

# FACILITATIVE MECHANISMS UNDERLYING THE EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING

Essay Review

## Facilitation and the invasibility of plant communities

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### Abstract

1. One of the most studied emergent functions of plant community diversity is the resistance of diverse communities to non-native invasions. As emphasized in this Special Feature, facilitation among native species is a key mechanism by which biodiversity increases various functions, including resistance to invasion. However, when diverse assemblages facilitate non-native species, diversity–invasibility resistance may be compromised.
2. Here, I review the scientific literature on plant invasion in which facilitative interactions, either among native and non-native plant species or among non-native species, affect community invasibility.
3. Native species can directly facilitate non-native species, and also generate net indirect facilitative effects through suppressing species that compete with non-native invaders, but examples of the latter are not common. Such direct and indirect facilitation among non-native species contributes to ‘invasional meltdown’ that restructures native communities.
4. In general, facilitative interactions between native and non-native species increased with environmental stress, suggesting that community diversity might resist invasion more effectively in environmentally favourable sites, whereas in environmentally severe sites, facilitative interactions may contribute to invasibility.
5. *Synthesis*. Native and non-native species can facilitate each other in direct and indirect ways, with important consequences for the invasibility of communities. Facilitative interactions may alter the fundamental relationship between diversity and invasibility, particularly in environmentally severe habitats.

### KEYWORDS

invasion assistance, invasion resistance, plant invasions, positive interactions

## 1 | INTRODUCTION

Expansions of non-native species negatively affect native species, communities and ecosystem functioning (Blackburn et al., 2019; Pyšek et al., 2012; Simberloff et al., 2013; Vilà et al., 2011). The ability of non-native species to invade new communities depends on the traits of the non-natives, their propagule pressure and the susceptibility of native communities to invasion (i.e. invisibility; Lonsdale, 1999). A key emergent function of community diversity

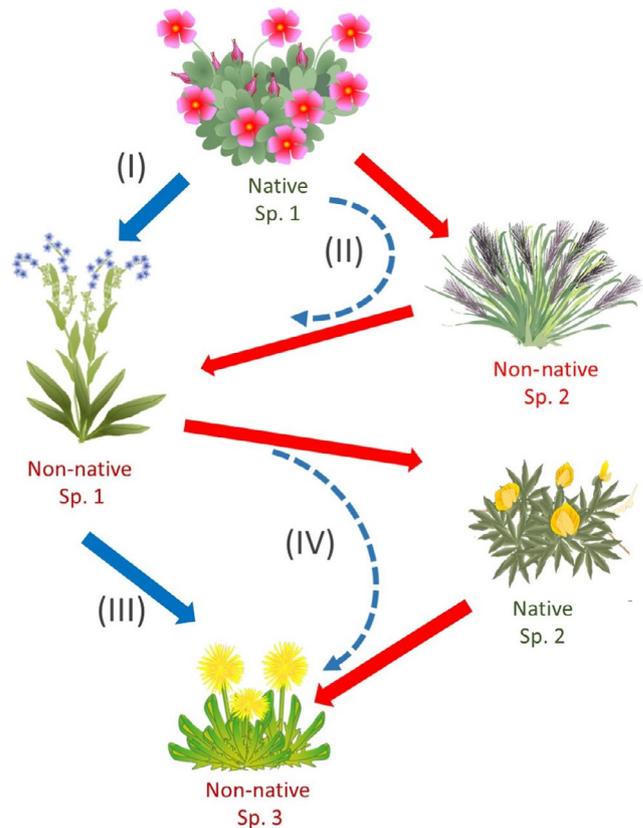
is its role in the invasibility of communities, where it has been widely shown that diverse communities better resist non-native invasions (e.g. Byun et al., 2013; Dukes, 2001; Hector et al., 2001; Kennedy et al., 2002; Maron & Marler, 2007; Naeem et al., 2000; Tilman, 1997; Yang et al., 2017; Zavaleta & Hulvey, 2004). Communities with higher species diversity are thought to more effectively use resources, and hence compete better with non-native invaders (see Maron & Marler, 2007; Naeem et al., 2000; Tilman, 1997, 2004). Communities with higher plant diversity also have higher probabilities of including

a highly competitive native species, which may resist invasion (i.e. Fargione & Tilman, 2005; Zhu et al., 2015). Either way, the process underlying these aspects of the diversity–invasibility relationships is competition.

