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Review

Review

Strengthening the Ties That Bind: An Evaluation of Cross-disciplinary Communication Between Invasion Ecologists and Biological Control Researchers in Entomology

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Abstract

To control non-native species, resource managers may import and introduce biocontrol agents. Like accidentally introduced insects, biocontrol agents must overcome several abiotic and biotic obstacles to establish successfully. They can also have varying efficacy and negative or positive impacts on native species and ecosystems. Given the similarities between accidentally introduced insects and biocontrol agents, researchers studying these organisms can more effectively communicate and actively link data to improve overall understanding and management of non-native species within the framework(s) of invasion theory. To assess interdisciplinarity between invasion ecologists and biocontrol practitioners that study insects in forests, we identified 102 invasion ecology and 90 biocontrol articles published from 2006 to 2018. These articles helped us determine which broad disciplines (invasion ecology, biocontrol, other control, other ecological, and nonecological) and publication formats (e.g., journals and books) the authors cited most. We found 1) invasion ecologists primarily cite other invasion ecology research; 2) biocontrol researchers cite biocontrol and invasion ecology research; 3) both disciplines primarily cited peer-reviewed journal articles; and 4) there was 65–70% overlap in the top 20 journals cited in primary invasion ecology and biocontrol literature. Though we found some cross-communication, it is currently mostly unidirectional, whereby invasion ecology informs biocontrol. We identify and discuss three areas—1) ecological principles governing success or failure of introduced species, 2) the invasion process, and 3) negative impacts on native species—for which the disciplines possess substantial overlap to demonstrate that biocontrol agents can provide invasion ecologists with an unconventional model to study the mechanisms of species invasion.

Key words: bibliometric analysis, insect invasion, interdisciplinarity, forest ecosystem, non-native species

As global ecosystems face the growing impacts of non-native species, researchers in invasion ecology strive to understand the mechanisms driving species invasions, with an invasive species defined here as '…an introduced species that has spread well beyond its arrival point and that perpetuates itself without human assistance' (Simberloff 2013). Having an improved understanding of the mechanisms driving successful species invasion (i.e., successful establishment of reproducing populations and spread into adjacent areas) can help better prevent, detect, and manage these important threats to our natural systems and resources (Jeschke et al. 2014). In early management programs, land managers often relied on chemical pesticides to control or eradicate non-native species, specifically non-native insects and plants in natural terrestrial habitats, which are the focus of this review article (Liebhold and Kean 2019). In the 1960s, Rachel Carson's 'Silent Spring' raised awareness of the environmental risks of many commonly used synthetic chemical applications, such as herbicides and pesticides (Carson 1962), which may have inspired some non-native species control programs to shift from chemical to microbial-based pesticides (Liebhold and Kean 2019) and integrated pest management (Ehler 2006), including biological control (Barratt et al. 2018). Integrated pest management is a decision-based method that uses multiple tactics to augment the control of a species in a way that is ecologically and economically sustainable (Ehler 2006). Importation biological control is one integrated pest management method in which non-native species are reunited with and controlled by antagonists (e.g., herbivores, predators, and parasitoids) from their native range (DeBach and Rosen 1991, Schulz et al. 2019). Antagonists native to the introduced range of the non-native species or regions other than the native range of the non-native species (i.e., new associations; Pimentel 1963, Hokkanen and Pimentel 1984) may also be introduced for control efforts via importation control. In some ways, importation biological control may be considered an intentional, though controlled, invasion since a species is deliberately introduced (Marsico et al. 2010, Heimpel and Mills 2017).

During the late 20th Century, biological control became more notable, with many researchers emphasizing importation biological control (DeBach and Rosen 1991), and a few experimenting with the concept of new associations (Pimentel 1963, Hokkanen and Pimentel 1984). Although invasive species are generally viewed as having a negative impact and biological control agents may be generally viewed as having a positive impact (though exceptions exist; see Van Driesche and Hoddle 2016), both are often, but not always (e.g., augmentation or conservation biological control using native antagonists), non-native to the region in which they are having, or are expected to have, an impact. Given this similarity, it could be hypothesized that the research fields of invasion ecology and biological control would naturally have a lot of overlap in research topics and ideas toward increasing scientific understanding (Grevstad 1999). Though the two fields often have different objectives, in principle, they have the same goals (e.g., to control or eradicate invasive species and to understand species establishment success or failure for making better predictions and management recommendations). Although invasion ecology is often more theoretical and, thus, can potentially be utilized to explain trends in biological control success or failure, biological control programs can provide underutilized datasets to better and more accurately inform ever evolving invasion theories (Marsico et al. 2010).

In this review, we further discuss the similarities between non-native species and biological control agents, with an emphasis on the stages of the invasion process (transport, introduction, establishment [colonization and naturalization], spread, and impact; Fig. 1; Catford et al. 2009, Blackburn et al. 2011, Schulz et al. 2019), ecological principles governing the success or failure of introduced species, and negative impacts on native species. With a focus on non-native insects in forested and other terrestrial natural environments, we also contribute to the non-native species management literature by evaluating the types of publications that biological control professionals and invasion ecologists primarily cite to assess current levels of communication between the researchers and their primary fields of study. Cross-disciplinary communication is anticipated for this subset of the literature that is focused on natural environments because the invasion ecology literature largely focuses on process and impact in natural systems. Past studies have evaluated the level of communication between invasion ecology and other related scientific disciplines (e.g., Vaz et al. 2017, Abrahams et al. 2019); however, no study has specifically evaluated cross-communication between invasion ecology and biological control in the last decade. By evaluating the current levels of communication and discussing similarities between invasion ecology and biological control, we hope to improve cross-disciplinary communication to advance our understanding of the basic processes and mechanisms contributing to invasion and non-native species success or failure. If interdisciplinarity between invasion ecology and biological control is high, we expect that there would be strong linkages between these fields that then contribute to enhanced theory in the field of invasion ecology and more successful integrated pest management.

