

Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning

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Summary

1. Viewing facilitation through the lens of the niche concept is one way to unify conceptual and empirical advances about the role of facilitation in community ecology.
2. We clarify conceptually and through examples from marine and terrestrial environments how facilitation can expand species' niches and consider how these interactions can be scaled up to understand the importance of facilitation in setting a species' geographic range. We then integrate the niche-broadening influence of facilitation into current conceptual areas in ecology, including climate change, diversity maintenance and the relationship between diversity and ecosystem functioning.
3. Because facilitation can influence the range of physical conditions under which a species can persist, it has the potential to mitigate the effects of climate change on species distributions. Whereas facilitation has mostly been considered as a diversity-promoting interaction by ameliorating abiotic stresses, if facilitated species' niches expand and become less distinct as a result of habitat amelioration, the forces that maintain diversity and promote coexistence in regions or habitats dominated by the facilitator could be reduced (i.e. the sign of the effects of facilitation on populations could be species-specific). Finally, shifting or broadening ecological niches could alter the relationship between diversity and ecosystem functioning.
4. A niche-based perspective on the effects of facilitation can foster a greater mechanistic understanding of the role played by facilitation in regulating species coexistence, range shifts and ecosystem functioning in a changing world.

Key-words: biodiversity and ecosystem functioning, climate change, competitive exclusion, environmental stress, foundation species, micro-habitat, niche overlapping, niche segregation, positive species interactions, spatial and temporal heterogeneity

Introduction

Theoretical and empirical research on positive species interactions over the last two decades has altered the once prevailing view that negative species interactions and the physical environment alone determined species' distribution and abundance (Bertness & Callaway 1994; Bruno & Bertness 2001; Stachowicz 2001; Callaway *et al.* 2002; Bruno, Stachowicz & Bertness 2003; Altieri, Silliman & Bertness 2007; Brooker *et al.* 2008; Silliman *et al.* 2011). Yet, despite substantial advances in our understanding of the mechanisms controlling switches in the intensity and

direction of species interactions (Bertness & Callaway 1994; Stachowicz 2001; Callaway 2007), formal inclusion of positive species interactions into broad theories of community structure and organization and ecosystem functioning is still in its infancy (Bruno, Stachowicz & Bertness 2003; Michalet *et al.* 2006; Bulleri, Bruno & Benedetti-Cecchi 2008; Gross 2008; Schöb, Butterfield & Pugnaire 2012; Dangles *et al.* 2013; Angelini & Silliman 2014).

Here, building on the facilitation-expanded niche model proposed by Bruno, Stachowicz & Bertness (2003), we explore the direct and indirect roles of facilitation in shaping community structure. Specifically, we evaluate how considering the niche-broadening effects of facilitation may

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require us to refine our current concepts and applications in prominent areas of ecology, such as climate change, species coexistence, and biodiversity and ecosystem function relationships.

Facilitation and expansion of the niche

The niche, a core principle in ecology, has been defined both in the abstract (i.e. as a set of constraints in n -dimensions) or as physical entity (i.e. geographically) (see summary by Chase & Leibold 2003). Which of these represents the proper way to conceive of the niche has been debated recently (Chase & Leibold 2003; Stachowicz 2012). Pragmatically, the 'correct' view depends on the biological context of the investigation (i.e. physiology, behaviour, ecology) and specific questions being addressed. Our aim is not to revisit this debate, but instead to consider the role of facilitation in driving the physical area occupied by a species: its realized geographic niche. We apply the geographic view of the fundamental niche, that is a physical space in which a species can develop self-sustaining populations if not constrained by negative biotic interactions (i.e. competition, predation and parasitism). The realized niche represents the space actually occupied by a species after accounting for interactions with other species (including positive interactions). Based on this definition, both the fundamental and the realized niche can be physically mapped in space. For an insight into how the impact of facilitation on the fundamental and realized niche changes with different niche concepts, see discussion by Stachowicz (2012) and Rodriguez-Cabal, Noelia Barrios-Garcia & Nuñez (2012).

Historically, species interactions were viewed as constraining the realized niche relative to the fundamental niche, but it is now clear that facilitation or mutualistic interactions can expand species' realized niche (Bruno, Stachowicz & Bertness 2003; see also Stachowicz 2012). In some cases, facilitation will simply counteract negative biotic interactions (e.g. by providing a refuge from predation), reducing the impact of niche-shrinking interactions and thus the gap between fundamental and realized niches. In other cases, facilitation can expand the fundamental niche by permitting persistence in locations that would be too physically stressful in the absence of a facilitator. For instance, on intertidal rocky shores, buffering of thermal and desiccation stress due to the presence of canopy-forming macroalgae and mussels makes upper shore levels suitable for many species not able to tolerate environmental conditions in open areas, and these effects intensify at the physically stressful edges of species' ranges (Bertness *et al.* 1999; Bulleri *et al.* 2002; Silliman *et al.* 2011). Likewise, in Alpine systems, the presence of nurse plants has been widely shown to mitigate adverse environmental conditions or resource limitation (Callaway *et al.* 2002; Cavieres *et al.* 2014), assisting plant colonization at higher elevations (Choler, Michalet & Callaway 2001). However, the persistence of populations in these expanded areas of the niche

may be constrained by novel biotic interactions among many species that take advantage of the habitat-modifying effects of a single facilitator.

