higher molars live in places with more gritty and abrasive vegetation), thus, the morphology has a direct relationship with its environmental condition. In this sorting process, the distribution of functional traits within a community moves toward an optimal environmental condition. These functional traits may be described in terms of their distributions within a community and descriptors of the distribution of community level functional traits have been defined as ecometrics (Eronen et al. 2010a; Polly et al. 2011). Thus, ecometrics are traits described at the community level that have a relationship with environmental condition. Ecometrics are spatially variable, because the composition of species and traits in communities vary through geography. If species are perfectly sorted, the trait distributions in communities will parallel variation in the environmental condition to which the traits are functionally linked (i.e., the ecometric correlation equals one). If the ecometric correlation is strong, one can estimate the most likely environmental condition given a specific ecometric value using a transfer function or likelihood estimation. If the ecometric correlation is not strong, one may still be able to estimate the most likely environmental condition, but the likelihood surface would be more flat, which would produce a more ambiguous reconstruction. The power of this approach is that functional trait measurements are transferable through space and through time, regardless of the specific species that make up the community. For this reason, ecometrics is a useful approach to reconstruct paleoclimate and paleoenvironment (Damuth et al. 1992).

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Terms

Functional trait: a behavioral, biochemical, morphological, phenological, physiological, or structural characteristic that has a physical or chemical interaction with a specific environmental factor. This characteristic is expressed as a phenotype of individual organisms and it is considered relevant to the response of organisms to the surrounding abiotic conditions. A functional trait is something that can be observed and measured.

Geographic sorting: the process by which trait distributions are arranged in geographic space along gradients of environmental conditions.

Taxon free: not depending on taxonomic identity (i.e., it is a descriptor based on trait values rather than on presence or absence of particular taxa). For example, using palms as indicators of frost-free conditions is a taxon-based approach, whereas using counts of stomatal density as indicators of carbon dioxide concentration is a taxon-free approach (Beerling et al. 2011).

Ecometric value: a statistic summarizing the distribution of a functional trait within a community at a single geographic location. Means, variances, proportions, and extremes have been used as descriptors in previous studies; however, any parameter that describes a distribution of functional traits may be used.

Ecometric patterning: geography, or spatial variation, of ecometric values across communities. Perfect patterning represents optimal distributions of populations and species. The lack of patterning could represent a lack of useable covariation, a mismatch between the trait and the environment, or it could result from the inappropriate choice of environmental correlates.

Ecometric correlation: product-moment correlation between ecometric variation and variation in the environmental condition. High correlations evince a close match between the functional requirements of local communities and their abiotic condition.

Ecometric likelihood: the probability of finding a particular environmental condition given the ecometric value of a community at any single geographic location.

Ecometric load: the amount of mismatch between the distribution of functional traits and the selective optimum for the local environment. High loads may indicate risk to changing environmental conditions. Note that high ecometric loads can be present even with high ecometric correlations if traits are weakly but consistently sorted.

Ecometric optimum: the optimal distribution of an ecometric trait in a particular environment. The optimum is more likely to be a distribution rather than a single trait value, especially in locally heterogeneous environments (e.g., a savannah habitat favors both large and small body sizes).

Transfer function: a function that represents the relationship between the ecometric trait values and a relevant environmental variable.

Theoretical and Historical Background

Functional traits are features that organisms use to interact with their environment and with other organisms (Diaz and Cabido 2001; Violle et al. 2007). Functional traits of species within a community ultimately mediate the relationship between organisms' morphology and their ecology and link organisms to biotic and abiotic conditions present at particular geographic locations at a particular point in time (Ricklefs and Travis 1980; Chapin 1993; Poff 1997). A certain combination of biotic and abiotic conditions will thus favor traits that maximize an organism's performance, either through natural selection or geographic sorting. Natural selection is an evolutionary process that acts on the variation in a population, where individuals that thrive in their environment produce the most offspring and disproportionately share their traits with the next generation (Darwin and Wallace 1858). Species that move geographically in response to environmental change may follow an environment for which they are already adapted and form new assemblages as a result (Jackson and Overpeck 2000). We are not concerned with the trait values of particular species, but with the distribution of traits within communities (e.g., mean, standard deviation, and range; Damuth et al. 1992). Even weak sorting processes can produce trait gradients at the community level, as has been demonstrated in climate gradients in plant leaf traits (Wolfe 1979; Reich et al. 1997; Wilf 1997; Wright et al. 2004; Royer et al. 2005; Wing et al. 2005; Cornwell and Ackerly 2009; Peppe et al. 2011), large mammalian herbivores dental traits (Janis and Fortelius 1988; Damuth et al. 1992; Fortelius et al. 2002; Mendoza et al. 2005; Damuth and Janis 2011; Eronen et al. 2010b, 2012), carnivoran locomotor traits (Polly 2010), snake locomotor traits (Lawing et al. 2012), and mammal life history, physiological, and range traits (Lawing et al. 2017). The study of functional traits that have a relationship with climate or environmental gradients at the community level has been termed ecometrics to distinguish it from ecomorphology of particular species or clades (Eronen et al. 2010a; Polly et al. 2011). Figure 17.1 shows a few examples of the morphology of ecometric traits.

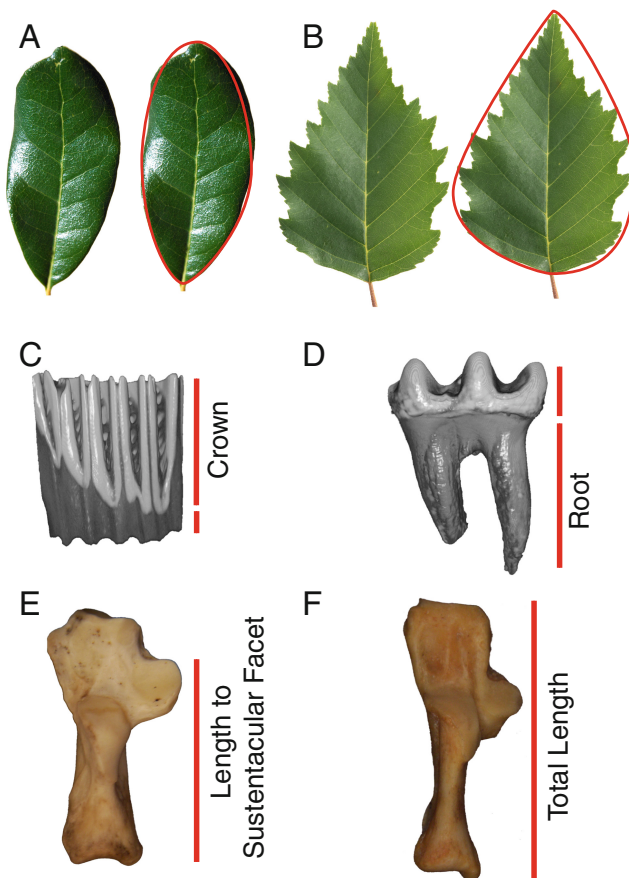


Fig. 17.1 A, Example of an entire leaf margin from a live oak leaf modified from an image by Jeremy Stovall. The leaf margin is entire when its margin is not punctuated. An easy way to determine if the margin is entire or to quantify the entirety of the margin is to overlay the image of the leaf with an oval, as is depicted in the figure with the red outline. Entire leaf margins are characteristic of hotter environments. B, Example of a non-entire leaf margin from a dwarf birch modified from an image by Fox Valley. Non-entire leaf margins are characteristic of cooler environments. C, Example of hypsodonty in a rodent modified from Tapaltsyan et al. (2015). Hypsodonty is measured by the crown to root ratio. Hypsodont rodents are grazers and are characteristic of arid environments with more gritty vegetation. D, Example of brachyodonty in a rodent modified from Tapaltsyan et al. (2015). Brachyodont rodents are browsers and are found in more wet environments with mixed vegetation. E, Example of a calcaneum from a raccoon modified from an image on boneid.net. Gear ratio is measured on the calcaneum and is the ratio of the length of the sustentacular facet to the total length of the calcaneum. The gear ratio for the raccoon is typical of a plantigrade animal and is characteristic for animals living in high vegetation cover (e.g., dense woodlands). F, Example of a calcaneum from a panther modified from an image on boneid.net. The gear ratio in the panther is typical of a digitigrade animal and is characteristic of animals that are adapted to run through open habitats

The relationship between the distribution of functional traits in a community and the corresponding environmental factors in the local environment is likely to be complex. Some trait-environment relationships favor a single ecometric optimum in each local environment such that all species tend to have the same trait value. Stomatal density on plant leaves

might be expected to have a single optimal value across all members of a community because carbon dioxide concentrations and evapotranspiration conditions are the same for all. However, locally heterogeneous environments are likely to favor a heterogeneous ecometric optimum. For example, savannah environments tend to favor a combination of large body masses (for animals that can travel long distances to procure food in a comparatively resource poor habitat and defend themselves in the open) and small body masses (for species that can subsist on the resources found in a limited area and can find cover in grasses or tree tops). The nature of the ecometric optimum will dictate how it should be measured. An optimum that favors a single trait value can always be adequately represented with the community mean, but an optimum that favors a complex distribution may be better characterized by variance, skewness, or other measure. Temporal variation in environmental conditions may also shape the distribution of the ecometric optimum. For example, Žliobaitė et al. (2016) recently showed that recurring extreme conditions (like drought) were better predictors of dental traits in Kenyan herbivores than average conditions, indicating that recurring limiting conditions may be important drivers of community functional trait distributions.

Historical Background

Bailey and Sinnott (1915) conducted the first study of community-level functional traits. They showed plant communities that have more leaves with ridges, or non-entire margins, occur in moist temperate climates that experience warm summers and cold winters. Conversely, plant communities that have leaves with no ridges, or entire leaf margins, occur in dry climates including tropic, alpine and arctic regions, moors, steppes, deserts, saline situations, and other physiologically dry climates. They used the proportion of species within a community with a specified phenotype as their metric to describe the community, what we refer to as an ecometric trait value.

