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Using limiting similarity to enhance invasion resistance: Theoretical and practical concerns

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Abstract

1. The control of invasive species is a central topic of both applied and theoretical research. Understanding how and which ecological theories can be used to improve invasion resistance of plant communities is essential, to design effective control strategies.
2. The theory of limiting similarity, stating that coexistence between species is more limited by competitive exclusion when species share niche properties, is often considered by applied ecologists as a possible approach to limiting plant invasions at the local scale.
3. The complexity of measuring ecological niche overlap between species as well as the difficulty of disentangling niche from fitness processes currently limit the demonstration and application of this theory. Limiting similarity appears to operate at a time-scale that is too long for efficient impact on invasive species' early establishment. It may also be ineffective against invasions in the long term, due to environmental changes and community instability. Finally, limiting similarity is not applicable to the most common situations, where there are multiple co-occurring invasive species or no prior identification of potential invasives.
4. *Synthesis and applications*. Whether the theory of limiting similarity, predicting competitive exclusion when species display niche similarities, can be successfully applied to limit plant invasions—or not—is an important issue for practitioners facing invasive species. In practice, using limiting similarity to design invasion-resistant plant communities appears to be complex, ineffective and unsuitable for most common situations.

KEYWORDS

biotic resistance, coexistence, competitive exclusion, ecological niche, fitness, invasive species, restoration

1 INTRODUCTION

Invasive species are a key driver of biodiversity loss world-wide (MacGeoch et al., 2010). Controlling them (as a conservation objective) is a central topic of both applied (Byun & Lee, 2017; Clements, Larsen, & Grenz, 2016; Clewley, Eschen, Shaw, & Wright, 2012; Connolly et al., 2018) and theoretical research (Catford, Jansson, & Nilsson, 2009; Davis, Grime, & Thompson, 2000; Hallett,

2006; Shea & Chesson, 2002; Tilman, 2004). Many studies suggest that more resources are invested in post-invasion control and impact reduction than in prevention or early intervention (Simberloff et al., 2013). In this regard, the establishment of a native resistant plant cover after a disturbance (e.g. after restoration activities implying vegetation clearing) is increasingly recommended to impair invasive plant species colonization and local spread (Byun, Blois, & Brisson, 2018). One of the ecological theories explored by applied ecologists seeking to improve the invasion resistance of plant communities is limiting similarity. The limiting similarity theory derives from the classical niche theory, which states that a species persists under a specific range of conditions (Hutchinson, 1959) and that an overlap in ecological niche with another species can prevent establishment in a community (Case, 1983; Diamond, 1975; MacArthur & Levins, 1967). Limiting similarity theoretically means that competitive exclusion will limit the coexistence of species sharing the same ecological niche (Abrams, 1983; Funk, Cleland, Suding, & Zavaleta, 2008; MacArthur & Levins, 1964, 1967). This hypothetical competitive exclusion is therefore considered as a possible way to reinforce the biotic resistance of native communities (Funk et al., 2008; Yannelli, Hughes, & Kollmann, 2017). In practical terms, attempts to apply limiting similarity involve reassembling plant communities so that the dominant species' ecological niche is similar to that of a target invader. Price and Pärtel (2013) examined experimental evidence of limiting similarity in invasion resistance and found partial support in artificial communities. In this paper, we go further by challenging the theoretical and practical issues raised by the application of limiting similarity to design invasion-resistant plant communities. We aim at answering the following question: Can we predict the competitive impact of a plant community by measuring niche overlap and therefore applying limiting similarity to enhance invasion resistance, and if so, would it be an efficient approach?