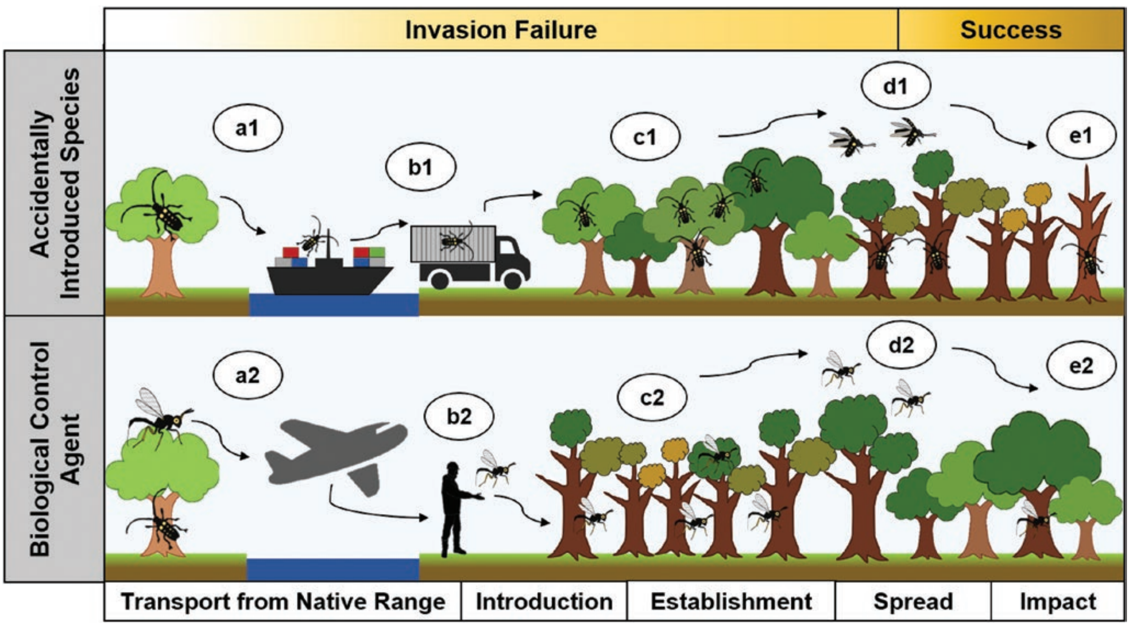

Fig. 1. Species that are accidentally introduced must avoid detection and survive transport from the native range to a novel range (a1) and remain undetected to become introduced in the novel range (b1). To successfully establish, the introduced species must have a sufficient number of propagules, succesfully identify an abundant host population and mates, acclimate or adapt to the new climate, and start and maintain a reproducing population that survives biotic resistance in the novel range (c1). After a species establishes, it may spread if there is an abundance of available hosts, environmental conditions are appropriate in adjacent areas, and the species can actively disperse and overcome geographic barriers (d1). With sustained, unobstructed (e.g., avoiding detection, tolerating antagonists, accessing abundant host populations) establishment and spread, an introduced species can impact the novel ecosystem (e1). Prior to introduction, importation biological control agents are carefully selected, assessed, and transported to a novel range (a2). If the biological control agents are approved for release and successfully reared, they are released into the novel range (b2), and they then follow a similar invasion process and obstacles as accidentally introduced species as they progress through the establishment (c2) and spread (d2) stages. Ultimately, the impact is based on the ability of the agent to successfully reduce populations of its target species (e2).

However, if interdisciplinarity is low, strengthening the shared aims and biological bases for both fields would 1) improve integrated pest management approaches, 2) aid decision-makers with policy modification and creation, and 3) improve early detection and rapid response practices (Reaser et al. 2020) and other strategies that can more effectively eradicate or control populations of non-native species.

Shared Characteristics of Non-native Species and Biological Control Agents

Non-native species studied in invasion ecology are often introduced intentionally or accidentally from other places around the globe, and they become invasive when they establish populations, spread in the novel environment, and negatively impact the ecosystems and economies where introduced (Lovett et al. 2016). Biological control agents are, in general, introduced deliberately into novel environments *via* planned releases (i.e., intentional invasions), where the agents are expected to establish and consume, thereby providing some control of a target non-native, invasive species' populations (Ehler 1998). We identify three predominant areas in which substantial overlaps exist among non-native, frequently invasive, species and biological control agents: 1) ecological principles governing the success or failure of introduced species, 2) the invasion process, and 3) negative impacts on native species.

Ecological Principles Governing the Success or Failure of Introduced Species

The invasion ecology literature has been building since the foundational book by Charles Elton (1958) was published, though it can be argued that the mathematical theory of invasions predates Elton by a few decades (Shigesada and Kawasaki 1997, Hastings et al. 2005). The literature in the field of invasion ecology now comprises numerous hypotheses that have been primarily developed to try to explain how and why non-native species successfully establish and spread in an environment (e.g., Richardson and Pyšek 2006, Catford et al. 2009, Enders et al. 2019, Schulz et al. 2019) and why biological control agents fail (e.g., Myers et al. 1989, Stiling 1993, Myers 2000). Perhaps in addition to thinking about invasion success in terms of non-native species success and biological control agent failure, researchers should directly think about how non-native species and biological control agents fail and succeed under the larger umbrella of introduced organisms. For example, Williamson (1998) proposed that a successful biological control agent should have a high reproductive rate, good searching ability, narrow host range, synchronization with the host's life cycle, climatic adaptability, and ability to survive at a low host density. These characteristics can be beneficial to the success of not only biological control agents, but also other non-native organisms that are introduced to a novel environment, such as invasive species.