However, facilitative interactions can also play a key role in exotic invasion. Facilitation occur when one species increases the performance of other species (Callaway, 2007). Facilitators may function directly by improving environmental conditions (e.g. ameliorating temperature and drought, providing protection from wind and increasing nutrient supply), or indirectly by decreasing herbivory or competition (e.g. Melfo et al., 2020; Michalet et al., 2015; Sotomayor & Lortie, 2015). Facilitative interactions among plants increase community richness and organization (Brooker et al., 2008, 2009; Cavieres et al., 2014) and their evolutionary trajectories (Gavini et al., 2019). As emphasized in this Special Feature, direct and indirect facilitative interactions are also important mechanisms in biodiversity–ecosystem function (BEF) processes (Caldeira et al., 2001; Cardinale et al., 2002; Knops et al. 1999; Mulder et al., 2001; Wright et al., 2017; Yang et al. 2015). As for competition, facilitation can operate in BEF processes through whole-community mechanisms (see Aguirre et al., 2021, this Special Feature) or by the inclusion of strong facilitators in diverse communities (Wright et al., 2017). Either way, facilitative interactions can affect how biodiversity either resists or promotes to non-native invasion (see also Bruno et al., 2003; Bulleri et al., 2008). Indeed, Fridley et al. (2007) identified facilitative effects of native species on non-native as an important driver of invasion that help to explain the ‘invasion paradox’ (i.e. fine-scale experiments tend to show a negative association between diversity and invasibility, but broad-scale observational surveys generally report positive correlations between native and non-native species).

The role of facilitation in non-native invasions emerged during the last two decades (Bruno et al., 2003; Richardson et al., 2000; Simberloff & Von Holle, 1999; Traveset & Richardson, 2014). Simberloff and Von Holle (1999) introduced the term ‘invasional meltdown’ to describe the promotion of non-native species by other non-natives, potentially increasing impacts and accelerating invasion overall. Facilitative interactions where non-native plants modify the environment in ways that favour the recruitment of other non-natives is an important mechanism in the invasional meltdown (Richardson et al., 2000; Simberloff, 2006; Simberloff & Von Holle, 1999). A recent meta-analysis of the interactions among non-native plant species found that negative and neutral interactions were the most commonly reported outcome (Kuebbing & Nuñez, 2015). Facilitative interactions were less frequent and positive mean effect sizes were rare, but some plant traits—nitrogen fixation, life cycle and functional group—corresponded with positive interactions among non-natives. However, despite the potential importance of facilitative interactions in BEF and in invasions, there have been no studies that have systematically assessed the role of facilitative interactions in the context of diversity and invasibility, the underlying mechanisms, and how these particular facilitative processes respond to variation in the abiotic environment.

Here, I review the literature on plant invasions, assembling examples of direct and indirect facilitative interactions among native



**FIGURE 1** Diagram illustrating the different type of facilitative interactions between native and non-native plant species during the invasion process. Blue arrows are for facilitative interactions and red arrows are for competitive interactions, straight arrows are for direct interactions and dashed arrows are for indirect interactions. From the top to the bottom: a native species (sp. 1) can directly facilitate a non-native species (n-sp. 1): interaction-type I. In other cases, this native sp. 1 can have a negative effect on a non-native species 2 that compete with non-native sp. 1, generating a net indirect facilitative effect on the latter: interaction-type II. Non-native sp. 1 can directly facilitate other non-native species sp. 3 (interaction-type-III), increasing community invasibility. In other cases, the non-native sp. 1 can compete with a native sp. 2, that in turn competes with a third non-native sp., generating a net indirect facilitative (interaction-type IV), also increasing community invasibility

and non-native plant species and among non-native species. I then organize these examples following to Figure 1, and then explore how these facilitative interactions vary with abiotic contexts and the consequences of these changes for the invasibility of plant communities.