Since Bailey and Sinnott (1915) demonstrated the variation in community leaf shape across a temperature gradient, researchers have used leaf shape and other traits to reconstruct paleotemperature. Most notably, Wolfe (1979, 1993) quantified the relationship between leaf margins and temperature, which led to many quantitative paleoclimate reconstructions from leaf assemblages, called leaf-margin analysis (e.g., Wilf 1997; Greenwood et al. 2004; Yang et al. 2007). Contemporary to and since Wolfe's work, researchers have been interested in identifying the function of leaf teeth (see Royer and Wilf (2006) for a history and discussion).

The ecometric approach has grown out of the formalization by Damuth et al. (1992) of "taxon-free" characterizations of

animal communities. These authors were interested in understanding long-term evolutionary and ecological processes. They argued that distributions of traits such as body size, dietary type, locomotor specialization, and predator-to-prey ratios serve as descriptive indices that can be used to compare important aspects of community function in the Paleozoic, Mesozoic, and Cenozoic or between faunal and floral realms in a single time period, because they capture information about productivity, resource availability, community physiognomy, and resource partitioning, comparisons that cannot be made if community function is characterized by the species that dominate it (such as grassland communities). They noted that what makes an approach “taxon-free” is the focus on distributions of traits for inferring paleoenvironment (i.e., the ecometric distributions), not the inferential pathways that lead to the understanding of the trait-environment relationship, which may be founded on taxon-based observations. The fact that many traits have a limited phylogenetic distribution (e.g., teeth are limited to vertebrates, leaf stomata are limited to plants) means that taxon-free approaches, including ecometrics, are not completely free of time, place, and taxon, but comparisons between communities that have no species in common are nevertheless possible. Andrews and Hixson (2014) recently reviewed and critiqued taxon-free approaches.

Ecometric Examples

One of the best-understood ecometrics is the molar crown height of herbivorous large mammals. Different diets vary in the amount of wear they produce: species that eat abrasive or tough foods, or foods of poor nutritive quality, usually have hypsodont teeth, which have a high crown relative to the root. Hypsodonty is a morphology adapted to high rates of tooth wear (Janis and Fortelius 1988). Proximal factors including abrasiveness of plant material, such as phytolith content and ambient grit and dust, are therefore likely to play a role in selection for tooth crown height (Janis and Fortelius 1988; Strömberg et al. 2013; Fortelius et al. 2014). Tooth crown height correlates with precipitation in the modern world and geologic past (Fortelius et al. 2002; Eronen et al. 2010a, b; Fortelius et al. 2014). Eronen et al. (2010b) used regression trees to show that there is a strong correlation (65.8%) between crown tooth height and regional precipitation, between diet and precipitation (66.5%), and when diet and tooth crown height are combined (74.2%). Community hypsodonty levels, therefore, have a strong correlation with annual precipitation, which affects both plant tissue properties and the amount of local grit (Fortelius et al. 2014) and may be used as a paleoprecipitation proxy that constrain regional details about vegetation patterns and climate models (Fortelius et al. 2002).

Together with other dental traits, hypsodonty can additionally be used to estimate more indirect properties like net

primary productivity (Liu et al. 2012) or more proximate ones like production of volcanic ash (Strömberg et al. 2013). Such complex combinations of proximal and distal environmental factors are likely to be associated with all ecometric traits (Polly and Head 2015). Žliobaitė et al. (2016) showed that dental traits are closely linked to vegetation greenness (normalized difference vegetation index [NDVI]) in addition to precipitation and temperature. This is reassuring as net primary productivity (NPP) estimates used in Liu et al. (2012) are computed using precipitation as an input and are highly dependent on it. NDVI is a direct observation of vegetation greenness and is independent of precipitation and temperature measurements. The NDVI depends on climatic conditions and reflects NPP and thus the availability and quality of herbivores' food. Using data from present-day seasonal environments in Africa, Žliobaitė et al. (2016) demonstrate that the dental traits show strong correlations to non-availability of preferred plant foods (e.g., during dry seasons or longer dry periods), rather than the properties of average foods consumed. This is the main functional link between climate and herbivore teeth and closely follows the suggestion by Owen-Smith (2002) (see also discussion in Liu et al. 2012 and Fortelius et al. 2014).

Other dental characteristics (such as dental wear patterns, dental structure, and tooth crown complexity) have also been used as estimates of diet in mammals (Fortelius and Solounias 2000; Evans et al. 2007; Eronen et al. 2010a; Wilson et al. 2012; Evans 2013; Saarinen 2014; Saarinen and Kärme 2017). Wilson et al. (2012) used the dental shape descriptor of orientation patch count (OPC), which is a measure of dental occlusal complexity that correlates well with feeding ecology in extant mammals, to determine the paleodiet of the extinct mammalian clade Multituberculata. They were able to identify a shift from a more carnivorous or omnivorous diet among early multituberculates into a more herbivorous diet around 85 million years ago. This shift coincided with the rise of angiosperms. Since vegetation patterns are driven by climatic conditions, these other dental characteristics could potentially be used as climatic proxies. Evans (2013) reviewed dental shape descriptors, which can be used in ecometric studies and will be useful for describing environmental conditions in the past.

Another well-studied trait in both endothermic and ectothermic vertebrates is body size, initiated by the work of Bergmann (1847). Mean body size in non-flying mammals has been shown to increase as temperature decreases, and therefore mean body size increases geographically toward the poles (Rodríguez et al. 2008; Eronen et al. 2010a). It has also been documented in ectothermic animals that body size is positively correlated with mean ambient temperature (Makarieva et al. 2005). This has allowed for the use of ectothermic animals, to be used to estimate paleotemperatures (Head et al. 2009; Polly et al. 2011; Head et al. 2013).

Table 17.1 Examples of ecometrics in plants, birds, mammals, and snakes. Environmental conditions are mean annual temperature (MAT), annual precipitation (AP), atmospheric carbon dioxide (pCO₂), net primary productivity (NPP), trophic position (TP), dietary classification (DC), and vegetation cover (VC)

Group	Functional Trait	Environmental Condition	Citation
Plants	Leaf margin	MAT	Wolfe (1979)
Plants	Leaf shape	MAT	Wolfe (1990), Royer et al. (2005), Peppe et al. (2011)
Plants	Stomata counts	pCO ₂	Beerling et al. (2002)
Birds	Body mass	MAT	Meiri and Dayan (2003)
Mammals	Body mass	MAT	Damuth et al. (1992)
Mammals	Tooth morphology	AP; TP; DC; NPP	Evans (2013)
Ungulates	Hypsodonty	AP	Fortelius et al. (2002)
Carnivorans	Limb proportion	VC; MAT; AP	Polly (2010)
Snakes	Body length	MAT	Head et al. (2009)
Snakes	Tail proportion	VC	Lawing et al. (2012)

Examples of ecometrics in plants, birds, mammals, and snakes are detailed in Table 17.1, showing the functional trait and the environmental condition for which it is related.

Ecometric Patterning

Geographic sorting of traits along environmental gradients is one of three processes by which ecometric patterning can emerge, along with evolutionary adaptation and extinction (Polly and Head 2015). Environmental gradients are shown to filter species geographically (Belmaker and Jetz 2012). The filtering effects of environmental gradients may sort species geographically by their traits, resulting in local communities with similar trait values that are correlated with local environmental conditions. The ecometric approach was formalized as a way of synthesizing data from the ecological present and geological past to measure responses of ecosystems to climate change in order to better predict the risks posed by global change over the next millennia (Eronen et al. 2010a; Polly et al. 2011). It has been used to investigate the impacts and risk of extinction (Wilson et al. 2012; Polly and Sarwar 2014; Polly and Head 2015) and to understand non-ecological processes (Lawing et al. 2017). The relative roles of geographic sorting, local adaptation, and extinction have been investigated by process-based simulation (Polly and Head 2015). Ecometrics and its paleontological precursors have been used to estimate paleobiotic conditions using traits (Damuth et al. 1992). For example, ectotherm body size (Head et al. 2009, 2013) and leaf shape (Wolfe 1993; Little et al. 2010) have been used as paleothermometers and tooth crown height, hypsodonty, has been used to estimate paleoaridity (Fortelius et al. 2002).

The ecometric approach may be used to forecast community responses to anthropogenic climate change (Barnosky et al. 2017). The concept of ecometric load, which is the mismatch between community-level functional trait

values and optimal performance, potentially allows us to estimate the vulnerability of a community to climate or environmental change when the optimal performance of the traits along an environmental gradient is known (Polly and Head 2015). If changing conditions increase the ecometric load, communities are more likely to become vulnerable.

Methods for using ecometrics to characterize paleoclimate and paleoenvironments have been expanded extensively. For example, Head et al. (2009) made a significant push forward on the construction of ecometric models and the application of the transfer function. Instead of solely using correlative models for inference, they used a mechanistic model from the physiology of poikilothermic metabolism along with modern observations of boid snakes and the temperatures they live in to predict paleotemperature at 58–60 Ma (Paleocene) in the neotropics. They found a minimum mean annual temperature of 30–34°C was needed in the Cerrejon Formation in Colombia during this time in order for the large boid, *Titanoboa*, to survive. This is several degrees warmer than the mean annual temperature of 26–27°C found in that area of the world.