By studying the characteristics and processes of successful invaders, invasion ecologists have developed the defense-free space (Gandhi and Herms 2010, Woodard et al. 2012), enemy release (Keane and Crawley 2002), increased resource availability (Sher and Hyatt 1999, Richardson and Pyšek 2006), and propagule pressure (Lonsdale 1999, Lockwood et al. 2005, Simberloff 2009) hypotheses, among many others. Although these hypotheses have been primarily developed for accidentally introduced non-native species, the overarching ideas behind all of these hypotheses are also applicable to biological control agents. In some cases, the field of biological control has an equivalent or near-equivalent hypothesis. For example, the defense-free space hypothesis in the invasion literature submits that a host in the introduced range lacks the defenses required to protect itself against non-coevolved organisms (Gandhi and Herms 2010, Woodard et al. 2012). In the biological control literature, the new associations hypothesis suggests that the most ideal biological control agents are related to coevolved antagonists of an undesirable species (Pimentel 1963, Hokkanen and Pimentel 1984). Specifically, the biological control agent should be related enough to recognize the undesirable species as a host, but distantly related enough that the undesirable species does not have the capability of defending against the biological control agent (Pimentel 1963, Hokkanen and Pimentel 1984).

Invasion ecologists also developed the propagule pressure hypothesis (Lonsdale 1999, Lockwood et al. 2005), whereas biological control researchers developed the concept of optimal release strategy (Shea and Possingham 2000). Both concepts aid in understanding the probability of establishment based on different release scenarios, including how many individuals are released at one time and how many releases occur over time. The biotic resistance hypothesis in invasion ecology (Levine et al. 2004) and the biotic interference hypothesis in biological control (Goeden and Louda 1976) are also similar; both hypotheses indicate that antagonists can reduce the success of non-native species, including biological control agents. Although importation biological control agents are first quarantined to ensure that they do not have any specialist antagonists that may impact success, antagonists in the novel range and, rarely, hitchhiking antagonists from the native range of the biological control agent, can impact agent introduction into the target system and its success (Goldson et al. 2014). Invasion ecology also has the enemy release hypothesis (Keane and Crawley 2002), which suggests that a non-native species is released from antagonists that limited its population in the native range. The field of biological control does not have a single hypothesis that directly considers the lack of or tolerance to higher trophic levels (e.g., hyperparasitoids and predators), which may also aid in the success of biological control agents (Schulz et al. 2019). However, biological control considers antagonists in the new associations (Pimentel 1963, Hokkanen and Pimentel 1984) and biotic interference (Goeden and Louda 1976) hypotheses, and Heimpel and Mills (2017) discuss effects of biotic resistance on biological control agents. Additionally, McEvoy (2018) discusses the activation-inhibition model in biological control, which incorporates multiple driving forces, including top-down effects from antagonists.

Not all hypotheses in invasion ecology have clear equivalents in the field of biological control. For example, the increased resource availability hypothesis (Sher and Hyatt 1999, Richardson and Pyšek 2006) proposes that a non-native species may succeed because it has an increased availability of resources in the introduced range. In importation biological control, researchers often select antagonists that have a coevolved relationship with the host in their native range, where the antagonist often subsists on low host population levels. However, in the introduced range, where the host may have larger populations due to unchecked population growth, the antagonist turned biological control agent may be successful due to increased host availability. Understandably, the field of biological control tends to be more applied and may focus less time on developing intricate theoretical hypotheses to understand, explain, and/or predict the success or failure of biological control agents. It should also be noted that the success of biological control must first be measured before it can be explained (McEvoy 2018). In many cases, postrelease evaluation of biological control agent effectiveness and success is not rigorously conducted (Müller-Schärer and Schaffner

2008), perhaps due to a lack of long-term funding. However, if a postrelease evaluation is conducted for biological control agents, it is important to invariably link the ecological concepts behind the hypotheses to show that, upon release into the naïve environment, many of the same ecological mechanisms are co-occurring with non-native species whether they are intentionally or accidentally introduced (Schulz et al. 2019). A push for shared theoretical frameworks between invasion ecology and biological control can result in improved rates of success in biological control planning and releases and provide invasion ecologists multiple models with which to test the plethora of theoretical hypotheses (Marsico et al. 2010).

The Invasion Process

Invasion processes have been well defined in the discipline of invasion ecology (e.g., Blackburn et al. 2011, Lockwood et al. 2013), but they are not as widely discussed within the biological control literature. We utilized the framework developed by Catford et al. (2009) to organize various classification systems of the invasion process, and we document 12 invasion ecology publications and three comparable biological control publications with explicitly noted processes (Table 1). In general, these processes are described as transport (i.e., organisms are accidentally or intentionally moved to an area where they are not native), introduction (i.e., undetected non-native organisms arrive in a natural ecosystem outside of their native range), establishment (i.e., non-native organisms establish reproducing populations in the introduced range), and spread (i.e., non-native organisms actively or passively disperse to other parts of the introduced range and establish new, reproducing populations) involved in successful invasion (Table 1; Fig. 1; Catford et al. 2009; Blackburn et al. 2011; Schulz et al. 2019).

About half of the invasion ecology publications included impact (i.e., the defined theoretical stage at which environmental and/or economic damage is perceivable by the human population) as the final stage of the invasion process, though some argue that non-native species are impactful at any stage in the process of invasion, and that success is ultimately governed by the ability and opportunity to disperse (e.g., Ricciardi and Cohen 2007; Jeschke et al. 2013; Ricciardi et al. 2013). Although some non-native species have impacts as soon as they arrive (e.g., pathogens) or after they have established but not yet spread, these impacts are localized to the area in which the propagules of the non-native species were initially introduced and established. Most non-native species, including insects, have little or no impact (Williamson and Fitter 1996; Aukema et al. 2011). Nascent establishing populations of non-native species may remain undetected, especially if they are small and/or cryptic (Stohlgren and Schnase 2006; Morais and Reichard 2018), or do not negatively affect important resources (e.g., non-native decomposers; Klimaszewski and Brunke 2018). The impacts of non-native species generally increase if the species are established and show broad dispersal and spread in the introduced range (Jeschke et al. 2014).