2 APPLICATIONS OF LIMITING SIMILARITY INVOLVE OVERSIMPLIFICATION

A species' ecological niche (hereafter termed 'niche') is usually defined as an n-dimensional hypervolume (Hutchinson, 1957), characterized by axes of resource use and/or environmental conditions within which populations are able to maintain a longterm average net reproductive rate ≥ 1 (Gause, 1934; Silvertown, 2004). Originally, this concept was introduced to emphasize the role of habitat and food in defining the niche of an animal (Chase & Leibold, 2003). Unlike in many animal communities, plants' coexistence is not explained by the trophic niche: all plants consume the same resources (light, water, CO₂, nitrogen, phosphorus, potassium and other macroand micronutrients; Silvertown, 2004). Two niches are hypothesized to be different if there are differences (a) in resource use across time and space, (b) in the ratios of limited resources required and (c) in the conditions for regeneration, or if there is complementarity of life-forms (Cody, 1986; Grubb, 1986; Tilman, 1982). Thus, the niche appears to be a complex, multidimensional concept that currently escapes comprehensive description. Niche differentiation is therefore usually described on a very limited number of axes, such as environmental (e.g. hydrology, salinity, soil texture or drought) or resource gradients (e.g. light or nitrogen) (Silvertown, 2004), although some studies also include space and/or time (Fargione & Tilman, 2005).

In demonstrations or applications of the limiting similarity theory, niche overlap between species is reduced to similarities quantified by measuring functional traits. The rationale is that these traits relate both to strategies of resource capture and to the effect on the overall pool of resources; they are effect and response traits (Goldberg, 1996; Lavorel & Garnier, 2002; McGill, Enquist, Weiher, & Westoby, 2006). Different groups based on similarities in growth form or other morphological or phenological trait similarities have been defined, assuming that species from the same group should have greater niche overlap and compete more intensively than species from different groups (Johansson & Keddy, 1991; MacArthur & Levins, 1967). However, most studies found no or very limited support for limiting similarity in invasion resistance (Abella, Craig, Smith, & Newton, 2012; Byun & Lee, 2017; Cleland, Larios, & Suding, 2013; Daneshgar & Jose, 2009; Emery, 2007; Eriksson,

Wikström, Eriksson, & Lindborg, 2006; Fargione, Brown, & Tilman, 2003; Funk & Wolf, 2016; Larson et al., 2013; Longo, Seidler, Garibaldi, Tognetti, & Chaneton, 2013; Öster & Eriksson, 2012; Prieur-Richard, Lavorel, Grigulis, & Dos Santos, 2000; Turnbull et al., 2005; von Holle, 2005; Yannelli, Karrer, Hall, Kollmann, & Heger, 2018). While such failures do not necessarily invalidate the limiting similarity theory, they are probably due to an inability to reach the domain of validity of this theory. For instance, there may be an insufficient degree of niche overlap between selected native and invasive species, or perhaps niche processes are not a determining factor in invasion resistance.

2.1 Getting the degree of niche overlap right is complex

What degree of niche overlap is required for competitive exclusion? is one key question that needs to be answered before limiting similarity can be applied successfully. Several categories of similarities between native and invasive species have been explored: in growth form (e.g. C3-grasses, C4-grasses, non-leguminous forbs and legumes; Emery, 2007; Fargione et al., 2003; Prieur-Richard et al., 2000; Symstad, 2000), in life longevity and phenology (e.g. annuals, perennials, early or late seasonal plants; Abella et al., 2012; Cleland et al., 2013; Larson et al., 2013), in morphology (e.g. woodiness, height, presence of taproot; Byun & Lee, 2017; von Holle, 2005) and/or in physiology (e.g. specific leaf area, relative growth rate, leaf dry-matter content; Byun & Lee, 2017). The findings from most studies do not support limiting similarity as an efficient, robust way to limit early establishment of invasive species. Among other explanations, this may be because the degree of niche overlap was insufficient to induce competitive exclusion.