## 2 | SELECTION OF RELEVANT LITERATURE

On 1 June 2020, a search was conducted using the ISI-Web of Knowledge database where the following search terms were used: *invasi\** OR *exotic\** OR *alien\** OR *introd\** AND *facilitat\** OR *positive interaction\**. These results were refined to include only articles within the disciplines of Ecology, Plant Sciences and Forestry. This search resulted in 535 studies. To minimize missing relevant studies,

I cross-referenced citations in all articles for other pertinent articles. All publications were screened for the evaluation of either direct and/or indirect plant–plant facilitation in terrestrial ecosystems. This generated 74 studies relevant to the role of plant–plant facilitation on the invasibility of plant communities (Table S1).

I organized the examples as indicated in Figure 1, starting with examples of native species that directly facilitate non-natives (interaction-type I, Figure 1). An alternative way by which facilitative interactions promote invasions occurs when native species have negative effects on non-native species that, in turn, competitively suppress other non-native species, which generates net indirect facilitative effects (interaction-type II, Figure 1). Subsequently, facilitated non-native species can directly facilitate other non-native species (interaction-type III, Figure 1), increasing community invasibility (i.e. invasional meltdown). In yet another indirect scenario, facilitated non-native species can have negative effects on native species that competes with other non-natives, thus generating net indirect facilitative effects among non-natives (interaction-type IV, Figure 1), which also increases invasibility of native communities. Interaction-types III and IV are consistent with ‘secondary invasion’ (O’Loughlin & Green, 2017), where the invasion success of secondary non-native invaders depend on the presence and influence of one or more other non-native primary invaders. Importantly, all these interactions have the potential to change with environmental contexts (i.e. Gallien & Carboni, 2017). Thus, I further reviewed how facilitative interactions involving non-natives change with the environmental harshness and the consequences of these changes on community invasibility.

### 3 | NATIVE SPECIES DIRECTLY FACILITATING NON-NATIVE SPECIES (I)

In a pioneering study, Maron and Connors (1996) analysed the effect of the native nitrogen-fixing shrub, *Lupinus arboreus* on the exotic grass *Bromus diandrus*, which has invaded grasslands through California, including coastal prairies. There, *Lupinus arboreus* fertilizes sandy soils with nitrogen-rich litter, and in experimental patches where *L. arboreus* was removed soil nitrogen was much higher than in adjacent sites with no *L. arboreus*. *Bromus diandrus* seedlings were larger when grown in soil from where *L. arboreus* was removed than in soil collected away from the native shrub. Interestingly, the non-native species was able to exploit environmental modifications generated by the native only after its death. In semi-arid shrublands dominated by *Chenopodiaceae* species in southern Australia, Lenz and Facelli (2003) found that invasive *Orbea variegata* (Asclepidaceae) planted under native shrubs benefitted from shade and lower temperatures. Other studies in arid or semiarid regions have shown that native species directly facilitate non-natives by different mechanisms including higher soil fertility and ameliorated microclimate (e.g. Griffith, 2010; Lucero et al., 2019; Madrigal-González et al., 2013; Rodríguez-Buriticá & Miriti, 2009).