Prior to transport and introduction, biological control program managers determine which antagonist species might best control the target species, identify parent populations of the selected antagonist species, and then evaluate the antagonists selected for release as biological control agents (Yek and Slippers 2014). The biological control agents encounter different obstacles than accidentally introduced non-native species because they are carefully and anthropogenically selected, and undergo a battery of testing before they are transported and released into the novel environment (Müller-Schärer and Schaffner 2008). For example, in the transport stage, non-native species that are accidentally transported must remain undetected, survive the transportation environment, and overcome geographical barriers (Blackburn et al. 2011). The human-aided, planned invasion of the biological control agent, however, removes these obstacles. Biological control agents need to survive and pass the human-interest assessment, specificity testing, and quarantine process to be transported and released into the novel range (Heimpel and Mills 2017). During the introduction stage, biological control agents likely are not limited by consumption of resources as the host species, to be controlled, are generally highly abundant. By contrast, accidentally introduced non-native species may have limited or no host availability in the area in which they arrive. In the introduction stage, biological control agents may also have the advantage as researchers have the ability to control the number, composition, and frequency of individuals that are released (Shea and Possingham 2000). Conversely, accidentally introduced species may experience limited early success due to low or inconsistent propagule pressure (Lonsdale 1999, Lockwood et al. 2005).

Non-native species and biological control agents face similar obstacles throughout the establishment and spread stages. Once released, biological control agents must overcome biotic resistance (e.g., antagonists), adapt to an altered climate, synchronize phenology with hosts and other abiotic and biotic factors, discover mates, successfully reproduce, and disperse throughout the range of their host, similar to that of accidentally introduced species. If the non-native species cannot overcome both abiotic and biotic obstacles, their populations may crash (Simberloff and Gibbons 2004), and they are considered to have failed. Since biological control agents are human-aided in introduction and establishment, they possess a higher success rate than other non-native species (Heimpel and Mills 2017). Whereas other non-native species follow the 25% invasion rule (previously the tens rule; i.e., 25% of the species that are introduced manage to establish and only 25% of those that establish successfully spread; Jeschke and Pyšek 2018), biological control agents more loosely follow a 'threes rule' in which about one-third of the species introduced do establish with great effort from humans (Williamson and Fitter 1996). Heimpel and Mills (2017) suggest that the threes rule is largely for entomophagous biological control agents, and a 'twos rule' (i.e., half of the species establish after introduction) is more appropriate for herbivorous biological control agents.

Impact is driven by distribution, abundance, and per capita effect of the introduced species (Parker et al. 1999). Impacts for invasive species are perceived as negative by humans, generally based on economic or ecological metrics, whereas, for biological control agents, which are also non-native, impacts are generally perceived as positive in the sense that the biological control agent controls a negatively viewed species. Figure 1 illustrates the similarities in invasion process between biological control agents and other non-native species. This framework of shared planned or unintentional invasion processes may encourage researchers to think about similar patterns of invasion between non-native species and biological control agents, strengthen the scientific linkages between the disciplines, and progress interdisciplinarity between researchers aiming to reduce non-native species abundance that reduces overall global biodiversity.

Negative Impacts on Native Species

Perhaps the closest similarity between non-native species and biological control agents can be observed when biological control agents

Table 1. A noncomprehensive list of publications with frameworks that describe the invasion process for non-native species and biological control agents according to various classification systems

Publication	Stages documented					
Stages as documented by Catford et al. (2009)	Transport	Introduction	Colonization	Naturalization	Spread	Impact
Definition	Species is transported outside the native range	Species is released in a new environment	Species survives in the new environment	Species has self-sustaining population	Species disperse from site of introduction	Species has socio-ecological impacts
Invasion Publications						
Williamson (1993)	Imported	Introduced		Established	Pest	
Richardson et al. (2000)	Geographic		Environmental	Reproductive	Dispersal	Environmental
Heger and Trepl (2003)	Immigration		Growth and reproduction of an individual	Population growth to minimum viable pop.	Colonization of new localities	N/A
Colautti and MacIsaac (2004)	Uptake/Transport	Release	Establishment		Spread	
Levine et al. (2004)	Introduction		Establishment		Spread	Impact
Lockwood et al. (2005)	Uptake/Transfer	Release	Establishment		Population Increase or Expansion	
Lodge et al. (2006)	Transport	Released Alive	Population Established		Spread	Impact
Mitchell et al. (2006)	Transport	Introduction	Colonization	Survival and Repro.	Spread	
Gurevitch et al. (2011)	Invader Demography			Rapid Population Increase	Range Expansion	Altered Landscape
Blackburn et al. (2011)	Transport	Introduction	Establishment		Spread	
Jeschke et al. (2013)	Transport	Release	Establishment		Spread	Impact
Lockwood et al. (2013)	Transport	Introduction	Establishment		Spread	Impact
Cassey et al. (2018)	Transport	Introduction	Establishment		Spread	Impacts
Biological Control Publications						
Müller-Schärer and Schaffner (2008)	Selection and Redistribution	Release	N/A			Agent Evaluation
Yek and Slippers (2014)	Parent Population N/A	Arrival	Survival	Reproduction	Persistence and Spread	N/A
Heimpel and Mills (2017)	Transport	Introduction	Establishment			Impact

N/A indicates that those particular stages were not included in the respective citations. Adapted from Catford et al. (2009).

