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Biotic resistance to exotic invasions: its role in forest ecosystems, confounding artifacts, and future directions

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Abstract Biotic resistance, the ability of communities to resist exotic invasions, has long attracted interest in the research and management communities. However, inconsistencies exist in various biotic resistance studies and less is known about the current status and knowledge gaps of biotic resistance in forest ecosystems. In this paper, we provide a brief review of the history and mechanisms of the biotic resistance hypothesis, and summarize the central topics and knowledge gaps related to biotic resistance with a special emphasis on forest ecosystems. Overall, although the amount of research efforts on biotic resistance in forest ecosystems has increased since the mid-2000s, aspects such as resistance to exotic pests and pathogens remain understudied. In addition, we synthesize ecological and statistical explanations of observed inconsistencies and provide suggestions for future research directions. Some of the observed inconsistencies on biotic resistance can be attributed to (1) the interactive or additive effects of other ecological processes and (2) the statistical artifacts of modifiable areal unit problem. With the advancement of new statistical knowledge and tools, along with availability of big data, biotic resistance research can be greatly improved with the simultaneous consideration of key ecological processes, the attention to various scales involved, and the addition of understudied systems.

Keywords Competition · Facilitation · Modifiable area unit problem · Pests · Pathogens

Introduction

The numerous ecological, economic and social impacts of invasive exotic (alien, nonnative, or introduced) species have compelled major interest in effective approaches to mitigate their establishment and spread. In particular, research has focused on the intrinsic ability of communities to resist or control

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invasions—a phenomenon termed biotic resistance. Interest in biotic resistance can be traced back to early ecology (Elton 1958; MacArthur 1955, 1972), which proposed that as the number of species in a community increases, more niche spaces are occupied and resources are more fully utilized, therefore enhancing the community's competitive resistance to invasion.

Understanding the degree and mechanisms of biotic resistance has important ecological and conservation implications for it provides useful information for the identification of communities that may be at risk of being invaded. Moreover, an understanding of biotic resistance can guide management efforts to enhance a community's ability to control established invaders or resist future ones (Funk et al. 2008). However, as biotic resistance research advances, it has become clear that this phenomenon is much more complex than expected. Native species are able to interact with exotics in multiple ways that either decrease or increase the probability of exotic establishment and spread. Inconsistencies among research findings on how biological diversity impedes invasion success, both within and across scales, further muddle our understanding (Fridley et al. 2007). Moreover, intrinsic ecosystem characteristics and underlying mechanisms that shape community composition and structure have been found to influence the ability of native communities to resist invasion (Alofs and Jackson 2014; Kimbro et al. 2013; Smith-Ramesh et al. 2016).

Because different ecosystems vary with regard to climate conditions, trophic levels, and interactions among resident species that can affect the biotic resistance of the ecosystem (Fraterrigo et al. 2014; Smith-Ramesh et al. 2016), current knowledge on biotic resistance may be biased toward specific ecosystems and thus may be inadequate for generalizations across ecosystems. For example, species with early successional traits and adaptation to disturbance are strong invaders in grassland communities, but under vastly different environmental conditions and disturbance regimes in forests, invaders require a different set of traits and adaptations (e.g., shade-tolerance) (Martin et al. 2009).

Here, we review and describe various interactions between native and exotic species that diminish invasion success (i.e., mechanisms of biotic resistance). We then review forest-specific biotic resistance literature, in order to elucidate system-specific processes. We further describe the ecological processes and statistical artifacts that may be causing the observed inconsistencies by masking the effects of biotic resistance. We end our review by proposing multiple fronts for future research to advance our understanding of biotic resistance.

Mechanisms of biotic resistance

Competition has been the most widely studied mechanism of biotic resistance, particularly in the plant invasion literature. In-depth theoretical and empirical studies of the mechanisms of competition show that native plants are able to decrease the performance of exotic plant species through direct reduction in available space, light and nutrients (i.e., niche complementarity). For instance, Maron and Marler (2007) found that assemblages with higher plant species richness not only displayed decreased soil moisture, light and nitrogen availability, but also lower invasibility than assemblages with lower species richness. Byers and Noonburg (2003) found that the sum of interspecific competitive effects in their competition model were a major driver of invasibility when resources were held constant. Indeed, the strength of competitive resistance in plant communities has been found to be closely related to abiotic factors, namely resource availability (Going et al. 2009; Shea and Chesson 2002). However, due to spatio-temporal variability in resource availability an exotic plant invader can still overcome competitive resistance by possessing an advantage over resident species at a given time or location (Shea and Chesson 2002).