Direct facilitative interactions with native nurses as the main mechanism underlying invasion have been reported in other abiotically harsh environments such as alpine habitats (Badano et al., 2007; Cavieres et al., 2005, 2008; Llambí et al., 2018, 2020) and the Patagonian steppe (Langdon et al., 2019). For instance, in the central Chilean Andes, Cavieres et al. (2005) showed that the native cushion plant *Azorella madreporica* facilitated the non-native herb *Taraxicum officinale*. The survival, growth and reproduction of *T. officinale* were higher within cushions than in open areas, and this corresponded with how *A. madreporica* created more stable substrates, with higher nutrient and water contents, and buffered temperatures (also see Llambí et al., 2018, 2020).

Examples of direct facilitative interactions of native species on non-natives in abiotically harsh and low-productivity environments are common (examples above), but there are examples from more productive environments (e.g. Nilsen et al., 2018; Saccone et al., 2010; Von Holle, 2005). For instance, the North American *Acer negundo* has invaded the Middle Rhone floodplains forest of France where it reaches much higher densities than in its native range (Reinhart & Callaway, 2004). Saccone et al. (2010) transplanted *A. negundo* juveniles into *Salix*, *Acer* and *Fraxinus* stands, as well as into experimental gaps, and showed that survival of *A. negundo* seedlings was directly facilitated in *Salix* and *Acer* communities where flooding disturbance was reduced by the interlocking stems of these native species. Recently, in highly productive temperate forests of North America, Nilsen et al. (2018) found that the highly invasive Eurasian species *Ailanthus altissima*, performed much better when experimentally planted with the native *Robinia pseudoacacia* than when in monoculture.

### 4 | INDIRECT FACILITATION BY NATIVES (II)

Indirect facilitative effects of native species on non-native invasive species in the literature include chains of seed-dispersal, pollination mutualisms, protection of exotics by natives from herbivores and herbivore preferences for natives that direct herbivores attention away from exotics (see White et al., 2006). Northfield et al. (2018) analysed the literature on biological invasions and identified eight possible ways in which native species might indirectly benefit non-natives, and in most cases the intermediate species between the native and non-native plants were from a different trophic level (e.g. pollinators, herbivores). Indirect interactions where the intermediate species is also a plant are scarce among the studies I reviewed, and there were no examples of native species indirectly facilitating non-natives by suppressing native competitors, a phenomenon that certainly deserves more attention.

Complex interactions among plant species, however, do yield fascinating examples of indirect facilitative interactions involving native and non-native species. Zarnetske et al. (2013) analysed interactions between the native grass *Elymus mollis* and the non-native grasses *Ammophila breviligulata* and *A. arenaria* in coastal

sand dunes in Oregon, USA. They found that *E. mollis*, in some cases, had an indirect facilitative effect on *A. arenaria* by suppressing *A. breviligulata*. Similarly, Metlen et al. (2013) and Metlen and Callaway (2015) reported that the non-natives *Centaurea stoebe* and *Bromus tectorum* were strikingly different in their associations with canopies of the native *Pinus ponderosa*. *Centaurea stoebe* was much less abundant under *P. ponderosa* than in surrounding open grasslands, whereas *B. tectorum* was more abundant under the tree. The more fertile soils beneath *P. ponderosa* facilitated both exotics and did not alter competitive outcomes, but *Pinus*' litter shifted competitive outcomes in favour of *B. tectorum* by inhibiting *C. stoebe* chemically. Thus, *P. ponderosa* modified interactions in ways that facilitated *B. tectorum*.

Suites of overlooked indirect interactions that appear to have very strong effects on invasions involve soil biota and their effects on interactions among native and plant species (Reinhart & Callaway, 2006; Waller et al., 2020). Generally, soil biota in non-native ranges have neutral or even positive effects on non-native invasive plants (Kulmatiski et al., 2008; Lekberg et al., 2018). Native species in these systems, on the other hand, are typically suppressed by soil biota, which potentially provide indirect competitive advantages to non-natives (Reinhart & Callaway, 2006). Allen et al. (2020) recently showed that in a grassland invaded by *Cytisus scoparius* in New Zealand, this non-native species had direct facilitative effects both on native and non-native species, but that indirect effects mediated through soil microbiota were stronger than the direct effects, particularly on other non-native species.