have nontarget effects. Van Driesche and Hoddle (2016) highlight five common types of non-target impacts: direct attacks on native species, negative food web effects, positive food web effects, hybridization with native species, and attacks on other biological control agents. Prior to the late 1980s to early 1990s, nontarget effects of biological control agents were not seriously considered, so biological control agents that were selected and released before that time often resulted in nontarget effects (Hajek et al. 2016, Van Driesche and Hoddle 2016). Both traditionally released biological control agents (e.g., Asian lady beetle [*Harmonia axyridis* Pallas (Coleoptera: Coccinellidae)]; Roy and Wajnberg 2008, Koch 2003) and adventive biological control agents (i.e., agents that were under consideration for release but establish themselves after unintentional introduction; Mason et al. 2017) have successfully established, spread, and resulted in intended and unintended impacts. In the future, these traditionally released and adventive biological control agents may be prime candidates to study for the purpose of determining how they successfully invade, as well as to test hypotheses in invasion ecology (Abram and Moffat 2018). It should be noted, however, that in the last several decades, biological control practitioners have greatly improved prerelease assessment of likely host range (Van Driesche and Hoddle 2016, Hinz et al. 2019), often opting for more specialist biological control agents due to their limited host range and, thus, limited potential for nontarget impacts (MacQuarrie et al. 2016). The strict national and international standards that have been developed to reduce the risks of accidental release of quarantined biological control agents and nontarget impacts have created additional, yet important, barriers to biological control implementation and, as a result, some biological control programs have been discontinued (Hajek et al. 2016). The remaining programs carefully quarantine and assess their biological control agents, but some nontarget effects are inherently unpredictable (Hajek et al. 2016), so elimination of nontarget effects is realistically unattainable.

Current Status of Cross-disciplinary Communication

We assessed the current level of communication between invasion ecologists and biological control professionals in entomology by determining what types of research publications each field primarily cites. To evaluate interdisciplinarity between or among fields of study, researchers often perform a bibliometric analysis, a form of analysis that measures and analyzes publications (Huang and Chang 2011). Specifically, we conducted a citation analysis of published biological control and invasion ecology literature from 2006 to 2018. This timeframe was selected because we wanted to evaluate the most current levels of communication between the two fields. A similar study was conducted on the pre-2006 invasion ecology literature (Pyšek et al. 2006), so we selected the timeframe immediately after that publication up to present time. Although citation analyses are limited in their ability to evaluate research quality, solidity, originality, and societal value—all values that can only be evaluated through a subjective peer review—they represent a satisfactory measure of impact (Aksnes et al. 2019), which might be used to assess quantity of communication across fields.

Citation Analysis

Publications were searched and collected from Google Scholar, a free, commonly used, web-based academic search engine that indexes closed- and open-access journals and that has a wider coverage of open access research than some research databases (Kousha and Thelwall 2008). To find publications that focused on non-native insects in forests and other terrestrial natural environments in each field, we performed keyword searches with relevant terms anywhere in the article. For biological control literature, we used a combination of Boolean search terms, including 'biological control' OR 'biocontrol' AND 'forest' AND 'insect'. To search for invasion ecology literature, we used a combination of related search terms: 'forest' AND 'herbivore' AND 'insect' AND 'invasive' OR 'non-native' OR 'alien'. Our samples were enriched toward studies that were focused in forest ecosystems, but research and review articles that included other natural environments were not excluded. Our search returned 17,200 biological control and 14,300 invasion ecology results. Google Scholar returns a less controlled collection of primary publications and gray literature (e.g., technical reports, abstracts, dissertations) than some other research databases, so a process of elimination was essential to find relevant primary literature. We limited our search to the first 500 pages (i.e., 5,000 references) of Google Scholar results, which contained most of the relevant publications. Publications within this first 500 pages were excluded if they 1) were not peer-reviewed, 2) were in a character-based language that is difficult to translate (e.g., Chinese), 3) focused on noninsect types of biological control (e.g., fungi, bacteria), 4) involved other noninsect animals, 5) focused on the rearing and release of native predators or parasitoids, or 6) were based in the medical or agricultural fields. We did not consider publications that were based in agricultural or medical settings, instead opting for research that was conducted in natural or semi-natural settings, in order to allow for more direct comparison with the invasion ecology literature. Although the study of invasive insects and their control (via biological control) in natural environments is still comparatively new and constitutes only a small portion of biological control programs (Van Driesche et al. 2010, Heimpel and Cock 2018), it, along with studies on the biological control of invasive plants in natural environments, is a logical subset of studies from both invasion ecology and biological control that should already represent substantial cross-disciplinary communication.

If a publication met the criteria and included both invasion ecology and biological control content, it was classified in the category (i.e., invasion ecology or biological control) that best fit most of the content in the publication. After reviewing the abstracts and articles, 102 invasion ecology (Supp Table S1 [online only]) and 90 biological control (Supp Table S2 [online only]) articles met the criteria and were selected for further assessment. We assessed the references within these primary invasion ecology and biological control publications to determine whether the authors cited biological control, invasion ecology, other control (e.g., pesticides, silvicultural management, host hybridization, genetic engineering of the invader), other ecological (e.g., conservation biology, population ecology, restoration ecology), or nonecological (e.g., economics, methods of statistical analysis, molecular analysis software, statistical packages, and software) literature. The first author manually categorized all 6,782 citations from the invasion ecology literature (Supp Table S1 [online only]) and 4,875 citations from the biological control literature (Supp Table S2 [online only]) in one of these five categories. If a citation fit into more than one category, it was placed in the category that best fit the information used by the authors of the primary publications. For example, if a citation included information on both the biology and history (i.e., invasion ecology) and biological control of a non-native organism, but the authors cited only the biological control aspect, then the citation was categorized as biological control literature to emphasize use of the citation. We then performed a Kruskal–Wallis test with post-hoc Pairwise Wilcoxon Rank Sum Test in R v.3.4.0 (R Core Team 2017) to compare the mean rank number of citations in each category within each type of primary publication.

The mean (± SE) number of citations per primary publication was 66.5 (± 3.5) for the invasion ecology publications, and 54.2 (± 5.7) for the biological control publications. The mean rank number of citations varied among the citation categories in the primary invasion ecology publications (H = 289.67, df = 4, $P < 0.001$, Fig. 2a) and primary biological control publications (H = 270.75, df = 4, $P < 0.001$, Fig. 2b). Overall, invasion ecology publications primarily cited other invasion ecology literature, followed by other ecology literature (Fig. 2a). The biological control publications primarily cited other biological control literature, followed by invasion ecology and other ecology literature (Fig. 2b).