Although there is a heavy focus on competition as a mechanism of biotic resistance, native communities are able to resist invasion through other ecological processes, such as consumption (i.e., herbivory and predation) and pathogeny. One of the earliest comprehensive reviews of various mechanisms of biotic resistance compared the effects of competition, the diversity of resident competitors, herbivory and soil fungal communities on exotic plant establishment and performance through a meta-analysis of 52 biotic resistance studies (Levine et al. 2004). The meta-analysis showed that competition, herbivory and competitor diversity had strong effects on invader establishment and performance. Evidence on the effects of mycorrhizal fungi and fungal pathogens, on the other hand, showed inconsistent trends, highlighting the species-specific nature of pathogeny as a mechanism of biotic resistance.

While the individual effect of these mechanisms is relatively well studied, the interactive and additive effects of these mechanisms in conferring biotic resistance is considerably less understood. Biotic resistance may be conferred indirectly, through interactions that alter the abundances of species that do interact directly with the exotic invader. Mitchell et al. (2006) propose a theoretical framework to assess and quantify the interactive effects of two species of enemies, mutualists, or competitors on an introduced plant.

Furthermore, we are beginning to understand how intrinsic differences among ecosystems influence biotic resistance mechanisms, and consequently the relative importance of each mechanism in any given ecosystem. Studies have shown important differences between marine, freshwater, and terrestrial ecosystems. Consumptive resistance appears to be a much stronger mechanism of biotic resistance than competition in aquatic ecosystems, presumably due to cross-ecosystem variation in typical levels of community saturation, the role of local coexistence mechanisms, and native traits (e.g., growth rate, size and nutritional quality) (Alofs and Jackson 2014; Kimbro et al. 2013).

Biotic resistance in forest ecosystems

Studies testing biotic resistance have been mostly centered around grasslands and aquatic ecosystems, rendering our knowledge of biotic resistance in forest ecosystems relatively rudimentary. In June of 2016, we used the online database Scopus to obtain all abstracts of journal articles published (N = 501), ranging from 1980 until present, related to biotic resistance. The following keywords were used in searching all titles, abstracts, and keywords: “Biotic resistance” OR “Invasion resistance” OR “Resistance hypothesis” OR “Invasion paradox” OR “Native-exotic richness relationships”. Individual abstracts were then classified for specific systems, i.e., forest, prairie, grassland, and other. Overall, grasslands (N = 85) and aquatic ecosystems (N = 100) dominated the literature, especially during the early period (Fig. 1). Abstracts in the “other” category, which predominantly consisted of studies that were not ecosystem-specific, also figured strongly in the literature. Forest ecosystems were not particularly neglected (N = 65). Articles on forest ecosystems emerged in the mid-2000s and have increased exponentially since then. Here we review the current knowledge of biotic resistance to invasions in forest ecosystems.

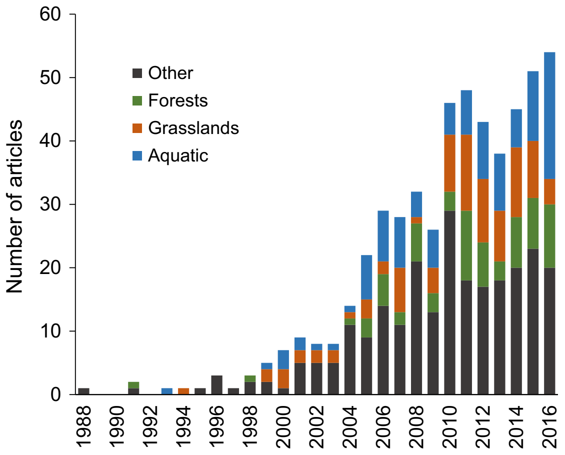

Fig. 1 Increase over time of the number of research articles focused on biotic resistance per year. *Stacked bars* indicate the number of articles each year specific to an ecosystem type (aquatic, grasslands, forests, other). The number of articles in 2016 are an estimate given the trends observed per month from January to June, when the literature retrieval took place

Content analysis of published research of biotic resistance

To obtain a comprehensive understanding of existing literature on biotic resistance in forest ecosystems, we performed an automated content analysis (ACA) on the 65 forest-centric abstracts using Leximancer 4.0 (Leximancer Pty Ltd., Brisbane, Australia). ACA is a novel literature synthesis technique that uses text-parsing software to classify large volumes of text into categories named *concepts*. We followed the steps detailed in Nunez-Mir et al. (2016) to perform ACA.