## 5 | NON-NATIVES DIRECTLY FACILITATING OTHER NON-NATIVES (III)

Vitousek and Walker (1989) provided one of the first examples of facilitation among non-native species. In nutrient-poor volcanic soils of Hawai'i, they found that the non-native nitrogen-fixing shrub *Myrica faya* increased nitrogen content in the soil, which facilitated seedlings of the non-native shrub *Psidium cattleianum*. Such facilitation did not occur in soil from under the native *Metrosideros polymorpha* (see also Carino & Daehler, 2002). Other studies have shown that shade, protection against herbivory, increases in soil nutrients and changes in soil microbiota can function as mechanisms underlying direct facilitative interactions among non-native species (e.g. Dornbusch et al., 2018; Jordan et al. 2008; Sheppard et al., 2018; Tecco et al., 2006, 2007). Notably, direct facilitation among non-native plants can also occur at the intraspecific level (e.g. Proença et al., 2019; Reijers et al., 2019; Reinhart et al., 2006).

The mentioned meta-analysis by Kuebbing and Nuñez (2015) reported that facilitative interactions among non-natives were not frequent, but they were more likely to occur when at least one of the neighbouring non-natives was a nitrogen fixer. Furthermore, woody non-natives were two or four times more likely to show facilitative interactions in response to other non-native plants than grasses or herbs (Kuebbing & Nuñez, 2015), reinforcing the idea that this interaction is

more likely to occur when one of the species substantially improves habitat conditions. In this context, Braga et al. (2018) reviewed literature citing Simberloff and Von Holle (1999), and showed that of 89 publications on vascular plants or algae, half of them reported that at least one non-native species had a positive effect on another non-native species, without reciprocal effects or mutually positive interactions, indicating common invasional meltdown. However, no distinctions were made between direct and indirect effects.

## 6 | INDIRECT FACILITATION AMONG NON-NATIVES (IV)

Indirect effects among non-natives are not commonly reported, but they occur and can be important for invasion success. For example, in field experiments, Flory and Bauer (2014) found that the invasive forb *Alliaria petiolata* more readily colonized plots without *Microstegium vimineum*, an invasive grass. However, *A. petiolata* produced three times more biomass and two times more siliques in plots invaded by *M. vimineum*. Facilitation of *A. petiolata* was associated with suppression of native species and more light, indicating that both biotic and abiotic modifications generated by *M. vimineum* may facilitate secondary invasion by *A. petiolata*. In New Zealand, Dickie et al. (2014) found that removal of invasive *Pinus contorta* facilitated another non-native conifer, *Pseudotsuga menziesii*, as well as non-native grasses by soil legacies related to shifts in soil nutrient content.

Indirect facilitative intraspecific interactions have also been reported. For instance, Saccone et al. (2010) found that in stands of the non-native *Acer negundo*, tree canopies strongly decreased competitive herbaceous species in the understorey, indirectly facilitating conspecific seedlings. Similarly, Siemann and Rogers (2003) showed that seedlings of the invasive *Sapium sebiferum* were indirectly facilitated by canopies of adult *S. sebiferum* by decreasing root competition from prairie grasses due to shade. Thus, the evidence presented above indicate that either direct or indirect facilitative interactions among non-natives play a crucial role in the invasibility of communities by generating the opportunities for other invaders.

## 7 | ENVIRONMENTAL CHANGES IN FACILITATION AND INVASION

Abiotic conditions that increase plant mortality and suppress the potential growth of plants (e.g. frosts, extreme heat, salinity and drought; see Lortie et al., 2004) appear to have fewer numbers of invasive species (Pauchard et al., 2009; Stohlgren et al., 2003).