Overlap in References

To further explore the level of communication between invasion ecologists and biological control professionals, we assessed the types of references cited in the primary invasion ecology and biological control publications. Using only the citations identified as 'biological control' or 'invasion ecology' in the primary publications, we tallied the journals and other resources (e.g., books, data repositories, dissertations, government reports, personal observations, and websites) that were cited for each primary publication type to show the proportion and distribution across the resources (Fig. 3). We also tallied the individual journals that were cited and identified the top 20 invasion ecology and biological control journals cited by the primary invasion ecology and biological control publications.

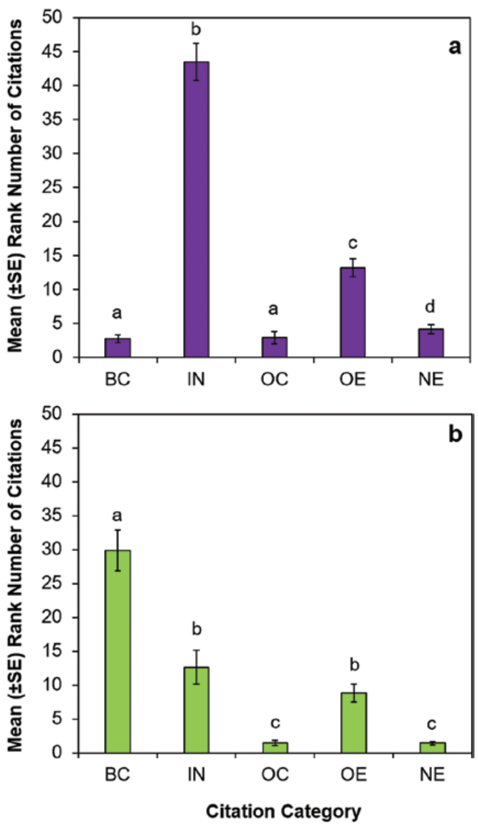

Fig. 2. Mean number of biological control (BC), invasion ecology (IN), other control (OC), other ecology (OE), and nonecological (NE) citations found within (a) 102 primary invasion ecology and (b) 90 primary biological control publications. The bars indicate standard error. Bars with the same letter are not significantly different.

Within the primary invasion ecology publications, we identified 4,438 citations that were classified as invasion ecology literature (Supp Table S3 [online only]). Most of these citations were from journals or books (Fig. 3a). We also identified 283 citations that were categorized as biological control literature in the primary invasion ecology publications of our dataset (Supp Table S4 [online only]). Like the invasion ecology citations, most biological control citations were from journals; however, about 22% of the citations originated from the USDA Forest Service (e.g., General Technical Reports and Research & Development publications), other governmental reports (e.g., state reports, USDA APHIS reports), and books, indicating the strong applied nature of this field in natural ecosystems (Fig. 3b). Within the primary biological control publications, we identified 1,136 citations that were categorized as invasion ecology literature (Supp Table S5 [online only]). Similar to the invasion ecology literature cited by the primary invasion ecology publications, most of the invasion ecology literature that was cited by the primary biological control publications was derived from journals or books (Fig. 3c). Finally, we identified 2,685 citations that were categorized as biological control literature within the primary biological control publications (Supp Table S6 [online only]). Of these citations, most were from journals, though the percentage of citations from books (13%) was nearly double that of the primary invasion ecology publications (7% across both invasion ecology and biological control citations) and about 1.5 times more than the invasion ecology citations (9%) in the primary biological control publications (Fig. 3d).

We identified 489 and 279 unique journals cited for invasion ecology content by the primary invasion ecology (Supp Table S3 [online only]) and primary biological control (Supp Table S5 [online only]) publications, respectively. Further, the primary invasion ecology publications cited 80 different journals (Supp Table S4 [online only]) and the primary biological control publications cited 346 journals (Supp Table S6 [online only]) with published biological control content. We found a 65% and 70% citation overlap in the top 20 invasion ecology and biological control journals cited by invasion ecologists and biological control practitioners, respectively (Fig. 4). Both invasion ecology and biological control publications primarily cited *Biological Invasions* and *Environmental Entomology* for information pertaining to invasion ecology. The journal *Ecology* was also in their top five cited journals. Both invasion ecology and biological control publications also primarily cited the journals *Biological Control, BioControl*, and *Environmental Entomology* for information on biological control. However, *Biocontrol News and Information*, *Biocontrol Science and Technology*, and *Entomologia Experimentalis et Applicata* were also regularly cited (37, 29, and 36 citations, respectively) by the primary biological control publications, but were not cited at all by the primary invasion ecology publications.

Disconnect Between Invasion Ecology and Biological Control?

Invasion ecology is inherently tied to many ecology- and management-based disciplines, including biological control (Ehler 1998), community ecology (Shea and Chesson 2002), restoration ecology (Gaertner et al. 2012), succession ecology (Davis et al. 2001), and the social sciences (Vaz et al. 2017), all of which fall under the umbrella of conservation science due to their efforts to conserve biodiversity. Nevertheless, some researchers have argued that invasion ecologists have intentionally or unintentionally dissociated themselves from these other disciplines, and, as a result,