The ACA results indicate that the most prominent concepts in the forest biotic resistance literature revolved around seedling recruitment and survival traits (Fig. 2). In many cases, seedling survival and recruitment were also explored against varying abiotic conditions, particularly soil conditions (e.g., Dechoum et al. 2015), highlighting the contingency of biotic resistance on abiotic conditions in forests. The concept map also shows a strong focus on how interactions at the community-level influence invasion (e.g., Brooks

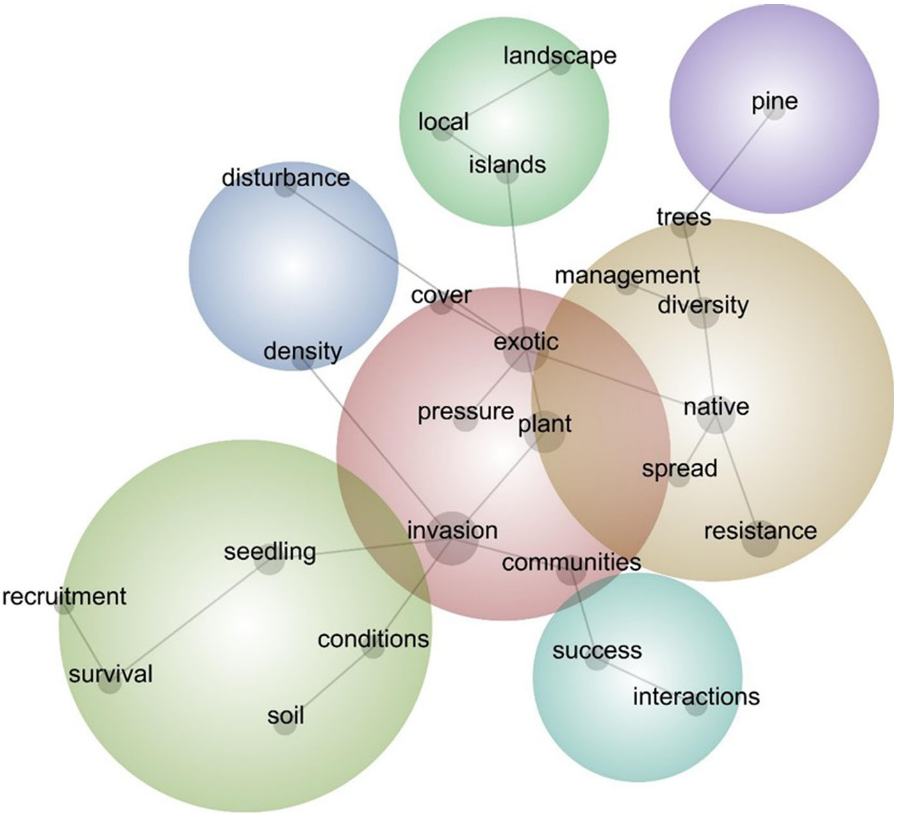

Fig. 2 Concept map of 65 forest-centric abstracts displaying the prominent concepts in the text. The position of each concept on the map is indicative of its relationship to other concepts. *Circle* size indicates the frequency of concept occurrence throughout the text. *Solid lines* represent the strongest direct associations among concepts. *Colored bubbles* highlight groups of concepts that fall within a common theme

and Jordan 2013; Green et al. 2011; Questad et al. 2012). Nonetheless, a cluster of concepts at the top of the map shows that features at the landscape scale are also considered, in addition to local scales (e.g., Butler et al. 2014; Yeo et al. 2014). Unsurprisingly, the diversity of native species, in particular trees, seems to be the most frequently studied mechanism of biotic resistance in the forest-specific literature. In fact, our map suggests that pine-dominated ecosystems may be the focus of a high proportion of forest-centric biotic resistance studies (e.g., Collins et al. 2007; Zas et al. 2011), though ironically pine species are among the most relevant exotic invaders (Nunez and Medley 2011). Furthermore, native diversity appears to be strongly associated to management, highlighting the practical implications and applicability of biotic resistance research in the context of forests.