2.2 Limiting similarity may have less impact than differences in fitness on early establishment success

A non-negligible role of limiting similarity has indeed been demonstrated in plant community assemblage (i.e. more trait divergence between species of a local assemblage than expected under a random null model; Armbruster, 1986; Fukami, Martijn Bezemer, Mortimer, & van der Putten, 2005; Mason & Wilson, 2006; Stubbs & Wilson, 2004; Wilson, 2007; Wilson & Whittaker, 1995; but see Mahdi, Law, & Willis, 1989), as well as in invasiveness (i.e. functional similarity to native species facilitates naturalization but hinders invasion; Divišek et al., 2018; Hamilton et al., 2005). However, its role in early establishment success at the local scale may be limited compared with the effect of differences in fitness (Funk & Wolf, 2016; Kunstler et al., 2012). Fitness advantage can arise from greater ability to effectively use resources in a specific range of environmental conditions (Freckleton & Watkinson, 2001; Keddy & Shipley, 1989; Mesléard, Ham, Boy, van Wijck, & Grillas, 1993), resulting in a competitive hierarchy (Fargione et al., 2007; Herben & Goldberg, 2014). Competitive hierarchies have been shown to occur within functional groups (Turnbull, Coomes, Hector, & Rees, 2004; Turnbull et al., 2005; Wedin & Tilman, 1993), contrary to the within-group equivalence predicted by limiting similarity (Hubbell, 2005). Accordingly, specific trait values—not necessarily similar to those of the target invader—such as high specific root length (Daneshgar & Jose, 2009; Funk & Wolf, 2016), large size or height (Byun & Lee, 2017), high growth rate (Symstad, 2000), or early access to limiting resources (Longo et al., 2013) have been linked to increased invasion resistance (Drenovsky & James, 2010). Moreover, competition can be intense between functionally distant species (e.g. between lianas and trees; Schnitzer, Kuzee, & Bongers, 2005).

Fitness inequality can also arise from a size-related competitive advantage generated through priority effects (Wilsey, Barber, & Martin, 2015), where the species established first sequester resources, thus depriving later colonizers (Byun, Blois, & Brisson, 2013; Fukami, 2015; Vance, 1984). Giving reassembled native species a short time advance (i.e. a few weeks) has been shown to create strong priority effects, successfully decreasing invasive species success (e.g. Byun et al., 2013; Grman & Suding, 2010; Vaughn & Young, 2015; Young, Stuble, Balachowski, & Werner, 2016). Several studies concluded that difference in fitness is more important than similarity in niche in determining invasion

resistance, at least in the short term (Byun et al., 2013; Byun & Lee, 2017; Firn, MacDougall, Schmidt, & Buckley, 2010; Funk & Wolf, 2016; Grman & Suding, 2010; Kunstler et al., 2012; Larson et al., 2013; Prieur-Richard et al., 2000; Wang, Ge, Zhang, Bai, & Du, 2013).

Moreover, disentangling niche from fitness processes is not easy, especially when only one invader is tested (e.g. Byun et al., 2013; Dukes, 2002; Sheley & James, 2010; Symstad, 2000; Walder, Armstrong, & Borowicz, 2018). When a resident species is the most effective in decreasing the success of an invader belonging to the same functional group, it is impossible to conclude on whether the effect is due to differences in niche or in fitness: the experimental design makes it difficult to rule out the possibility that a similar response could have been observed with invaders from other functional groups, which would support differences in fitness as being more important than niche similarity.

3 LIMITING SIMILARITY MAY TAKE TOO LONG TO ACT

There are several reasons to believe that limiting the establishment of an invasive species demands rapid and robust inhibition of invasive species seedling emergence and survival. The seedling stage offers a critical window of opportunity to control invasive species effectively, for two main reasons. First, the seedling stage is the most vulnerable stage in the life cycle of plants (Baskin & Baskin, 1998; Fenner & Thompson, 2005). Second, invasive species often exhibit a high growth rate (Dawson, Fischer, & van Kleunen, 2011; Marushia, Cadotte, & Holt, 2010; Rejmánek & Richardson, 1996) and strong priority effects (Dickson, Hopwood, & Wilsey, 2012; Stuble & Souza, 2016; Wilsey et al., 2015), thus rapidly becoming competitively superior after establishment (Martin & Wilsey, 2012).