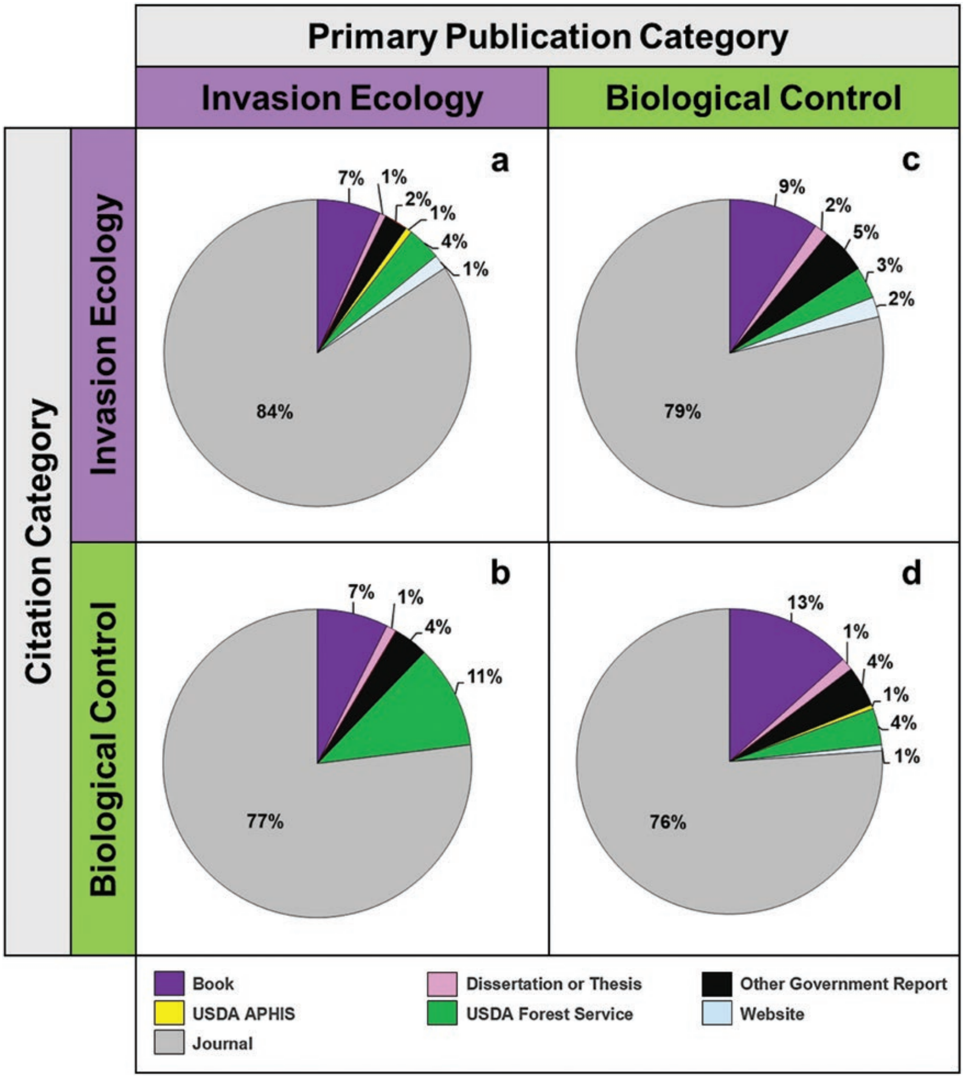

Fig. 3. Pie charts illustrating the types of references (i.e., books, dissertations and theses, journals, government reports, USDA Animal and Plant Health Inspection Service [APHIS] reports, USDA Forest Service reports, and websites) that were commonly cited by each primary publication type: (a) invasion ecology literature cited by primary invasion ecology publications, (b) biological control literature cited by primary invasion ecology publications, (c) invasion ecology literature cited by primary biological control publications, and (d) biological control literature cited by primary biological control publications. Data repository and personal observation data are not included because they made up less than 1% of the citations.

the field has become too parochial (Davis et al. 2001). Therefore, there is a need to improve intra- and interdisciplinary communication and reduce redundancy in terms and hypotheses between and among fields (Catford et al. 2009, Gurevitch et al. 2011, Schulz et al. 2019), which will progress and advance the field of invasion ecology, thereby leading to improved detection and management of non-native species (Vaz et al. 2017). We specifically evaluated the current levels of communication between and within the fields of invasion ecology and biological control to determine if the fields are maximizing their linkages. Primary invasion ecology articles largely cited other invasion ecology literature followed by other ecological literature (Fig. 2a). This indicates that there is an opportunity to diversify the research that is read and cited by invasion ecologists. Specifically, there exists a timely opportunity to strengthen linkages to other fields and incorporate their findings to improve basic and applied understanding and applicability in invasion ecology.

Similarly, primary biological control publications predominantly cited related literature (Fig. 2b), but they also cited invasion ecology literature more frequently than invasion ecology publications cited biological control literature. Biological control research typically focuses on a target prey species, an invasive species, and would therefore, cite relevant ecological research conducted on the invasive organism to best identify and study the biological control agent. It should be noted that most (>80%) of the invasion ecology publications in our study focused on invasive herbivorous insects, whereas most of the biological control publications focused on entomophagous biological control agents that target herbivorous insects. This lack of invasive entomophagous insects in the invasion ecology literature and herbivorous biological control agents in the biological control literature may be a function of real differences in research interest between researchers in the two fields (e.g., perhaps a lot of invasive species research is on invasive pests impacting important forest plant species or forest resources, and control efforts in forests are focused on insect pests of these ecologically and economically valuable forest trees). Also, it is possible that our search terms or other limitations (e.g., less controlled results) of the Google Scholar

Fig. 4. The top 20 invasion ecology and biological control journals cited by the primary invasion ecology and biological control publications. The top circle includes the invasion ecology journals cited by the primary invasion ecology publications (left side) and primary biological control publications (right side). The bottom circle includes the biological control journals cited by the primary invasion ecology publications (left side) and primary biological control publications (right side).

search engine resulted in unbalanced trophic levels in the groups, though we view this as unlikely since we searched through 5,000 potential manuscripts from each category to select our sample of studies. Still, future studies may aim to use a more controlled search engine and/or less specific search terms.

Invasion ecologists and biological control researchers in entomology primarily cited the journals, *Biological Invasions* and *Environmental Entomology*, for most of their information regarding invasive species. There was a 65% citation overlap in the top 20 invasion ecology journals cited by invasion ecologists and biological control practitioners. In comparison, there was a 70% overlap in the top 20 biological control journals cited by invasion ecologists and biological control practitioners. The field of invasion ecology may be slightly more diversified in journals and citations because the field includes theoretical and applied research. However, the field of biological control, although similar to invasion ecology in that it is rooted in theory, tends to be more applied and less frequently theoretical, perhaps because it is a more mature field. Invasion ecologists also used the same key journals (e.g., *Biological Control*, *Biocontrol*, and *Environmental Entomology*) as biological control researchers to cite biological control research. These are the predominant journals for biological control-focused publications, so it is expected that these journals would be frequently cited.