We further explored the interrelationships among these concepts through a concept co-occurrence matrix (Online Resource 1), which allowed us to assess the strength of the associations between concepts. To gain more insight into the major topics discussed in the literature, we focused on the concepts most strongly associated to *invasion* and *resistance*. Unsurprisingly, the concepts most closely associated to both concepts were *exotic*, *plant* and *native*, highlighting the plant-centric focus of biotic resistance research previously pointed out by other reviews of the literature (see Levine et al. 2004). More insightful, however, is the association between *resistance*, *native* and *diversity*. The strong association of *resistance* with these concepts evidences the perceived importance of diversity as a mechanism for resistance to invasion (Guo et al. 2015). The concept management was also tightly connected to diversity. The two concepts occurred jointly in about half of the total number of text segments containing the concept *management*, possibly evidencing the maintenance of native richness as a preferred management strategy to increase resistance to invasion at both the community and landscape scale. In fact, in regards to scale, the concept *community* was among the most strongly related to both *invasion* and *resistance*. This finding highlights the typical prevalence of studies at smaller scales, and indicates a need for more studies at the landscape and regional scales.

Current understandings of biotic resistance in forest ecosystems

In general, forests are relatively less easily invaded than other terrestrial ecosystems (e.g., grasslands) (Martin et al. 2009). In fact, high resistance to invasions in old-growth, closed-canopy forests is a widely-held concept (Brothers and Spingarn 1992; Fei et al. 2008; Rejmánek 1989; Von Holle et al. 2003). Although ecological theory (Elton 1958) and empirical evidence (Bufford et al. 2016; Tilman 1997) suggest that this perceived superior resistance is due to competitive resistance, a number of studies report positive relationships between native and exotic diversity (e.g., Gilbert and Lechowicz 2005; Howard et al. 2004; Stohlgren et al. 1999). These studies highlight the importance of abiotic factors and native species composition and abundance (Iannone et al. 2015). For instance, Howard et al. (2004) showed that in pine barrens and mixed hardwood communities, abiotic conditions generally associated with favorable environments for high native diversity (i.e., mesic, fertile soils) correlated with increased invasion by shade-tolerant exotics. Another environmental factor that may influence the relative strength of biotic resistance mechanisms is disturbance. Undisturbed forests have not empirically shown superior resistance to invasion (Martin et al. 2009; Martin and Marks 2006). In fact, disturbance has been found to strengthen the pressure of herbivory on exotic grasses that establish on disturbed sites (Maron and Vila 2001). Nonetheless, other studies show that the opposite may also be true, as exemplified by the inversely proportional abundances of an endemic predator and an exotic snail in an insular rainforest (Lake and O'Dowd 1991). Disturbance (or lack thereof) may play a larger role on how biotic resistance hinders the rate of invasion or spread, rather than the establishment of an exotic species (Martin and Marks 2006). Similarly, the effects of native diversity on exotic pest outbreaks are inconsistent with expectations founded on ecological theory and empirical evidence based on studies with native pests (Jactel et al. 2005). These studies argue that mixed forests experience fewer outbreaks than single-species stands because the presence of non-host trees makes it difficult for pests to locate their host species, whether physically or by obstructing odor recognition, and because there is more predation due to the greater diversity and abundance of natural enemies in mixed forests (Jactel et al. 2005). However, some studies have found that native forest diversity has no effect on pest outbreak (e.g., Smith et al. 2015), while others have found positive associations (e.g., Liebhold et al. 2013). Similar to plant invasion, the observed differences in pest-native tree relationship could very likely be the result of different scales studied. Diverse forests appear to harbor more pests due to the increased probability of presence of suitable hosts (Liebhold et al. 2013). Furthermore, diverse forests maybe more prone to "associational susceptibility," by which polyphagous exotic pests (e.g., gypsy moth, Asian longhorned beetle) move onto less palatable species at high densities (Brockerhoff et al. 2006).

Evidence for consumptive resistance is equally inconsistent in its support for the role of this mechanism in decreasing invasion success. Although herbivory has been found to hinder establishment and performance of exotic producers in other ecosystems (e.g., Levine et al. 2004; Parker et al. 2006), in forests, empirical studies show that generalist herbivores may either not have a significant effect on invasion success (e.g., Bufford et al. 2016) or promote invasion as certain exotics have greater tolerances (Ashton and Lerdau 2008; Eschtruth and Battles 2008). Yet, Webster et al. (2008) showed that chronic herbivory decreases invaders' ability to adapt to drought; and Lombardero et al. (2012) found that stands of the exotic *Pinus radiata* were more vulnerable to herbivory and disease than its native congener, as the natives have evolved resistance to native herbivores. On the other hand, consumptive resistance through predation of exotic consumers may be a stronger mechanism of biotic resistance. For instance, insectivorous birds were found to limit invasion of an exotic spider in a Hawaiian forest (Gruner 2005), while predation from *Elatophilus nigricornis* decreased the impact of exotic insect *Matsucoccus feytaudi* on maritime pine stands (Jactel et al. 2006).