Competitive exclusion via limiting similarity, which may take several generations (Passarge, Hol, Escher, & Huisman, 2006), may therefore act at too long a time-scale to successfully hamper invasive species colonization (Abrams, 1983; Price & Pärtel, 2013; Stohlgren, Barnett, Jarnevich, Flather, & Kartesz, 2008; Symstad, 2000). Seedlings are not necessarily functionally similar to adults (Hooper & Dukes, 2010), meaning that it would take too long for the resident species to affect functionally similar invasive species. In support of this, Price and Pärtel (2013) found less effect from limiting similarity on invader colonization (germination, establishment or seedling survival) than on performance (biomass, cover or growth). Limiting similarity thus appears to be an inappropriate approach to hindering the early establishment of invasive species.

But is limiting similarity any more appropriate for limiting invasive species success in the long term? Its long-term efficiency relies heavily on the stability of the community over time, achieved by maintaining species assumed to prevent the development of similar invasive species. Yet, species dominance in a community can decrease over time through succession, raising the risk that species selected for their similarities with the target invasive species will lose their dominance. In this case, a reasonable hypothesis is that the environmental conditions will also become unfavourable for the invasive species. A more appropriate strategy could be to foster a diverse community where a few species are likely to respond favourably to changes in environmental conditions, especially if the community sown is dominated by perennials (Byun & Lee, 2017; Corbin & D'Antonio, 2004; Naeem et al., 2000). This might be a surer bet than relying on the capacity of one or a few species resembling the invasive to maintain dominance under changing conditions.

4 LIMITING SIMILARITY CAN ONLY BE APPLIED TO A SINGLE TARGET INVASIVE SPECIES

The concept of limiting similarity is only applicable to control a single invasive species (or a group of species occupying the same niche). This implies that the target invasive species has previously been identified. The scope is thus narrowed to situations where the target invasive species (a) is present at the site prior to management or restoration actions (and its propagules are potentially present in the

soil), or (b) poses a direct threat to the site through being established nearby. However, previously unnoticed invasive species can emerge from persistent seed banks (e.g. Honig, Cowling, & Richardson, 1992; Pyke, 1990; Shen, Liu, Baskin, Baskin, & Cao, 2006) through the soil disturbances generated by restoration activities (Fumanal, Gaudot, & Bretagnolle, 2008). Invasive species established several kilometres away can reach the site through long-distance dispersal abilities (Buchanan, 1989; Renne, Barrow, Johnson Randall, & Bridges, 2002; Stansbury, 2001). Moreover, there are far more situations where several invasive species co-occur than single-invaded habitats (Kuebbing, Nuñez, & Simberloff, 2013). The application of limiting similarity may therefore be ineffective in a wide range of common situations, such as when potential invaders are not yet identified and when multiple invaders co-occur.

All these arguments suggest that the application of the theory of limiting similarity to design invasion-resistant plant communities does not seem relevant in most cases. Research efforts should focus on strategies that quickly and significantly reduce invasive species colonization, and that are efficient when there are multiple co-occurring invasive species. Establishing a community displaying a great diversity of functional traits would allow a more effective and stable use of resources over time and space—and the occupation of most of the niches (Sheley, Svejcar, & Maxwell, 1996). Also, when increasing the number of species in a community, theoretically, the probability of a species being present to be a strong competitor to invasive species increases (Lavorel, Prieur-Richard, & Grigulis, 1999). Diverse communities may therefore exhibit an increased invasion resistance when fully established. However, diverse communities would include slow growing, low competitive species that would compromise invasion resistance at the first stages of growth. Therefore, in a case where invasive species are already present in the immediate vicinity and thus threatening the site, this strategy may be less effective. Combining this strategy with approaches giving a rapid and strong invasion resistance, for example through priority effects (Hess, Mesléard, & Buisson, 2019), would seem a more promising way of effectively hinder invasive species' early establishment.

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AUTHORS' CONTRIBUTIONS

M.C.M.H. and F.M. initiated the study. All authors contributed critically to the development of concepts and writing of subsequent drafts, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data have not been archived because this article does not use data.

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