The effects of faunal sampling, extinction, and extirpation on ecometric patterns were investigated by Polly and Sarwar (2014) using resampling and rarefaction methods with calcaneum gear ratios. Gear ratios are related to the locomotor style of an animal and, in turn, related to the animal's habitat (see also Curran 2018). Polly and Sarwar (2014) showed that extinction, extirpation, and range change have minimal effects on ecometric correlations when they affect less than a quarter of the species in North American carnivoran communities. If the correlation between gear ratio and an environmental variable, such as vegetation cover, is either high or low, then extinction of more than 25% of species will alter the correlations, but the strongly and weakly correlated environmental variables will still be distinguished. Local extinctions, extirpation, caused a decline in ecometric correlations; however, up to 75% of species could be lost this

way before ecometric patterns were completely lost. This result suggested that even in fossil faunal assemblages with a small proportion of the total fauna, the ecometric patterns may still be recoverable if enough independent assemblages are considered. These authors also showed that global extinction and large-scale extirpation have a less predictable effect on ecometric correlations than do local extinctions. How the ecometric pattern is affected by global extinction depends on which organisms go extinct and what their ecometric correlation was. So, if a species, such as a polar bear, is a large contributor to local ecometric means, and if its range is correlated to an extreme of the environmental variable, such as zero vegetation cover, then its extinction could drive correlation up or down dependent on the circumstance.

Ecometric Modeling

Polly et al. (2016a) used stochastic modeling to assess the role of population level processes in the formation of ecometric patterns. They systematically varied parameters like local selection intensity, probability of dispersal, probability of extirpation, gene flow, and ancestral trait value to understand the interaction between geographic sorting processes, trait selection, and clade dynamics in producing ecometric patterns. These authors introduced the concept of ecometric load, an analogy with genetic or mutational load, as the mismatch between the distribution of functional traits in a community (or a group of communities) and the selective optimum for those traits in the local environment (Polly et al. 2016a). In cases where ecometric load can be measured, it may help predict whether environmental change is likely to make a community more vulnerable to reorganization or extinction. Interestingly, their models frequently produced parallel trait evolution in different clades, rather than the kinds of phylogenetically correlated trait distributions that are observed in many clades. For example, calcaneum gear ratio, which has strong ecometric sorting in the real world, also has a strong phylogenetic correlation with about 60% of its variance being explained by phylogeny (Polly et al. 2017). The lack of phylogenetic correlation in the models suggested that empirically observed examples of trait-based phylogenetic sorting of species into communities in the modern world results from large-scale turnover in environments.

Ecometrics and Ecogeographical Rules

Ecogeographical rules often describe patterns that we would classify as ecometric. Ecogeographic rules are hypotheses about how morphological variation changes along environmental or

geographic gradients. They may be rules regarding within-species variation or between-species variation. Across species variation has been the most important component of variation to consider for the ecometric approach.

The most notable ecogeographic rule is Bergmann's Rule (Bergmann 1847; Blackburn et al. 1999). It states that body mass correlates with temperature and this has been demonstrated both intraspecifically (Ashton 2002; Freckleton et al. 2003) and interspecifically (Blackburn and Hawkins 2004; Diniz-Filho et al. 2007). Other ecogeographical rules include Allen's rule (length of appendages in endotherms positively correlate with temperature; Allen 1877), Gloger's rule (pigmentation is correlated with humidity within endothermic species; Gloger 1833), Fox's rule (among small Australian mammals during community assembly, it is more likely that species entering a community will represent different functional groups; Fox 1987) and Jordan's rule (there is an inverse relationship between meristic characters and water temperature; Lincoln and Clark 1982). See Gaston et al. (2008) for a review of ecogeographic rules.

Implementing and Ecometric Analysis

In order to document the existence of an ecometric pattern, three types of data are required: geographic ranges of species, abiotic conditions, and functional trait measurement of species. The spatial resolution of the data and the density of sampling of traits and environmental variables within local communities will depend on the scale of the functional relationship and on the question being addressed. Here we focus on ecometric patterns that emerge at regional, continental, or global scales, but the same principles could be applied to patterns that emerge on landscape scales. To simplify large-scale analysis, we recommend measuring trait distributions by sampling the trait once for each species making up the local community and making the assumption that each species has the same trait value everywhere it occurs. Finer scale analyses might benefit from sampling the frequencies of traits among the individuals in a local community to account for variation in abundance of the species making up the community, or from measuring the local values of traits within each community. Because of our choice of scale, our analysis requires information about the geographic range where species are known to live or where they have the potential to live. For our purposes, local community composition includes all the species whose ranges overlap at a sampling point, an assumption that is reasonable for coarse scale analysis, but which might be unreasonable for a finer-scale landscape analysis.

Geographic Range

Geographic range data are often available from field guides and are becoming more readily available online as spatial shapefiles. For example, NatureServe (www.natureserve.org) and International Union for Conservation of Nature host a website that has an option to download spatial data that depict the ranges of species as polygons (www.iucnredlist.org). The ranges are typically drawn by experts and represent the general areas of occupation of a species. Species occurrences may be used to draw range maps, if no range maps are available, so long as the occurrence data are relatively randomly distributed across the entire environmental range of the species. Once the geographic ranges are obtained, a sampling scheme for measuring the trait-environment relationship needs to be determined. Sampling sites may be systematically or randomly scattered across the extent of the study area. A list of species that occur at each sample site should then be compiled. Some sources of data for geographic ranges include the NatureServe and IUCN for mammals, birds, amphibians, coral and some fishes (www.natureserve.org, www.iucnredlist.org). Plant distribution data for North America and Europe are available from USDA PLANTS database (plants.usda.gov) and from the European Environmental Agency (eea.europa.eu). The Global Biodiversity Information Facility contains species occurrences (longitude and latitude) of both plants and animals (www.gbif.org). A geographic information system (GIS) is useful to work with geographic ranges and other geographic information. Open source systems are available, such as QGIS, DIVA, or even R. Proprietary software is also available; the most popular products are developed through ESRI. Researchers should check with their institutions for GIS services and licensing.

Environmental Data

Environmental factors can be measured directly in the field at sample sites or collected from maps representing the geographic variability of the environmental condition. For every sample site, the environmental variables that are functionally linked to the trait of interest should be sampled. PRISM Climate Group and WorldClim databases provide relatively high-resolution datasets of climate for the globe (www.prism.oregonstate.edu and www.worldclim.org). Global potential vegetation is available from UW SAGE (www.washington.edu/research/tools/sage/); global historical vegetation coverage is available from Oak Ridge National Laboratories (<https://doi.org/10.3334/ornl daac/419>); global digital elevation models and annual productivity are available from NASA (earthobservatory.nasa.gov/) and USGS (nationalmap.gov/

elevation.html); global soil distributions are available from International Institute for Applied Systems Analysis (www.iiasa.ac.at/); global land cover is available from the European Space Agency (www.esa.int/); global nitrogen deposition is available from Oak Ridge National Laboratory (www.ornl.gov); global freeze and thaw status is available from the National Snow and Ice Data Center (nsidc.org/); global terrestrial ecosystems are available from World Wildlife Fund (www.worldwildlife.org). In addition to all of these data sources, there are numerous others to find online and in the published literature. One may use any reliable map as a reference for the environmental condition at sample localities.

Functional Traits

Functional traits, such as body size, locomotor strategy, dentition, or shape, should be measured or categorized for each species that has the functional trait of interest within each community. Ideally, one would measure the traits from all the species that occur at each sampling location; however, a species value may be used for all of the locations in which that species occurs. Species values for traits may be collected from measuring specimens directly or from obtaining measurements from the published literature. Typically only one value for each species is necessary; however, if there is strong geographic variation, the analysis can include species values that are geographically explicit. If the functional trait is variable within species to the extent that it causes performance differences, then individuals should be sorted along the environmental gradient, but if that variation does not cause performance differences with respect to the environmental gradient, then it is reasonable to ignore the within species variation. The functional traits may be continuous (e.g., size, shape, or ratios of morphological elements) or categorical (e.g., locomotor strategy, substrate use, or dentition type) in nature.

The equipment necessary for collecting the measurements of functional traits greatly varies depending on the trait of interest. One may collect trait data from published literature, and thus, no equipment is necessary. If measurements are taken directly from specimens, the researcher might want to photograph specimens or use calipers to take direct measurements from specimens. If photographs are taken to investigate specimens, the orientation of the camera and the orientation of the specimen should be consistent for all photographs and photos should include a scale. For classifications or counts, no equipment is necessary, unless the researcher requires magnification. For geometric morphometrics, a camera and scale bar, a 3D scanner, or other digitizing equipment is necessary.

Data Analysis

For each sample site, a list of the relevant species that co-occur there must be assembled. The distribution of functional traits in the community members can then be measured. For the remaining examples, we will use the trait mean to summarize that distribution, but other distributional statistics such as variation, standard deviation, range, or median may be appropriate depending on the expected relationship between the trait and its associated environmental parameter. It is useful to assemble data from all sampling sites into a table with the mean trait values and the associated environmental values in columns and sites in the rows. If there is more than one environmental variable associated with the trait of interest, then in this table each variable requires its own column. Ecometric correlation can easily be calculated from this table as the Pearson's correlation coefficient (r), or a nonparametric equivalent, of the two columns as a measure of correspondence between the environmental parameter and the ecometric trait. If the performance relationship between trait and environment is known, the ecometric load can be calculated as the mean absolute difference between the observed trait means and the expected values for all rows in the table (i.e., the residual between the observed and expected values). Note that ecometric load is largely independent of the ecometric correlation, except insofar that a weak correlation requires at least some mismatch between performance optimum and realized trait mean and thus cannot have a load of zero (Polly et al. 2016a). Ecometric patterns with strong correlations can also have strong loads. Establish a transfer function to determine the specific relationship between the two variables (i.e., it estimates function coefficients). If there are fossil localities to estimate past abiotic conditions, then apply the transfer function to the mean of the functional traits measured from the fossils at a single fossil site. Calculate confidence limits for the estimated abiotic condition.

Ecometric estimates of paleoenvironment can be made from a regression-based transfer function or from a likelihood distribution of environmental values given an observed ecometric value. If regression-based methods are used, reduced major axis (RMA) regression may be the most appropriate if there is uncertainty in the independent variable. Transfer functions are prediction equations derived from regressing the environmental variable of interest onto the predictive trait value. Different transfer functions are used depending on the type of trait variable and the type of environmental variable. Other considerations include the type of predicted relationship between the trait and environment and the statistical fitting procedures.