On gradients of abiotic stress, or low productivity, facilitative interactions in general are more frequent as the environmental conditions become more stressful. Competitive interactions are generally more common or more intense where abiotic stress is lower (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Brooker et al., 2005). This has been codified as the stress gradient hypothesis

(SGH; see Callaway et al., 2002; Dohn et al., 2013; He et al., 2013). The idea is that stressful environments restrict plants from acquiring resources, and any amelioration of these conditions favour growth to the extent that amelioration outweighs the negative, competitive impacts of neighbours. This has important implications for the invasibility of communities.

In riparian habitats of floodplain forests of southwestern Virginia, USA, Von Holle (2005) found that in non-flooded and nutrient-rich upland zones of these forests understory native species competitively resisted non-natives, but in the abiotically harsher flooded streamside zones understory natives facilitated non-natives. Similarly, Van Riper and Larson (2009) found that the nitrogen-fixing invasive *Melilotus officinalis* often acts as a nurse species for both native and non-native species in North American grasslands. In the sparse vegetation of 'badlands', they found consistent and strong positive relationships between *M. officinalis* and both native and non-native species. In contrast, in less stressful prairie soils, *M. officinalis* showed no facilitative effects, but instead had weak competitive effects on other species (see also Goergen & Chambers, 2012). In alpine systems of the Andes of central Chile, the cushion plant *Azorella madreporica* facilitates the non-natives, *Cerastium arvense* and *Taraxacum officinale*. However, this interaction changes along an elevation gradient, with greater facilitative effects on both non-natives at more stressful higher elevations (Badano et al., 2007). Indeed, *C. arvense* occurred only in cushions at the highest elevation, suggesting that *A. madreporica* expanded the distribution of this exotic species to the most environmentally stressful part of the gradient. Von Holle (2013) investigated the relationship between native richness and non-native species performance along a salinity gradient in coastal heathlands of northeastern USA, and found that at a high-stress site, native species facilitated the performance of several non-natives: *Achillea millefolium*, *Cirsium* spp., *Rosa rugosa*, *Rumex acetosella*, *Taraxacum officinale* and *Vicia sativa*. However, at a low stress site, native species exerted a negative effect on those target non-natives, concurring with expectations derived from the SGH. Considered together, these studies indicate the amelioration of extreme abiotic conditions by native nurses can indeed make stressful habitats invulnerable, with larger positive effects as abiotic stress increases.

Other studies of facilitation and invasion are not consistent with the SGH. Kleinhesselink et al. (2014) showed that the nurse native shrub *Ericameria ericoides* increased organic matter and decreased wind speeds under its canopy across a stress gradient in a coastal dune in northern California, USA. Although the shrub facilitated the growth of the non-native invasive grass *Bromus diandrus*, this positive effect did not increase along the stress gradient, inconsistent with the SGH. Reisner et al. (2015) showed that along an environmental stress gradient in the Northern Great Basin floristic province of Oregon, the native shrub *Artemisia tridentata* negatively interacted with native species in the low stress end of the gradient, but showed facilitative interactions in the high stress end. However, the interaction with the non-natives *Bromus tectorum* and *Lepidium*

*perforatum* was negative along the entire gradient. Recently, Lucero et al. (2020) explored an aridity gradient across the Mojave and San Joaquin deserts, USA, where the native shrub *Larrea tridentata* was shown to have exceptionally strong facilitative effects on the non-native invasive grass *Bromus madritensis* ssp. *rubens*, but the facilitative effects were less positive as aridity increased.

Highly invasive species may not display responses in importance and intensity consistent with the SGH for several reasons. First, the intensity of facilitation may be so high across entire gradients, as noted by Lucero et al. (2020), that changes along these gradients are difficult to discern. Second, the mechanism driving facilitation may not be the mechanism that varies along the gradient. For example, non-native annual grasses often respond very favourably to increased soil nutrients (Besaw et al., 2011; Maron & Marler, 2007; Yoder & Caldwell, 2002), yet canopy-driven increases in soil nutrients may not change along aridity gradients. Finally, many exotic species are released from a suite of biotic constraints in their non-native ranges, and the resulting very high abundances and performance may obscure variation in interactions along gradients. Indeed, He et al. (2013) noted in their meta-analysis that non-native species showed competitive interactions either as target or as neighbour species, particularly at low stress. Clearly, there is a need for more studies of interaction among natives and non-natives across environmental stress gradients in which drivers of severity gradients, mechanisms for facilitation, and functional and phylogenetic similarities between interacting species are addressed.