Controversies in biotic resistance

As evidenced in the sections above, from its early stages, biotic resistance research has displayed contradicting evidence regarding the ability of native communities to resist biological invasions, not only in forests, but also in all other ecosystem types. This inconsistency is more clearly illustrated by the patterns observed when testing the relationship between native and exotic richness, an indicator of competitive resistance. Empirical and theoretical studies have shown that the association between native diversity and invasion are inconsistent, varying across scales and ecosystems of study (Fridley et al. 2007; Guo 2015; Herben et al. 2004). Generally, at small spatial scales, at which interactions between individuals take place, plots or units with more native species contain less exotic species than those with lower native diversity (e.g., Chen et al. 2010; Tilman 1997), as predicted by the classical theory of biotic resistance. However, some studies have shown the opposite pattern under the same conditions, a positive relationship between native and exotic diversity (e.g., Cleland et al. 2004; Jauni and Hyvönen 2012; Zeiter and Stampfli 2012).

Studies performed at larger spatial scales further add a layer of complexity, as at these scales the relationship between native diversity and exotic species is almost consistently positive (see Herben et al. 2004; Stohlgren et al. 2003). The combination of these observed patterns leads to what is called the "invasion paradox," which states that negative relationships should be expected at small spatial scales, while a positive relationship is expected at larger scales (Fridley et al. 2007). Here, we further review the underlying ecological processes and statistical artifacts that could help to better explain the observed invasion paradox.

Processes diluting the biotic resistance effects

Ecologists have proposed a number of underlying processes able to mask or counteract the effects of biotic resistance occurring at the local scale, and therefore generate positive relationships. Two of the ecological processes identified, facilitation and biotic acceptance, generate positive relationships at both the small and large scale. Facilitation and biotic acceptance represent opposing views to pathways by which diversity begets diversity. Facilitation refers to positive interactions among native species and between natives and exotics that enhance establishment and survival of exotic species (Bruno et al. 2003), while biotic acceptance refers to the situation where favorable environments, presumably indicated by high native richness, are able to maintain large numbers of species, regardless of origin (Stohlgren et al. 2006).

The role of facilitation on invasion success was first brought to the forefront in Bruno et al. (2003). The authors proposed that positive interactions among native species could result in habitat changes that can increase or decrease favorability for exotic invaders. Through facilitation, positive effects from natives to exotics may outweigh the effects of competition in particularly stressful environments. Early support for the role of facilitation showed that the influence of facilitative interactions could explain contradicting patterns among differing environmental conditions. Von Holle (2005) found positive relationships between native and exotic species richness in harsh, stressful streamside areas, yet negative relationships in the more benign upper terrace plot. The author summoned facilitation to explain these contradictions, stating that the occurrence of facilitation in stressful environments is a well-known mechanism of survival.

"Biotic acceptance" was coined and upheld as the antithetic process to "biotic resistance." Formally proposed in Stohlgren's and co-authors' "Scale and plant invasions: a theory of biotic acceptance" (2006), the hypothesis of biotic resistance states that coexistence is a stronger force than competitive exclusion, and therefore favorable environments are able to harbor high numbers of exotic species regardless of the number or abundance of natives. The authors found native species richness to be positively correlated to invasion at the county, state, region and national scales. Therefore, they argue that the strength of biotic acceptance is highest in areas with high species richness and optimal conditions for growth (in the case of plants). An observational study on old-field plant communities (Souza et al. (2011) contributed toward the biotic acceptance hypothesis by providing more evidence to support the claims made in Stohlgren et al. (2006). Souza and co-authors found positive native-exotic relationships at all scales, with native and exotic species richness being more strongly related at the regional scale. They also found regional exotic richness to be strongly related to local exotic richness. Regarding underlying mechanisms, the authors found that mean foliar cover at the landscape scale was the most important factor influencing the slope of native-exotic richness relationships, indicating that the favorability of the environment rather than heterogeneity shaped explained the positive patterns observed.

Statistical artifacts

One of the chief unresolved issues in the biotic resistance research is the change in the direction of the native-exotic richness relationship when moving from small to larger scales. Instead of summoning ecological processes, an alternative camp of thought attributes this scale dependency in the observed patterns to statistical artifacts. This line of research stipulates that sampling effects, simple numerical constraints, and inappropriate null models may produce an artificial negative relationship between native and exotic diversity at the small scale that becomes positive as scale increases. The modifiable areal unit problem (MAUP), a statistical artifact defined as the effect of aggregation of data on statistical measures, may explain the positive relationship between native and exotic diversity at large scales. In that case, the effect of biotic resistance may be artificially masked by MAUP as scale is increased (Dixon Hamil et al. 2016).