Transfer functions have been typically calibrated with modern distributions of species and their functional traits.

For optimal use of the transfer function, for both reconstructing abiotic condition and tracking trait distributions through time, the functional trait should be either directly fossilizable or able to be estimated from fossil specimens. For example, hypsodonty may be estimated directly from fossil specimens (Fortelius et al. 2002) and body size may be accurately estimated from fragmentary skeletal and dental remains (Alexander 1989; MacFadden 1990).

Strengths of Approach

Econometrics allows us to quantify the dynamic relationships between organisms and their environment. Arguably, the primary strength is that ecometric traits are predictable and transferable through space and time. Since econometrics uses taxon-free descriptors of community characteristics, it allows for the comparison of community changes in the modern world to those in deep time (Eronen et al. 2010a; Polly et al. 2011). The species that make up the community in the modern world do not need to be the same as those that make up the paleocommunity; the only thing the two communities need to share is the functional trait under study. Because econometrics focuses on traits that are directly related to environmental conditions, it can be applied to questions across geographic and temporal scales (Wolfe 1994; Weiher et al. 1998; Thompson et al. 2001; Fortelius et al. 2002). Some examples of questions include how have environmental conditions changed in the past, what are the past rates of change in environmental conditions, how were specific environmental conditions distributed across a landscape, how do communities assemble and why are there consistent trait distributions across communities of very different taxonomic composition, what drives diversity gradients and do they change through time, and how does extinction impact traits distributions. The quality of crossing spatial and temporal scales allows econometrics to be applied from local to global community levels and for the comparison of ecometric patterning across scales. In addition, many ecometric traits are easily measured on both animal and plant fossils (Alexander 1989; MacFadden 1990; Fortelius et al. 2002; Royer et al. 2005; Head et al. 2009), so we can begin to integrate across different depositional environmental and data types.

Biases and Shortcomings

The incomplete nature of the fossil record may influence the quality of data in ecometric studies. However, Polly and Sarwar (2014) showed that even if only 25% of the species of a community are found in a fossil locality, the ecometric patterns still appear. Taphonomic issues with the fossil

preservation should also be taken into account, because the functional traits used in ecometric studies need to be measurable or inferred from the fossil remains. It has often not been the case where this is an issue (Alexander 1989; MacFadden 1990; Fortelius et al. 2002; Royer et al. 2005; Head et al. 2009; Peppe et al. 2011; Wilson et al. 2012) and there are various ways to remove the taphonomic influence from the fossil, thus returning it, or a model of it, to its original state (i.e., retrodeformation methods; Webster and Hughes 1999; Angielczyk and Sheets 2007).

Several important assumptions are made with the ecometric approach, including, that the ecometric relationship doesn't change through time and that the full range of morphologies and environmental conditions are represented (i.e., they are not truncated – there are no biased extinctions and only analogous climate conditions). If these are reasonable assumptions for the ecometric trait in question, one may use an ecometric relationship to reconstruct paleoclimate and paleoenvironment, given a couple more assumptions about the fossil localities. The community of fossils within the fossil localities being studied should represent the actual community of species that co-occurred with the depositional environment. In addition, the functional traits should be measurable in the preserved fossils. More work is needed to quantify coefficients describing the relationship between functional traits and environmental conditions to understand if and how they change through time and space.

More research needs to be done concerning intraspecific variation. Intraspecific variation, at least in regards to carnivorous calcaneum gear ratios, is high, and it does not follow community level ecometric patterning. Models seem to support the idea that this is possible due to the high level of gene flow within populations, but the overall signal at the community level overshadows the intraspecific variation of the populations.

Ecometrics Example

In this section we provide an example of how mean annual temperature can be estimated from the distribution of body masses in North American mammals using a likelihood approach. In addition to presenting the method, we also discuss the theory for why ecometric distributions are related to local environment and how our methodology is related to that theory.

When the relationship between trait performance and environment is known, the likelihood function can, in theory, be determined *a priori* (Arnold 1983). Performance-environment relationships can sometimes be estimated for traits recovered in fossils using tools such as finite element analysis, hydrodynamic or mechanical principles, or

functional morphological experimentation (e.g., Baumiller et al. 1991; Rayfield 2007; Wroe 2008; Shino and Suzuki 2011; Stayton 2011; Polly et al. 2016b). However, in many cases the performance-environment relationship is unknown, even when the trait-function relationship is well understood. For example, the functional role of hind-limb gear ratio of mammals is understood (it is related through physical lever principles to the efficiency of hind limb extension, and thus to the mechanics of walking, springing, climbing, and running), but its distribution in a particular environment is difficult to predict *a priori* because it is likely to be influenced by a combination of factors such as vegetation physiognomy, terrain ruggedness, substrate, snow cover, and predator-prey interactions (Klein et al. 1987; Polly 2008, 2010; Crête and Larivière 2003). In such cases, likelihoods can be estimated directly from empirical data by making the assumption that the distribution of traits in modern communities is close enough to equilibrium to be representative. Polly and Sarwar (2014) found this to be a reasonable assumption for carnivore limb ratios, but care should be taken before generalizing that result to other traits.

Likelihoods for paleoenvironmental parameters can be estimated empirically by projecting environmental variables into an ecometric space, which is a mathematical space whose axes are statistical descriptors of the distribution of traits in local communities (Fig. 17.2A). Ecometric space is in some ways the conceptual opposite of Hutchinson's (1957) niche space, in which a species' niche is the volume it occupies in a multidimensional space whose axes are environmental variables. Translated into ecometric terms, the niche of a species is circumscribed by the performance of the functional traits that relate it to the environmental factors. An ecometric space inverts that relationship by mapping the distribution of environmental parameters on trait-based axes, except that those axes describe the distribution of traits in community assemblages rather than the traits of a single species. Figure 17.2A shows mean annual temperature mapped into an ecometric space whose axes are defined by the distribution of log body mass (kg) of mammals.

To create this ecometric space we sampled mammal faunas at 50 km intervals across the entirety of North America. At each sampling point we calculated the mean and standard deviation of the body masses (kg) of the local mammals from the data compiled by Smith et al. (2003) and we recorded the local mean annual temperature (MAT) from Hijmans et al. (2005).

Estimating the likelihood of MAT from community trait characteristics is then a three-step process. First, the trait data should be binned so that a frequency distribution of the environmental variable can be calculated. The number of bins is arbitrary, but it should be coarse enough to encompass a reasonable number of communities in the densest areas of the trait space, yet fine enough to be biologically

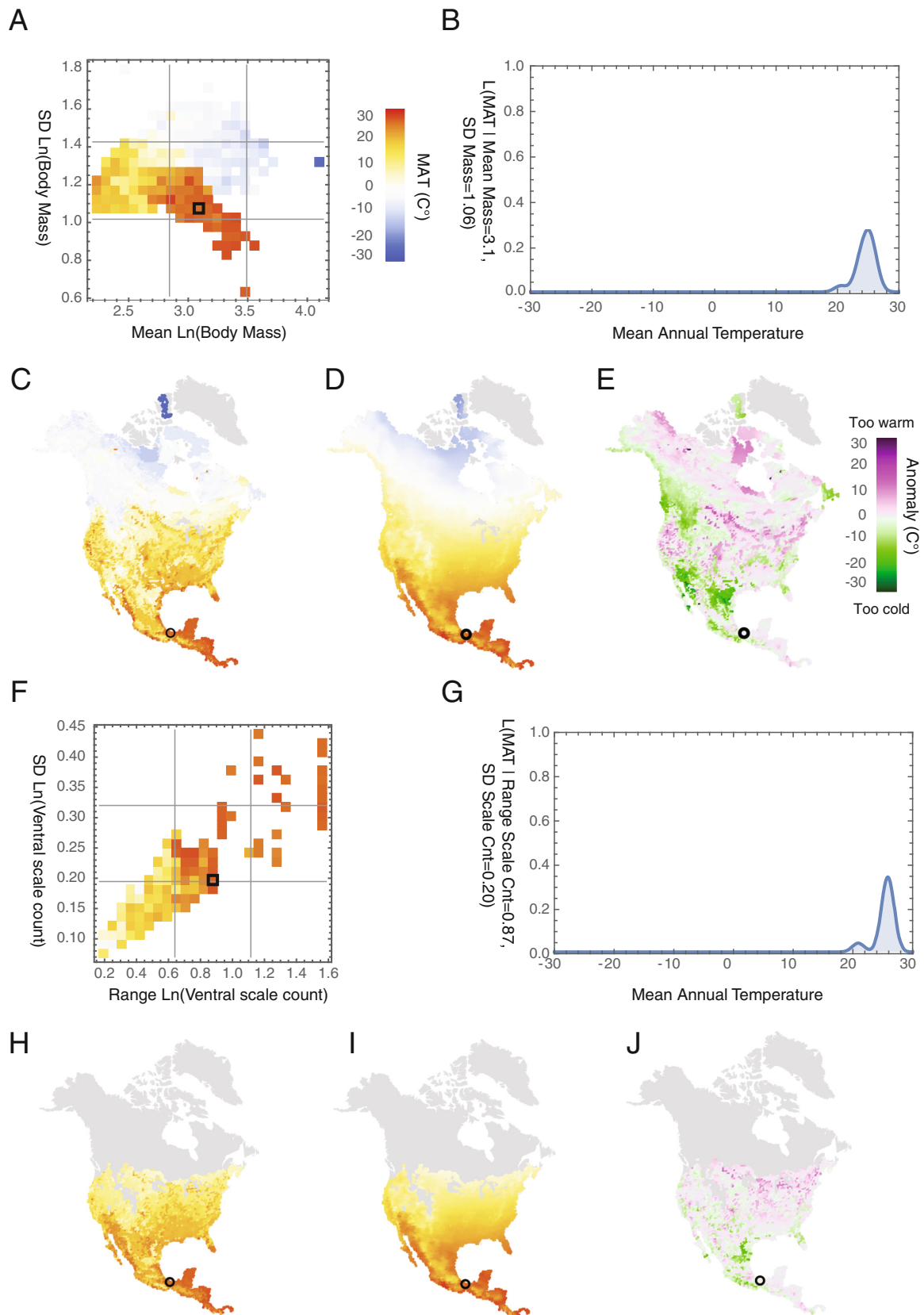


Fig. 17.2 A, Ecometric space for community-level mammalian body mass showing the maximum likelihood estimation of mean annual temperature (MAT) for each bin. B, Likelihood function for MAT based on mammal body mass at the point in Central America highlighted by the black circles in C–E. C, MAT estimated from mammalian body mass. D, Observed MAT. E, anomaly between estimated and observed MAT. F, Ecometric space for snake body size showing the maximum likelihood estimate for MAT in each bin. G, Likelihood function for MAT at the same point in Central America based on snake size. H, MAT estimated from combined mammalian body mass and snake size. I, Observed MAT. J, Anomaly between combined estimate and observed MAT

meaningful. The ideal bin size would be about as wide as the standard errors of the means and standard deviations in the bin. We divided our ecometric space into 625 bins (25×25).