## 8 | FACILITATION, DIVERSITY AND THE INVULNERABILITY OF PLANT COMMUNITIES

As noted above, facilitation has the potential to change the relationship between biodiversity and the ecosystem function of resistance to invasion, particularly considering that non-native species have been shown to respond very differently to experimental diversity gradients (Wilsey et al., 2009, 2014). Using a modelling approach, Bulleri et al. (2008) showed that regardless of the relationship between native species richness and resource consumption or depletion, facilitation by natives always increased invasibility, particularly when resources are scarce and the diversity of native species is relatively high. This is because at higher native species richness, there are higher chances of having an effective facilitator species when resources are limiting—the portfolio effect. Northfield et al. (2018) also used a modelling approach to show that positive indirect effects of native species on potential invaders were more frequent in communities with higher species richness and resource availability. These two theoretical studies suggest that facilitative interactions, either direct or indirect, might explain the departure from the expected negative relationship between diversity and invasibility observed at plot scales in some studies (Belote et al., 2008; Knight et al., 2008; Souza et al., 2011).

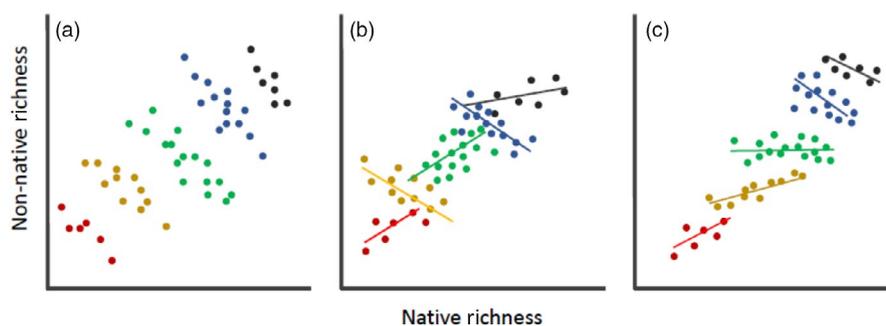
Experimental studies also show that facilitative interactions are important in the invasibility of communities. For instance, Badano et al. (2015) compared the relationship between species diversity

and invasion success within and outside alpine nurse cushions in the Andes, an estimate of the facilitative effects of the cushions. Because cushion plants have strong facilitative effects in alpine systems globally, harbouring higher species richness than open areas (Cavieres et al., 2014), it was expected that the diversity of species within cushions would resist invasion more than the less diverse plant assemblages in open areas surrounding cushions. In contrast, they found that the non-native *C. arvensis* was positively correlated with increasing diversity of native species within cushion plants, but that this relationship was negative or absent in the surrounding open areas. Thus, competitive interactions derived from high diversity were important to resist invasion in the absence of cushions, but this did not appear to function in microhabitats created by cushions. Both the portfolio effect—inclusion of strong facilitators with increasing diversity—and the diversity effect of increased pollinator visitation in more diverse patches were considered as potential mechanisms (Badano et al., 2015). El-Barougy et al. (2020) planted the invasive *Ipomoea carnea* in native annual communities representing gradients of species richness, phylogenetic diversity and phylogenetic relatedness to *I. carnea* in Egypt. They found positive relationships between native species richness and the invader performance, indicating facilitative effects of some natives on *I. carnea*. Interestingly, this interaction was stronger with greater phylogenetic distance to the resident native species. Thus, the phylogenetic richness and distance of the native community to exotics may affect the emergence of competition or facilitation in the resistance or susceptibility of native communities to invasion (see Gallien & Carboni, 2017 and references therein).