MAUP, in fact, refers to two separate but related problems: the zoning and the scale effect (Openshaw and Taylor 1979; Wong 2009). The zoning effect occurs when analyses using units of different shapes, orientation and/or configurations produce different results. On the other hand, the scale effect occurs when units are aggregated and analyses performed on a smaller number of units. The configuration (zoning) and number (scale) of units interact with the spatial distribution of the data at its original resolution. As a result, the relationship between spatially-distributed variables is either magnified or diluted. For instance, Fotheringham and Wong (1991) found that slightly negative relationships at the original resolution could become moderately positive as units were aggregated into larger scales. These findings echo the contradicting patterns observed across scales in the relationship between native and exotic species richness, stressing the need to be aware of this statistical artifact when studying these relationships.

The term "MAUP" was coined by Taylor and Openshaw in 1979. However, the concept had already been identified and discussed in the literature decades prior. For example, Yule and Kendall (1950) present the results of three experiments that test the mechanisms through which MAUP is produced. From these experiments, the authors showed that at their largest scale (99 counties aggregated into 6) correlation coefficients ranging from 0.999 to 0.999 could be observed. They concluded that although spatial autocorrelation and the zoning configuration interact in predictable ways that could explain the variety of correlation coefficients observed, the relationship between spatial autocorrelation and correlation coefficient is much more complex and elusive.

Although relatively well studied in other fields, MAUP has had relatively less attention in the ecological fields, despite the fact that it is highly relevant to any study featuring aggregated data or cross-scaled spatial processes or phenomena. There are, however, a few studies that have focused on the MAUP effects in the context of ecology. An early introduction of MAUP to the landscape ecology community, Jelinski and Wu (1996), explores the impacts and implications of scale and zoning effects on landscape analyses. In this study, the authors explore the scale effect by aggregating pixels, and zoning effects by creating different zoning configurations at the small scale and large scale. The authors found that increasing scale for the most part decreased spatial autocorrelation across landscapes, while changing the zoning configuration had mixed effects on spatial autocorrelation depending on the landscape, reflecting intrinsic differences in the spatial distribution of these landscapes.

Another study exploring the effects of MAUP in an ecological context, Lechner et al. (2012), tested how the resolution of remote sensing environmental data affects the perceived intrinsic scale at which the interaction between an ecological attribute and an environmental factor occurs. The effects of MAUP on the identification of intrinsic scale were tested through a simulation model that compared the relationship between species diversity and vegetation cover for a correct landscape and a set of apparent landscapes, created by aggregating and processing pixels. The authors found that the apparent landscapes, using different pixel sizes, displayed different correlation curves, evidencing the presence of MAUP in this use of remote sensing data.

These findings demonstrate that MAUP may have serious implications for the application of certain spatial analysis methods or simulation models that involve aggregation. In particular, remote sensing is vulnerable to MAUP as the pixels of the image are certainly modifiable units that depend on the capacity of the sensor and available technology. The influence of MAUP on ecological research warrants more attention than it is currently given.

Moving forward

To improve our understanding of biotic resistance, both in forests and other ecosystems, it is necessary to study the interactions of the aforementioned ecological processes, along with a need for better frameworks for handling statistical artifacts. Moreover, we advocate the following perspectives in advancing our knowledge in biotic resistance, particularly in forest ecosystems.

Invasion potentials versus degree of invasion

It is still questionable whether native-exotic richness relationships can be used to evaluate invasibility or even degree (or level) of invasion (DI). In other words, does a negative native-exotic relationship actually indicate biotic resistance is at play? Furthermore, does a positive relationship indicate the opposite? It is becoming increasingly clear that both DI and potential invasibility of a community are determined by multiple factors, including the proximity to exotic species pools, disturbance, human population density and migration (Rejmánek 2003), location, and history (Davies et al. 2005). Communities that are equally resistant may show different DI if the source of exotic species is remote or the time is not “right” (e.g., late succession) (Williamson 1996), therefore displaying contradicting native-exotic relationships.