Second, the MAT observations in each trait bin were themselves binned to tabulate their frequency distribution. The number of temperature bins is also arbitrary (we used a bin size of 1°C). Once binned, a discrete probability density function (PDF) can be estimated by dividing the bin counts by the total number of observations. A continuous PDF can also be fit to the frequency data. Figure 17.2B shows a continuous PDF for temperature in communities with a mean \ln body mass between 3.05 (21.11 kg) and 3.13 (22.87 kg) and a standard deviation between 1.05 and 1.10 (black box in Fig. 17.2A) based on a Gaussian kernel density estimate with bandwidth of 1°C .

With these pieces in place, a maximum likelihood estimate of the environmental variable (MAT) can be made by measuring the trait (body mass) mean and standard deviation at a site of interest and then finding the environmental value that maximizes the PDF. The maximum likelihood estimates of MAT for all the sampling locations in North America are shown in Fig. 17.2C, compared with the real MAT values in Fig. 17.2D. This estimate (MAT at sampling locations) is reasonable, but tends to be too low in high elevation areas and too warm at lower elevations (see anomaly map in Fig. 17.2E). On average, the discrepancy between the real MAT and the estimate based on mammal body masses was 3.9°C , which serves as an approximate standard error (but one that is probably underestimated because the likelihood functions were estimated from the same data on which they were tested).

One of the primary advantages of using likelihood and ecometric spaces is that the likelihoods of alternative reconstructions can be compared. For example, the maximum likelihood estimate of MAT for the Central American location highlighted by the black circles in Fig. 17.2C–E is 24.95°C with $L(24.95) = 0.274$ derived from the PDF for that location (Fig. 17.2B). The real MAT is 25.3°C , which has $L(25.3) = 0.265$, which is clearly much more plausible with a likelihood ratio of 0.967 than an MAT of 20°C , where $L(20.0) = 0.024$ produces a likelihood ratio of only 0.088. This approach can be developed into a formal likelihood ratio test of alternative hypotheses about paleoenvironment, and it can be combined with prior probabilities from independent paleoenvironmental proxies into a Bayesian framework (Polly and Head 2015).

The second advantage of the likelihood approach is that incommensurable traits can be combined. Mammalian body mass distributions were fairly good predictors of MAT, as might be expected by extrapolating Bergmann's rule, which postulates that subspecies in colder climates will have larger body mass than their conspecifics elsewhere (Bergmann

1847; Scholander 1955; Mayr 1963), to the level of species and communities. However, homeothermic mammals are well-insulated from climate and their body size may not be as good predictors of MAT as that of ectotherms (Head et al. 2009). Because large ectothermic animals require warm ambient temperatures to sustain their growth rate, the size range of species in hot climates is expected to be greater than in cold climates (Makarieva et al. 2005). Using a dataset of ventral scale count as a proxy for size assembled by Lawing et al. (2012), we repeated the likelihood estimation for MAT in North America using the range of log scale count and its standard deviation as the dimensions of the ecometric space (Fig. 17.2F). These two parameters are both measures of dispersion and are therefore correlated, yet pick out different aspects of the distribution of body size in local communities. These data yield a similar likelihood function for the site in Central America, but with a narrower peak of predicted MAT (Fig. 17.2G). Because the likelihood functions are probabilities, they can be combined by multiplying them and renormalizing so that the area under them is 1.0. The resulting function gives the likelihood of MAT given the distribution of body masses in mammals and the distribution of ventral scale counts in snakes. This combined likelihood function provides a better estimate of temperature than either trait does alone (Fig. 17.2H–J). The mean anomaly between estimated and real temperature based on the combined estimate is only 2.4°C , much better than with mammals alone. Sacrificed is the ability to estimate MAT in the northern part of the continent where the climate is too cold for snakes to live.

A fully worked ecometrics example and R code is documented in Appendix I.

Future Prospects

Several aspects of ecometrics need to be addressed with future research. These areas include—intraspecific variation (but see Polly et al. 2017 for a recent example), abundance, phylogenetics, combining multiple ecometrics, conservation, and ecosystem services. Polly et al. (2016a) took first steps to identify and define a theory of ecogeography, moving from pattern to process with ecometric modeling. They used modeling to simulate the effects of changing microevolutionary processes on the ecometric patterning seen at the community level. As this area of interest progresses, eventually we hope to be able to observe ecometric patterns and determine which microevolutionary and macroevolutionary processes caused the patterns we see.

Another future development in the field of ecometrics is the prospect of marine ecometrics (Wallin 1991; Yasuhara et al. 2015). Due to the depositional environments found in marine systems, marine fossils are the majority of fossils found

(Sepkoski 1978). Marine fossils are often used in isotopic studies to reconstruct paleoecology (Bowen 1964; Anderson and Arthur 1983; Krantz et al. 1987; Wefer and Berger 1991; Rodrigues et al. 2014; Huyghe et al. 2015; Reich et al. 2015). The changes in isotopic fractionation may follow geographical gradients similar to an ecometric (Marchais et al. 2013; Lynch-Stieglitz et al. 2015; Mackenzie et al. 2014; Beard et al. 2015). However, the isotopic fractionation process is not a morphological trait, it is a metabolic functional trait, and as such, follows different biological, physical, and chemical rules.

New advances in remote sensing capabilities could alter the accuracy of our estimates of both species geographic ranges and the environmental condition in which they occur. Remote sensing appears like it will be quite useful when studying changes in plant community structures over large geographic regions. It allows for a level of detail in which single plants are recognizable across regional scales (Jones and Vaughan 2010).

Geometric morphometrics will also allow for the study of ecometrics when a particular functional trait changes size across age, but doesn't change shape (or vice versa). New advances will also allow for 3D modeling of functional traits. This may allow for the identification of aspects of the morphology that are better ecometrics than those being used. It can also allow for better ecometrics since we will no longer be using linear or volumetric measurements, but instead use the full 3D shape. Recent work by Polly (2010) and Wilson et al. (2012) has shown that this is a viable avenue of future inquiry.

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Appendix 17.1. Ecometrics Workflow and R Code

This section demonstrates an ecometric modeling workflow using the R Statistical Programming Language. To demonstrate these models in R, we will work with spatial data. There are special functions in two packages, *raster* and *sp*, that allow for relatively quick processing of spatial information (Bivand et al. 2013; Hijmans 2015; Pebesma and Bivand 2005). We will use climate data from the worldclim database (Hijmans et al. 2005) and we will use trait data body mass and hypsodonty from the PanTHERIA database (Jones et al. 2009) and from Eronen et al. (2010b). The code below can be typed directly into an R console or can be

entered into an R script file. A bold word indicates that the word is a function. To start the analysis, load the two required libraries. If they are not installed yet on your computer, install them with the function `install.packages()`.

```
library(raster)
## Loading required package: sp
library(sp)
```

Load the sampling locations and look at the first six rows of data with the functions `read.csv()` and `head()`. The first function `read.csv()` is a wrapper for another function called `read.table()`, which can be used in place of `read.csv()`, if the data are in tab delimited format. Use the `help()` function to see the documentation associated with each function.

```
points <- read.csv("data/SamplingPoints.csv")
head(points)
## GLOBALID Longitude Latitude
## 1 103148 -42.1727 83.26264
## 2 103149 -38.3442 83.26264
## 3 103150 -34.5156 83.26264
## 4 103151 -30.6871 83.26264
## 5 103152 -26.8586 83.26264
## 6 103235 -79.4690 82.81348
```

Plot the sampling locations with the function `plot()` to visualize the geographic distribution of the sampling locations. In this example, we use 50 km equidistant points sampled across North America (Fig. 17.A1). These are the same points used in Polly (2010).

```
plot(points[,2:3], col = "gray", pch = 16)
```

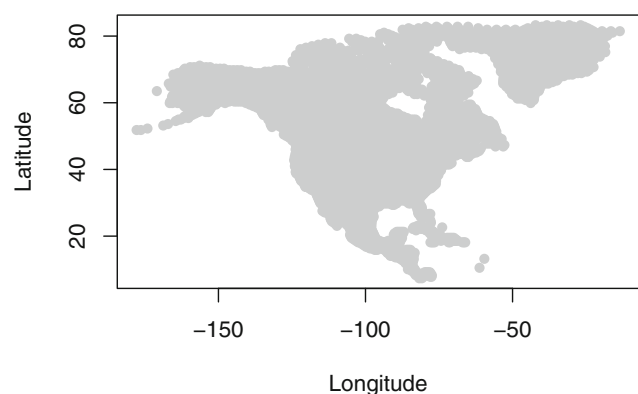


Fig. 17.A1 An example of output in the R Statistical Programming Language from calling the `plot` function for plotting the latitude and longitude of 50 km equidistant points sampled from across North America

Download raster climate data from the worldclim database using the `getData()` function from the package `raster` that we loaded with the `library()` function (Hijmans et al. 2005; Hijmans 2015). In this example, we download the 10-minute resolution, but if you would like to try a higher resolution data set, then change the argument named `res` to 2.5 or 0.5. Extract the temperature and precipitation for each sampling location using the `extract()` function.

```
bioclim <- getData("worldclim", down-
load = T, path = "data", var = "bio", res = 10)
```

Extract the temperature for each sampling location.

```
temperature <- extract(bioclim[[1]], points[,2:3])
```

Calculate the temperature range for all the sampling localities to make a plot of the temperature. We add one to the range to make the range equal to index values that we can use to subset the color function. The R language starts the subset of data at an index value of 1.