Citation choice may be linked to publication access or a lack thereof. Many of the most cited publications were available online through portals, such as the USDA Forest Service (always publicly available as required by law), ResearchGate, or the Entomological Society of America journals, which can be accessed free online or with a society membership. Journals that were cited by primary biological control publications and not the invasion ecology publications, may be due to limited access or are underutilized by those outside of biological control research. Further, some biological control researchers, as employees of private companies or state and municipal governmental organizations, potentially have more restricted journal access than researchers in academia. This provides another opportunity to strengthen interdisciplinary research. As open access matures and becomes more prevalent, while also combined with search engines like Google Scholar or Open Knowledge Maps (2019), more researchers may be able to diversify and improve their ability to find and access quality, relevant empirical literature wherever it is published, thereby reducing this gap in anticipated overlap among journal citations. Though we do not analyze field-specific conference settings or presentations here, future research may aim to evaluate whether there are differences in conference settings between fields. If biological control professionals and invasion ecologists are found to largely attend different conference settings, they may be neglecting valuable opportunities to actively seek out cross-disciplinary collaborators. While small and informal efforts have started to occur at some conferences, more directed efforts may be necessary to promote this form of cross-disciplinary communication.

Overall, there appears to be some cross-communication between the disciplines, but it is mostly unidirectional with invasion ecology informing biological control. As such, opportunities exist to strengthen inherent linkages and communication methods among researchers, practitioners, and the public to jointly advance the elucidation of natural phenomena and the discipline of ecology as a whole. To date, few published studies (e.g., Williamson and Fitter 1996, Memmott et al. 1998, Grevstad 1999, Yeates et al. 2012) have explicitly used biological control introductions to answer questions in invasion ecology, indicating that biological control datasets are an underutilized resource. For example, biological control agents can provide researchers with a way to empirically test hypotheses in invasion ecology (Ehler 1998, Marsico et al. 2010) and study microevolution (Yek and Slippers 2014) and predator functional responses (Dick et al. 2017).

Cross-disciplinary Communication Is Where Great Ideas Emerge

Invasion ecology and biological control have the potential for complete intellectual overlap, though the fields tend to differ in their approach to research and management. Whereas invasion ecology tends to focus on the theoretical nature of the invasion of non-native species, biological control focuses on the applied nature of invasion and how to manage it, which could help invasion ecology close the knowing-doing gap (Esler et al. 2010, Matzek et al. 2014). If a biological control agent is being introduced from another region, it is going to have to overcome similar obstacles as other non-native species to succeed. It is at this intersection that invasion ecologists can learn a lot from biological control research. Biological control agents are highly variable, ranging from herbivores to predators and parasitoids, so researchers can evaluate how species in these different trophic levels succeed in novel environments (Schulz et al. 2019).

Since biological control agents tend to follow the same path of invasion and encounter similar obstacles, we can learn a lot about the process of invasion using information from the controlled releases of biological control agents (Ehler 1998, Marsico et al. 2010, Yek and Slippers 2014, Abram and Moffat 2018). Many non-native, invasive species are not detectable until they have already established and spread, so it is difficult to determine how many individuals and introductions were required for the species to successfully establish (i.e., propagule pressure). Early monitoring of biological control agents, besides being best management practices (Hajek et al. 2016), may inform researchers about patterns and processes that occur during the rarely monitored introduction and establishment stages (i.e., lag phase; Epanchin-Niell and Liebhold 2015) of accidentally introduced non-native species (Fagan et al. 2002, Yeates et al. 2012). Data collected on biological control agents can also help researchers better understand general mechanisms of invasion, and test particular invasion hypotheses to assess their future empirical value. Information on the native range, biology of the biological control agent, number of releases, population establishment success, and ability to successfully control its host target are just a few of the variables that can provide information and help researchers test hypotheses (Marsico et al. 2010). We are not advocating for researchers to release biological control agents for the sake of testing invasion hypotheses, but rather use biological control agents that are going to be released anyway to enhance the theoretical underpinnings of each stage and the overall processes involved in invasion ecology.

Conclusions

The field of invasion ecology has periodically been criticized for its detachment from other disciplines, with researchers advocating improved communication between invasion ecology and other biological disciplines (e.g., Davis et al. 2001, Shea and Chesson 2002, Vaz et al. 2017). Although we found that invasion ecology is making some progress in terms of relating other ecological literature to species invasions, the field is not maximizing its linkages with the related field of biological control. Improved communication between biological control and invasion ecology will help further the successes of biological control agents and reduce the success of other non-native species by improving early detection and rapid response (Reaser et al. 2020) and management programs of new and existing populations of non-native species. This review article has demonstrated that there are still opportunities for further enhancements in communication in invasion ecology and biological control. To the benefit of invasion ecology, biological control studies can improve understanding of early lag phases of invasion by utilizing release data of biological control agents. To the benefit of biological control, theoretical underpinnings from invasion ecology, including mathematical theory that may foster more parsimonious explanations of outcomes (Shigesada and Kawasaki 1997, Hastings et al. 2005), may make preselection of agents more efficient. We encourage researchers to use the suggestions presented in this article to forge a path forward of increased dialogue.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

Table S1. List of 102 primary invasion publications used for analysis, including the number of references cited in each category.

Table S2. List of 90 primary biological control publications used for analysis, including the number of references cited in each category.

Table S3. List of the 497 journals and other references cited by the 102 primary invasion ecology publications as containing information from the field of invasion ecology.

Table S4. List of the 85 journals and other references cited by the 102 primary invasion ecology publications as containing information from the field of biological control.

Table S5. List of the 287 journals and other references cited by the 90 primary biological control publications as containing information from the field of invasion ecology.

Table S6. List of the 354 journals and other references cited by the 90 primary biological control publications as containing information from the field of biological control.

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