In addition, for native species to competitively resist invaders, they need to build up sufficient biomass or cover so as to exhaust or limit resources, such as nutrients and light. For instance, in communities with high levels of native species diversity, certain levels of disturbances may reduce biomass and therefore create gaps that exotics can still invade (Williamson 1996) while natives continue to persist, producing a positive native-exotic relationship. Reported contradictions in the diversity-invasibility relationship may be a result of differing levels of biomass or cover. Competition is linearly related to both aboveground and belowground biomass, but not species diversity. Communities with high biomass may be saturated, with most niches occupied. In such habitats, interspecific competition is likely to be very strong, thus displaying high biotic resistance. However, high diversity does not necessarily equate with high biomass. When biomass is low, a positive relationship between biomass and diversity is observed; but when biomass is high, a negative relationship emerges (Grime 2006).

Resistance to low versus high impact invaders

Not all invaders were made equal. The damage caused by a single high-impact exotic invasive species (e.g. *Microstegium vimineum*) may vastly outweigh that of multiple low- to moderate-impact invasives. In parallel, the processes that influence the establishment and spread of high impact invaders, may differ from those that determine that of low/moderate-impact invaders. Therefore, mechanisms of biotic resistance may differ in their efficacy depending on the potential impact of the invader. Specific comparisons of biotic resistance to high- versus low/moderate-impact invaders have not been pursued and may represent an interesting avenue for future research. Current evidence suggests that certain mechanisms of biotic resistance, namely herbivory and predation, may have an effect on the rate of spread or abundance of high-impact invaders (e.g., Bajer et al. 2015; Dorn and Hafsadi 2016). On the other hand, the ability of established resident exotic species to contribute to a community’s resistance may be positively related to their potential impact (Henriksson et al. 2016), providing an additional layer of complexity.

Big data and novel statistics

Many variables related to propagule pressure, socioeconomic invasion drivers, biological and geophysical complexity can affect the realization and the prediction of biotic resistance for a specific ecosystem. To better understand biotic resistance and its relationship to other mechanisms, advances are needed in both of the following fronts. The first is the need for big data at the regional to continental or even global scales. The two common attributes in big data, large volume and high heterogeneity, can facilitate new insights in life science research that are imperceptible from small datasets (Howe et al. 2008; Shneiderman 2014). Big data will not only allow the exploration of large numbers of explanatory variables with sufficient statistical power, but also unveil across scale generalities and emergence of novel patterns that cannot be observed with small observational or experimental datasets.

The second is the advancement of statistical tools. To better understand biotic resistance, we believe the following statistical approaches can be beneficial. Due to variability in multiple exogenous factors, not all study sites have approached maximum levels of invasion. For this reason, statistical procedures such as extreme value analysis, quantile regression, and frontier analysis, which are used to define the outmost relationship between the responses and explanatory variables (Battese and Coelli 1995; Resnick 2007) should be considered if the purpose is to unveil the biotic resistance patterns. On the other hand, if a study aims to uncover the contribution of known or unknown variables to biotic resistance, machine learning based statistical models, or Bayesian models, or the combination of the both should be considered. Selecting important variables from a large number of potentially correlated variables is a common challenge in fields that utilize massive datasets. Statistical and computational methods, collectively referred to as machine learning, have been developed to address this problem in the last 20 years (Jordan and Mitchell 2015). Bayesian models, on the other hand, not only can generate the full posterior distribution of estimated parameters alleviating potential model overfitting by identifying variables that have high levels of uncertainty, but also allow for stochasticity at multiple levels and capture uncertainties due to "unobservable" latent variables and parameters through the inclusion of hierarchical structure (Beaumont 2010; Clark 2005).

Highly managed forests and plantation forest systems

Forests managed intensively for timber production tend to have fewer canopy species and differences in their species composition and structure, compared with 'natural' forests (e.g., Crow et al. 2002). However, despite the potentially reduced richness in canopy tree species, this may not be obvious in studies comparing the overall richness of vascular plants (Paillet et al. 2010). For example, uneven-aged managed forests had fewer canopy species but more vascular plant species overall than unmanaged old growth forests (Crow et al. 2002). This is thought to be the result of selective encouragement of desirable tree species while unwanted species are suppressed, combined with effects of overstory thinning and disturbance of the forest floor, caused by management and harvesting, which lead to an increase in understory species (Crow et al. 2002). Planted and plantation forests tend to have an even lower richness of canopy tree species because they are typically managed as single-species stands, while understory plants may or may not be reduced, for example if management practices suppress the understory (e.g., Bremer and Farley 2010; Brockerhoff et al. 2008; Carnus et al. 2006). Meanwhile, significant areas of planted and plantation forests are distributed worldwide. For example, most of Europe's forests were cleared in the industrial revolution and much of its current forests were re-established by planting and were intensively managed (Perlin 2005). Similarly, planted forests are massive in China, where different tree species and combinations of different species groups were used (Fang et al. 2001).Therefore, due to the wide distribution and economic and ecological importance of plantation forests, it is important to understand biotic invasions in these forests.