Calculate the color value associated with each temperature value and the temperature values associated with even breaks to assign legend values. Figure 17.A2 is a map of the mean annual temperatures.

```
temp_range <- 1 + max(temperature, na.rm = T) -
min(temperature, na.rm = T)
colfunc_temp <- colorRampPalette(c(
"darkblue", "blue", "gray", "yellow",
"red"))(temp_range)[1 + temperature - min
(temperature, na.rm = T)]
```

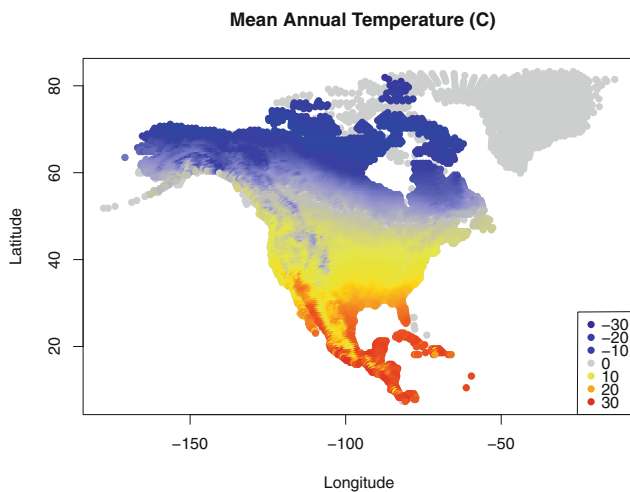


Fig. 17.A2 A heat map of the mean annual temperature (°C), where the hotter colors represent warmer places and cooler colors represent colder places

```
h <- hist(temperature, breaks = 5)
plot(points[,2:3], col = colfunc_temp,
pch = 16, main = "Mean Annual Temperature
(C)")
legend("bottomright", legend = h
$breaks/10, pch = 16, col =
colorRampPalette(c("darkblue", "blue", "gray",
"yellow", "red"))(length(h$breaks)))
```

Extract the precipitation for each sampling locality.

```
precipitation <- extract(bioclim[[12]], points
[,2:3])
```

Calculate the precipitation range for all the sampling localities to make a plot of the precipitation. Also, calculate color value associated with each precipitation value and the precipitation values associated with even breaks to assign legend values. Figure 17.A3 is a map of the precipitation values.

```
precip_range <- 1 + max(log(precipitation),
na.rm = T) - min(log(precipitation), na.rm = T)
colfunc_pr <- colorRampPalette(c("brown", "green"))
(precip_range)[1 + log(precipitation) -
min(log(precipitation), na.rm = T)]
h <- hist(log(precipitation), breaks = 5)
plot(points[,2:3], col = col-
func_pr, pch = 16, main = "Precipitation (mm)")
legend(-36.25, 60.5, legend = round(exp(h$breaks)),
pch = 16, col =
colorRampPalette(c("brown", "green"))(length
(h$breaks)))
```

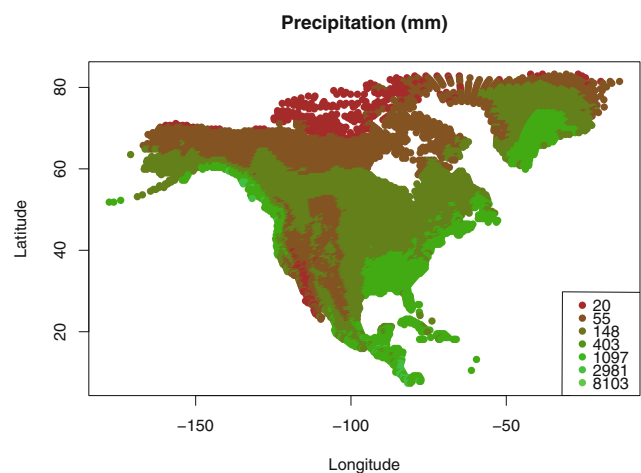


Fig. 17.A3 A heat map of the annual precipitation (mm), where greener colors represent wetter places and browner colors represent drier places

Compile the climate variables into a new data.frame called `climate`. Remove the variables that are taking up memory with the `rm()` function if your memory is getting sluggish.

```
climate <- cbind(points, temperature, precipitation)
#rm(bioclim, temperature, precipitation, points)
```

Visually check the climate variables for normality and if they are not mostly normally distributed, transform them for normality (Fig. 17.A4).

```
head(climate)
## GLOBALID Longitude Latitude temperature precipi-
tation
## 1 103148 -42.1727 83.26264 -169 139
## 2 103149 -38.3442 83.26264 -170 141
## 3 103150 -34.5156 83.26264 -175 149
## 4 103151 -30.6871 83.26264 -185 166
## 5 103152 -26.8586 83.26264 -180 139
## 6 103235 -79.4690 82.81348 -207 90
```

```
hist(climate[,4], main = "", xlab = "Mean Annual
Temperature", col = "gray")
```

Temperature appears to be reasonably normally distributed, so now we check precipitation (Fig. 17.A4).

```
hist(climate[,5], main = "", xlab = "Annual Precipita-
tion", col = "gray")
```

Precipitation appears to be log distributed (Fig. 17.A5). We log transform this variable to get it closer to normality (Fig. 17.A6).

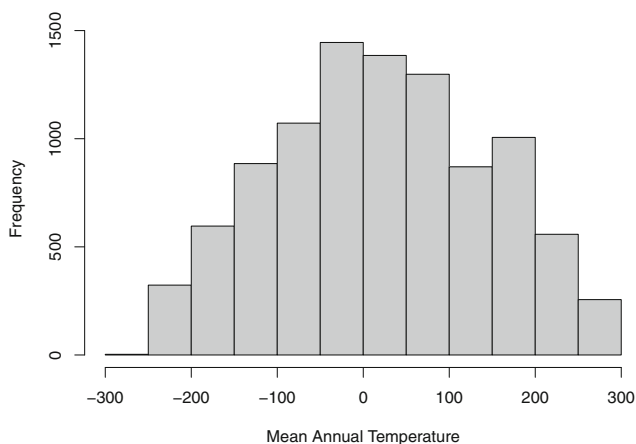


Fig. 17.A4 A histogram of the mean annual temperature ($^{\circ}\text{C} \times 10$) of all of the sampling locations

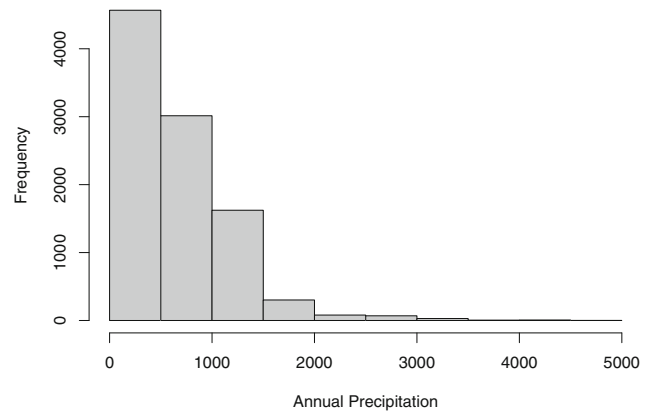


Fig. 17.A5 A histogram of annual precipitation (mm) of all the sampling locations

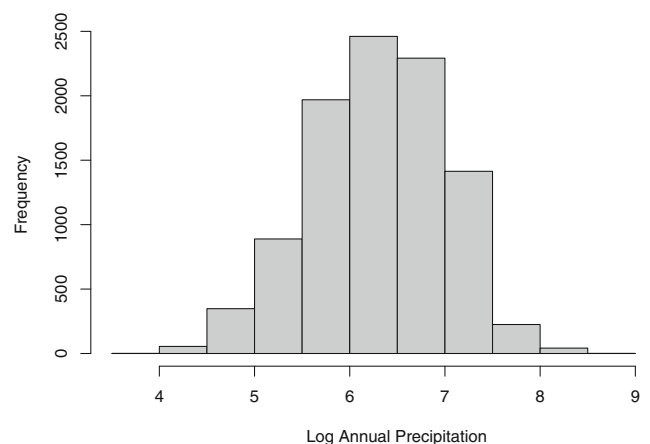


Fig. 17.A6 A histogram of log annual precipitation (mm) of all sampling locations

```
climate[,5] <- log(climate[,5])
hist(climate[,5], main = "", xlab = "Log Annual Pre-
cipitation", col = "gray")
```

Next, we read in the trait data from a folder called `data`. We assign the row names of the new data frame to the names of the taxon within the dataset. We look at the first six rows of the trait data frame with the `head()` function. The two traits that we use in this example are body mass and hypsodonty index. Body mass is reported in grams and is the mass of any adult reported in the PanTHERIA database (Jones et al. 2009) from live or freshly-killed specimens. These include captive, wild, provisioned, or unspecified populations and include male, female, and sex unspecified individuals. The mean for each species is reported for each species. The second trait that we use is an index for hypsodonty from Eronen et al. (2010b).

```
traits <- read.csv("data/NA mammal Traits.csv")
rownames(traits) <- traits$TaxonName
head(traits)
##      TaxonName BodyMass hypsodonty_index
## Didelphis virginiana Didelphis
virginiana 3.387760          1
## Aplodontia rufa      Aplodontia rufa 2.906448
## Sciurus carolinensis Sciurus carolinensis
2.736715          1
## Sciurus griseus      Sciurus griseus 2.847480
## Sciurus niger          Sciurus niger      NA
## Tamiasciurus douglasii Tamiasciurus
douglasii 2.352183          1
```