Von Holle (2013) suggested a conceptual diversity–invasibility model that included both facilitation and competition between the native community and non-native invaders. Her model produced an overall positive relationship between native diversity and exotics at the landscape scale (Figure 2). At smaller, community scales, natives promoted exotics in some habitats, but competitively resisted exotics others habitats. However, the model predicted positive relationships

between native and non-native species diversity at small scales regardless of native richness. Based on the concepts and empirical results discussed above, I propose a conceptual model derived from those published by Shea and Chesson (2002) and Von Holle (2013). I propose that facilitative interactions play a more important role in the invasibility of communities in more abiotically stressful and species-poor habitats. In contrast, in more benign environments, facilitation produced by high species diversity resists invasion, ideas that are consistent with several BEF studies (Byun et al., 2013; Dukes, 2001; Hector et al., 2001; Kennedy et al., 2002; Maron & Marler, 2007; Naeem et al., 2000; Tilman, 1997; Yang et al., 2017; Zavaleta & Hulvey, 2004). Supporting this, Davies et al. (2007) analysed native and non-native species richness at three spatial scales in different sites on serpentine soil in California. At the smallest spatial scale, the relationship between native versus non-native richness was positive at sites with low productivity, and negative at sites with higher productivity. These patterns are consistent with the importance of facilitative interactions in abiotically stressful sites with low productivity, and the importance of competitive interactions in less stressful sites. A meta-analysis (Stotz et al. 2016) reported that diversity-based biotic resistance invasion was generally the most common result in the literature, but the magnitude of biotic resistance increased with increasing temperature and precipitation. This suggests that the diversity-based resistance generally operates in environmentally moderate and species-rich sites, whereas diversity-based facilitation generally increases invasibility in abiotically stressful sites (also see Smith & Côté, 2019). These results suggest a need to conduct experiments that incorporate variability in species richness at different spatial scales across environmental stress gradients.

Finally, although native facilitator species provide habitat for both native and non-native species, it seems likely that in some cases a key facilitator may further increase the number of native species, potentially increasing resistance to invasion. This may result in a unimodal relationship between species diversity and



**FIGURE 2** Conceptual diagrams of the relationship between non-native and native richness at different spatial scales. Environmental conditions are more similar within each cluster of the same-coloured points than between clusters. Biotic interactions are responsible for the structure within clusters and abiotic extrinsic factors are assumed to be responsible for the overall (large spatial scale) relationship between non-native and native richness. (a) Shea and Chesson (2002) model of the diversity–invasion relationship across spatial scales, where higher numbers of native species lead to lower potential niche opportunities for invaders, assuming competition structured communities. (b) Von Holle (2013) model where higher numbers of native species can lead to greater or lower potential niche opportunities for invaders, given that both facilitative and competitive interactions occur. (c) A combination of the two previous models and including the stress gradient hypothesis, where facilitative interactions are more likely to occur in species poor environmentally harsh habitats, while competitive interaction predominate in species rich communities

invasion success as suggested by Bruno et al. (2003), where the shape of the curve (symmetrical vs. skewed) would depend on the level of richness at which the facilitator include a strong native competitor or resources start to decrease turning competition with natives intense enough to reduce invasions. However, as far as I know, there is no evidence for this potential scenario that certainly deserves more attention.

In sum, both direct and indirect facilitative interactions have important consequences for the invasibility of plant communities, particularly in stressful environments. Thus, it is important to include facilitative interactions in the models that analyse BEF and the diversity-invasibility relationships (e.g. Wright et al., 2017). This will increase our predictive power for determining habitat susceptibility to particular invasions and help to prioritize management of non-natives with a higher likelihood of facilitative interactions.

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## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

This study does not include data.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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