Given that habitat invasibility can be inversely related to biodiversity, the reduced richness of tree species in intensively managed and plantation forests is a potential concern; however, comparisons of invasions of these forests and natural forests do not provide unequivocal evidence of the occurrence of such a relationship. There are examples of managed forests that contain more exotic plant species than equivalent unmanaged old-growth or second-growth forests (e.g., Crow et al. 2002). Similarly, single-species forests (such as plantation forests) tend to be more invaded by exotic plants and more invasible than mixed forests with less disturbance (Chytrý et al. 2008). Plantation forests may also have a higher degree of invasion by exotic insects than natural forests. For example, in exotic pine plantation forests in New Zealand, approximately 25% of insect species were exotic, compared with only 7% in adjacent natural forest remnants (e.g., Pawson et al. 2008). This difference is not primarily explained by differences in the number of exotic beetles feeding on pines as this study concerned primarily Carabidae and Scarabaeidae with species that use the exotic plantation forest as habitat but feed on resources other than pine trees. The greater richness of exotic beetles is probably more related to the habitat disturbance that occurred before planting and, to some degree, because the understory includes many exotic plants (Brockerhoff et al. 2003) which provide opportunities for invasion by exotic insects. It would be of interest to determine the relative importance of these factors in explaining the greater invasion of these single-species exotic plantation forests, but it is clear that they are less resistant to invasion than adjacent mixed native forests. On the other hand, there are surprisingly few exotic pine-feeding insects in pine plantations in New Zealand, contrary to expectations regarding the invasibility single-species forests of exotic tree species; however, this appears to be more an effect of New Zealand's geographic isolation and distance from the main source regions of pine-feeding insects.

Improvement of biotic resistance to insect and pathogen invasions

Compared to plant invasions, relatively little is known about biotic resistance to insect and tree disease invasions. Comparing different regions of the world, more such exotic species are established in some areas than others though these patterns reflect not only geographical variation in biotic resistance but also variation in propagule pressure (Liebhold et al. 2013). One aspect that differentiates herbivorous insects and tree pathogens from invasive plants is that their ability to reproduce is constrained by the availability of host plants. This has several implications for resistance to invasions. For example, there have been relatively few invasions of insects and diseases on native trees in the southern hemisphere because the primary source of trade and travel from the northern hemisphere brings insects and diseases that are poorly adapted to the taxa of trees in the southern hemisphere (Brockerhoff et al. 2010). Conversely, most insects invading northern hemisphere forests have originated from other parts of the northern hemisphere where they often feed on trees in the same genera or families (Mattson et al. 2007; Yamanaka et al. 2015). A consequence of the close association between insect herbivores and plant taxa is that greater diversity of plants at the genus or family level increases the number of potential hosts and therefore the opportunity for a greater number of insects to invade richer forests. Based on observations in the United States, a positive relationship between native tree species richness and the number of invasive forest insects was noted (Liebhold et al. 2013); however, it is not clear whether this necessarily increases the probability of insect invasions. A study at the plot scale has found that there was an inverse relationship between tree species richness and the degree of invasion by an exotic tree-feeding insect on chestnut (Guyot et al. 2015).

Conclusion

Although the number of studies focused on biotic resistance has increased exponentially since the late 1980s, many unresolved complexities and knowledge gaps remain. First, most research has focused on the ability of plant communities to resist invasion through competition. Meta-analyses of the literature show that herbivory and predation are also able to confer resistance to invasions. In fact, the relative importance of these mechanisms has been found to be ecosystem-specific. Second, empirical and theoretical studies have shown inconsistencies in the relationship between native diversity and invasion across scales and ecosystems of study. Ecological processes such as biotic acceptance, the antithesis to biotic resistance, and facilitation could counteract or mask the effects of competition and/or consumption. Furthermore, inconsistencies observed as scale is increased may be the result of statistical artifacts, in particular the aggregation effects associated with the modifiable areal unit problem (MAUP). Finally, research gaps that present fruitful venues for future research include invasions in plantation systems and the role of biotic resistance in impeding exotic pest outbreaks. In order to continue the advancement of biotic resistance research, it is necessary to consider the difference between invasion potential and degree of invasion, as well as the use of big data and novel statistical methods.

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