Now we read in shapefiles containing polygons that represent the geographic ranges for all of the species of interest. These specific shape files were obtained from IUCN Redlist using their spatial data download option (www.iucnredlist.org). If you are dealing with large shapefiles, then this step will take a reasonable amount of processing time.

```
geography <-
shapefile
("data/TERRESTRIAL_MAMMALS/TERRESTRIAL_MAMMALS.
shp")
```

Next we create a list of species at each sampling locality by first turning the sampling points into spatial points with the function `SpatialPoints()`. We assign the coordinate reference system of our spatial points to a proj4string to match the coordinate reference system of the spatial polygons representing the geographic ranges. We then create a list with the function `over()`. If you are dealing with large shapefiles, keep in mind that the `over()` function will take a reasonable amount of time to process.

```
sp <- SpatialPoints(climate[,2:3], proj4string = CRS
(proj4string(geography)))
o <- over(sp, geography, returnList = T)
```

The sample size at each site is calculated by determining the length of the vector returned for each site. The ecometric for body mass and hypsodonty index are summarized for the community level distribution. Here, we summarize with the mean.

```
richness <- unlist(lapply(o, function(x) length(
traits[x$binomial, "hypsodonty_index"])))
ecometric_bodymass <- unlist(lapply(o, function(x)
mean(traits[x$binomial, "BodyMass"],
na.rm = T)))
ecometric_hypsodonty <- unlist(lapply(o, function(x)
mean(traits[x$binomial, "hypsodonty_index"], na.rm =
T)))
```

First Approximation with Transfer Function

Now we create a model describing the relationship between traits and climate. First, we consider the relationship between hypsodonty and precipitation. We build a simple linear model to describe the variation in precipitation due to the variation in hypsodonty using the function `lm()`. We only use sites that we have data for more than five species. We look at a summary of the model using the function `summary()`. Both the intercept and the coefficient (here the coefficient represents the slope of the linear relationship) are not zero ($p < 0.001$). The amount of explained variation (R^2) is 30%. We then make a scatterplot of those variables to look at the general spread of data and add the linear model with the function `abline()` (Fig. 17.A7).

```
model_mass <- lm(climate[richness > 5, 4] ~
ecometric_bodymass[richness > 5])
summary(model_mass)
## Call:
## lm(formula = climate[richness > 5, 4] ~
ecometric_bodymass[richness > 5])
## Residuals:
##      Min       1Q   Median       3Q      Max
## -170.72  -65.22  -24.73   43.71  375.19
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)      471.512     6.571   71.76 <2e-16 ***
## ecometric_bodymass[richness > 5] -153.559     2.304
-66.64 <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.'
0.1 ' ' 1
## Residual standard error: 92.6 on 8651 degrees of
freedom
```

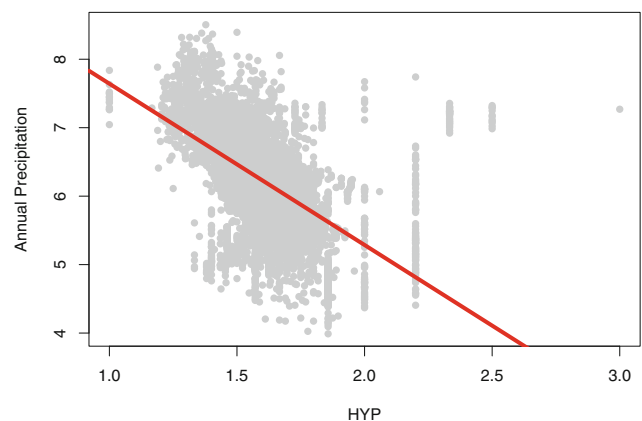


Fig. 17.A7 A scatterplot of hypsodonty and log annual precipitation with a trend line

```
## (15 observations deleted due to missing data)
## Multiple R-squared:  0.3392, Adjusted R-squared:
0.3391
## F-statistic:  4440 on 1 and 8651 DF,  p-value: <
2.2e-16
plot(ecometric_bodymass[richness > 5], climate[rich-
ness > 5,4], ylab = "MAT", xlab = "Body
Mass", pch = 16, col = "gray")
curve(model_mass$coefficients[1] + model_mass$coeffi-
cients[2] * x, col = "red", lwd = 4,
add = T)
```

From this model, we can see there is some predictive power in this transfer function, but the linear model does not capture the relationship well. In the next section we will show how to estimate annual precipitation from hypsodonty with a maximum likelihood approach that better captures the relationship between annual precipitation and hypsodonty.

Now we create a model describing the relationship between the body mass and temperature. We build a linear model to describe the variation in body mass due to the variation in temperature using the function `lm()`. We look at a summary of the model using the function `summary()`. Both the intercept and all the coefficients are significantly different from zero ($p < 0.001$). The amount of explained variation (R^2) is approximately 34%. We then make a scatterplot of those variables to look at the general spread of data and add the model with the function `curve()` (Fig. 17.A8).

```
model_mass <- lm(climate[richness > 5,4] ~
ecometric_bodymass[richness > 5])
summary(model_mass)
## Call:
## lm(formula = climate[richness > 5, 4] ~
```

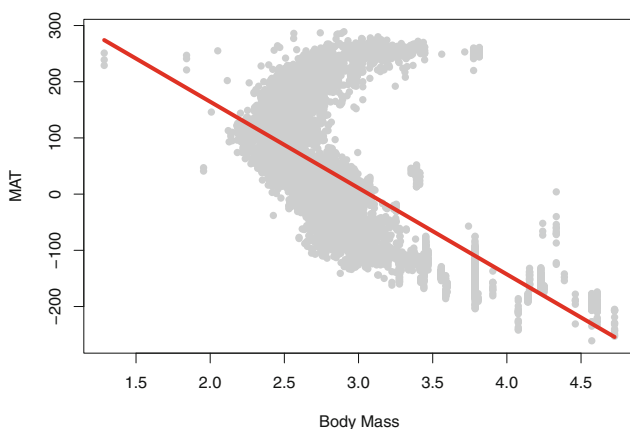


Fig. 17.A8 A scatterplot of body mass and mean annual temperature with a trend line

```
ecometric_bodymass[richness > 5])
## Residuals:
##   Min     1Q   Median     3Q      Max
## -170.72  -65.22  -24.73   43.71  375.19
## Coefficients:
##              Estimate Std. Error t value Pr(>|t|)
## (Intercept)      471.512     6.571   71.76 <2e-16 ***
## ecometric_bodymass[richness > 5] -153.559     2.304
-66.64 <2e-16 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.'
0.1 ' ' 1
## Residual standard error: 92.6 on 8651 degrees of
freedom
## (15 observations deleted due to missing data)
## Multiple R-squared:  0.3392, Adjusted R-squared:
0.3391
## F-statistic:  4440 on 1 and 8651 DF,  p-value: <
2.2e-16
plot(ecometric_bodymass[richness > 5],
climate[richness > 5,4], ylab = "MAT", xlab
= "Body Mass", pch = 16, col = "gray")
curve(model_mass$coefficients[1] +
model_mass$coefficients[2] * x, col = "red", lwd
= 4, add = T)
```

From this model, we can see that, again, there is some predictive power in this transfer function, but the linear model does not capture the relationship well. In the next section we will show how to estimate mean annual temperature from body mass with a maximum likelihood approach that better captures the relationship between the two.

The coefficients that were estimated in both of these models can be used to estimate paleotemperature and precipitation. Confidence limits can also be calculated given the input dataset. It is important to note that the size of the confidence limits will vary with climate. For example, between 5 C and 28 C, there is a stronger relationship with body size than below or above those temperatures. Hypsodonty has high variability throughout the precipitation range present in North America; however, there is a central tendency about the average relationship between precipitation and hypsodonty index that is useful in reconstructing paleoprecipitation with confidence limits.

Maximum Likelihood Estimation

Although transfer functions, while easy to apply and adequate for first approximations, assume a fairly simple one-to-one relationship between environment and trait means. Combining different traits that have functional relationships with the same environmental factor is also

awkward with conventional regression-based transfer functions, especially if the traits are fundamentally different in kind or scale (e.g., body mass measured in kg and humerus shape measured in Procrustes units).

An alternative strategy is to estimate the likelihood of environmental parameters given the distribution of traits in a community (Lawing et al. 2012; Polly and Head 2015). This approach, like many likelihood or Bayesian methods, requires far fewer assumptions about the statistical distributions of variables and it allows otherwise incommensurable data to be combined into the same estimate.

To begin, we need to create another variable at the community level, namely the standard deviation, to use in the maximum likelihood estimate of temperature.

```
sd_ecometric_bodymass <- unlist(lapply(o,
function(x)
sd(traits[x$binomial, "BodyMass"], na.rm = T)))
```

We create bins using the body mass variable and extract the break points for each bin.

```
#bin the community level trait distribution into 25X25
#first take the range of each
mtemp <- range(ecometric_bodymass, na.rm = T)
sdtemp <- range(sd_ecometric_bodymass, na.rm = T)
#get the break points for the mean and sd
mbrks <- seq(mtemp[1], mtemp[2], diff(mtemp)/25)
sdbbrks <- seq(sdtemp[1], sdtemp[2], diff(sdtemp)/25)
#assign bin codes for each
mbc <- .bincode(ecometric_bodymass, breaks = mbrks)
sdbc <- .bincode(sd_ecometric_bodymass, breaks =
sdbbrks)
```

We calculate the temperature for each bin.

```
#calculate the data for the raster
obj <- array(NA, dim = c(25, 25))
for(i in 1:25){
  for(j in 1:25){
    dat <- round(temperature[which(mbc==i & sdbc==j)]/
10)
    obj[26 - j, i] <- mean(dat, na.rm = T)
  }
}
```

Next, we create a raster to store the body mass and temperature data for bins.

```
#make a raster
r <- raster(extent(0, 25, 0, 25), resolution = 1)
```

```
#set the values to the obj
r <- setValues(r, obj)
```

Plot the raster and highlight the bin that we will use to extract data to show an example of that maximum likelihood estimate (Fig. 17.A9).

```
#make an empty plot
plot(1:25, 1:25, type = "n", xlim = c(1, 25), ylim = c
(1, 25),
xaxs = "i", yaxs = "i", asp = 1, axes = F, xlab = "",
ylab = "")
#add the rectangle/box
rect(0, 1, 25, 25, lwd = 3)
#add the raster data
plot(r, col = colorRampPalette(c("darkblue", "blue",
"grey", "yellow", "red"))(round(maxValue(r) -
minValue(r))), add = T)
#this is mean = 3.1, 12, and sd = 1.08, 10
rect(11, 9, 12, 10, lwd = 4)
```

The colors in this raster plot show the Mean Annual Temperature (MAT) maximum likelihood estimate given the associated mean and standard deviation of each bin.

We extract the data for the highlighted bin and plot the kernel density with a Gaussian kernel (Fig. 17.A10). This shows the distribution of the likelihood surface.

```
#grab all the data for that box
dat <- round(temperature[which(mbc==12 & sdbc==10)]/
```

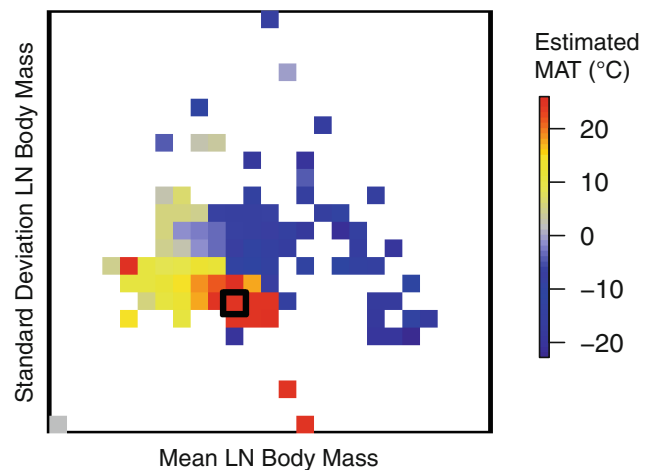


Fig. 17.A9 Ecometric space for the trait body mass with mean body mass on the x-axis and standard deviation of body mass on the y-axis. The colors represent the estimate of mean annual temperature for each mean and standard deviation combination. The hotter colors represent higher mean annual temperature and the cooler colors represent lower mean annual temperatures

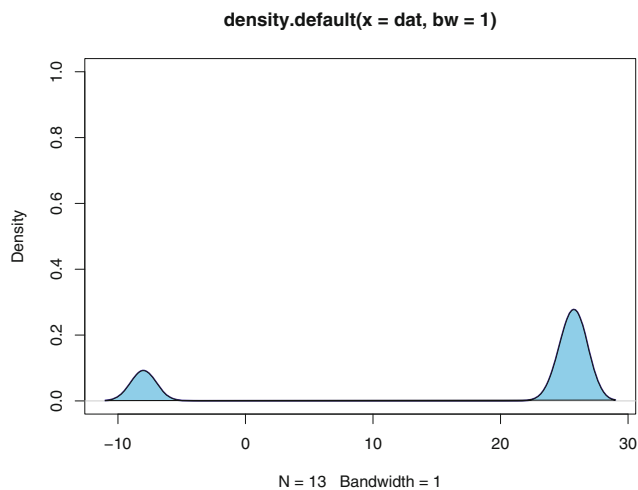


Fig. 17.A10 Kernel density estimation from one combination of mean and standard deviation of body mass

```
10)
#plot the kernel density with gaussian kernel,
bandwidth = 1
mod <- density(dat, bw = 1)
plot(mod, ylim = c(0,1), col = "darkblue", lwd = 2)
polygon(mod$x, mod$y, col = "skyblue")
```

This likelihood surface shows a bimodal distribution of the most likely temperature. Although it is bimodal, it is much more likely that the temperature falls on the warm end of the spectrum, as opposed to the cold end.

Next, we calculate the maximum likelihood for all bins.

```
modmax <- array(NA, dim = length(points[,1]))
mod <- list()
for(i in 1:length(points[,1])){
  if(!is.na(mbc[i]) | is.na(sdbc[i])){
    dat <- round(temperature[which(mbc==mbc[i] &
sdbc==sdbc[i])]/10)
    mod[[i]] <- density(dat, bw = 1)
    modmax[i] <- mod[[i]]$x[which.max(mod[[i]]$y)]
  }
}
modmax <- round(modmax*10)
```

We only use bins with more than the number of species specified as the cutoff. Here we use seven. This means that there needs to be at least seven species recorded at each location to be included in the estimate.

```
cutoff <- 7
```

To plot the maximum likelihood temperature estimate from the ecometric values, we create a color palette for the temperature estimates. In addition, we save the histogram

with five break points to a variable to use in plotting (refer back to Fig. 17.A4).

```
colfunc_eco <- colorRampPalette(c("darkblue",
"blue", "gray", "yellow", "red"))(temp_range)[1 +
modmax - min(modmax, na.rm = T)]
h <- hist(temperature, main = "", xlab = "Mean
Annual Temperature", col = "gray", breaks = 5)
```

We map the maximum likelihood temperature estimate from body mass (Fig. 17.A11).

```
plot(points[,2:3], col = "gray", pch = 16)
points(points[richness > cutoff, 2:3], col =
colfunc_eco[richness > cutoff], pch = 16)
legend(-31.5, 61, legend = h$breaks/10, pch = 16,
col = colorRampPalette(c("darkblue",
"blue", "gray", "yellow", "red"))(length(h$breaks)))
```

Next we plot the actual temperature to compare with the estimated temperature (refer back to Fig. 17.A2).

```
plot(points[,2:3], col = "gray", pch = 16, main = "Mean
Annual Temperature (C)")
points(points[richness > cutoff, 2:3], col =
colfunc_temp[richness > cutoff], pch = 16)
legend(-31.5, 61, legend = h$breaks/10, pch = 16,
col = colorRampPalette(c("darkblue",
"blue", "gray", "yellow", "red"))(length(h$breaks)))
```

We plot the anomaly to visualize the difference between the estimated and actual Mean Annual Temperature (Fig. 17.A12).

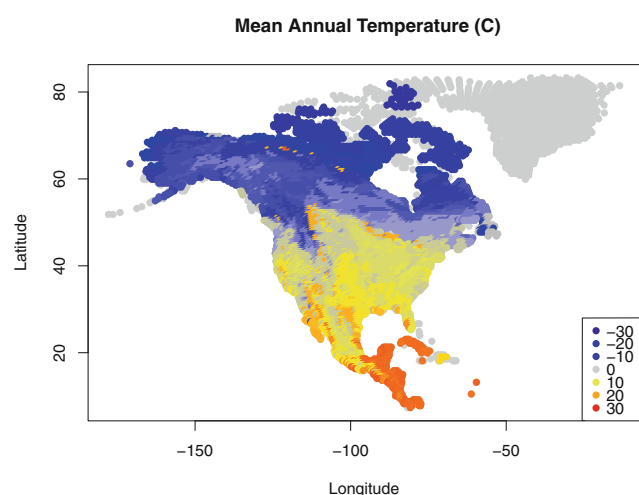


Fig. 17.A11 A heat map of the estimate of mean annual temperature (°C) from the mean and standard deviation of body mass. The hotter colors represent higher temperature estimates and the cooler colors represent lower temperature estimates

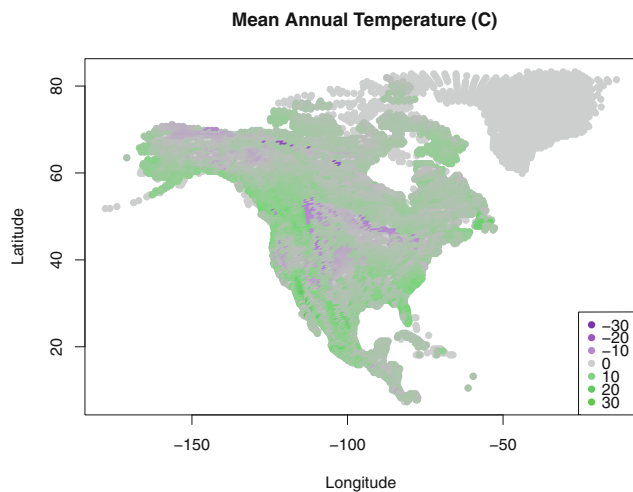


Fig. 17.A12 Anomaly between the observed mean annual temperature and the estimated mean annual temperature. The purple colors represent negative anomalies, up to -30°C . The green colors represent positive anomalies, up to 30°C

```
plot(points[,2:3], col = "gray", pch = 16)
anom <- temperature - modmax
colfunc_anom <- colorRampPalette(c("purple", "grey",
"green"))(max(anom, na.rm = T) -
min(anom, na.rm = T)) [1 + anom - min(anom, na.rm = T)]
points(points[richness > cutoff, 2:3], col =
colfunc_anom[richness > cutoff], pch = 16)
legend(-31.5, 61, legend = h$breaks/10, pch = 16,
col = colorRampPalette(c("purple", "grey", "green"))
(length(h$breaks)))
```

The anomaly between the estimated Mean Annual Temperature and the actual Mean Annual Temperature shows that most of the temperature estimates are less than 1°C divergent from the actual Mean Annual Temperature.

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