Indirect consequences of facilitation-induced niche broadening

Indirect consequences of facilitation on species coexistence and diversity have received little attention. For instance, potential negative effects of beneficiaries on the benefactor are not commonly considered (but see Schöb *et al.* 2014). Furthermore, when extended beyond the pairwise effects of facilitators on associated species, net effects become more complex and contingent. The traits of foundation species (*sensu* Dayton 1972) such as plant density, height and chemical composition often alter the interactions between associated species at different trophic levels, each of which use the foundation species as habitat (seagrass, Duffy 2006; cottonwoods, Whitham *et al.* 2006; kelps, Steeneck *et al.* 2002). So, while, for example, the direct effects of seagrass density on associated crustaceans and fishes are both positive, net effects could be negative because seagrass indirectly increases predation on small crustaceans by facilitating predatory fishes. In contrast, we know little about how the presence of a foundation species can influence the direction and intensity of competitive interactions among associated species (but see Soliveres *et al.* 2011; Michalet *et al.* 2015). The broadening of niches by facilitation has the potential to increase overlap among potential competitors; this has major implications for the net effect of facilitators on species diversity and coexistence at various spatial scales.

Changes in the geographic scale of the niche due to the onset of more benign environmental conditions depend on species-specific traits. For example, in rocky intertidal, alpine or desert communities, desiccation and temperature are two (related) primary environmental stressors that limit species distributions, and stress-tolerant species can influence the distribution of other species by ameliorating these stresses. These habitat modifiers could affect the niche of associated species in three ways: (i) broaden the niche of species sensitive to both stressors along both axes (Fig. 1a,b); (ii) broaden the niche size along a single axis in species that are sensitive to just one of the two stressors (e.g. temperature in Fig. 1c,d); (iii) cause negligible changes to the niche of species tolerant to both desiccation and temperature (Fig. 1e,f). However, increasing strength of negative interactions among facilitated species reduces the potential expansion of the niche due to facilitation. Thus, foundation species, via a generalized expansion of the fundamental niche of many species, could increase niche overlap (Fig. 1g,h), thereby imposing greater constraints on the realized niche of one of the species. Importantly, expansion of the fundamental niche due to facilitation is likely to alter the intensity of competitive interactions among species characterized by different stress tolerance and competitive ability.

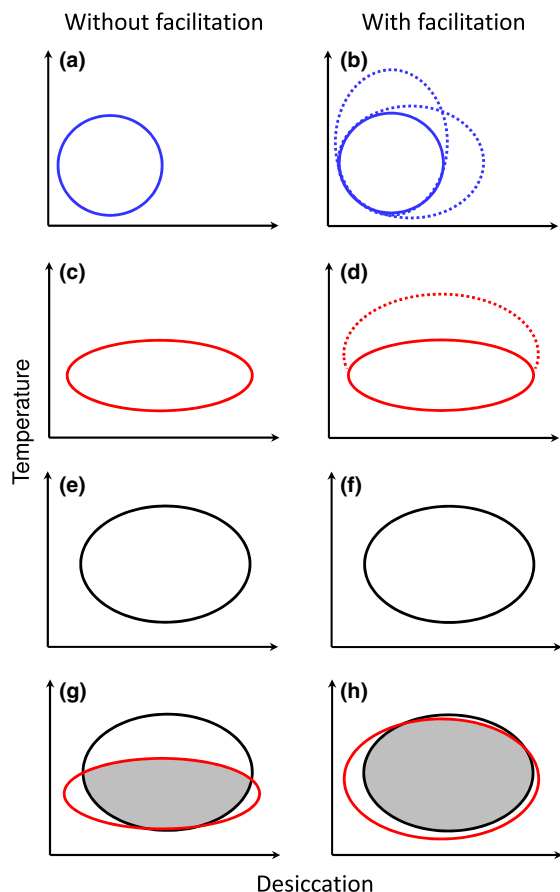


Fig. 1. The fundamental niche in a system composed by three species characterized by different tolerance to two major environmental stressors (e.g. temperature and desiccation), in the absence and presence of facilitation by a foundation species. The fundamental niche of a species susceptible to both heat and desiccation is expanded (blue line) along both axes by foundation species that maintain stress levels within its tolerance range (a, b). Some species can be tolerant to some forms of stress (e.g. desiccation), and the expansion of their fundamental niche (red line) can be expected to occur along a single axis (c, d). No major changes in the fundamental niche due to the presence of a foundation species are expected for species well adapted to live in harsh environments (black line; e, f). Fundamental niche overlapping (grey area in g, h) can be used as a proxy to predict the intensity of competition and, hence, realized niche breadth. Facilitation can benefit competitive, stress-sensitive species (e.g. red line), expanding the surface area over which their fundamental niche overlaps with that of stress-tolerant species (black line; g, h). Stress-tolerant species may, in contrast, be expected to be negatively influenced by a foundation species (e.g. a canopy-forming species that reduces stress), since this will increase the surface area over which their niche overlaps with species that exhibit a markedly positive response to the reduction of physical stress (g, h). Dashed lines in (b) and (d) represent facilitation broadened niches.

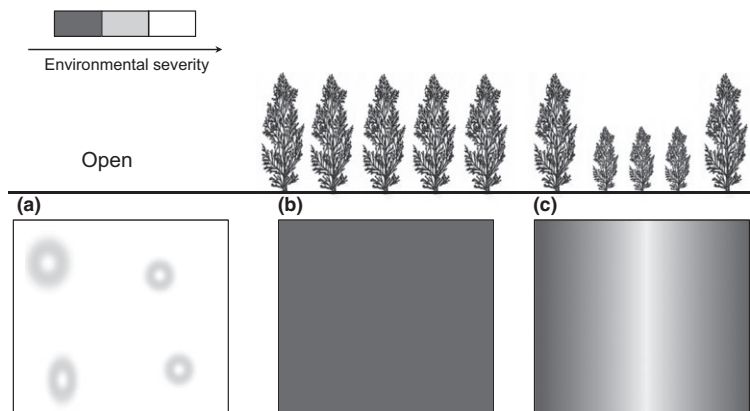
On intertidal rocky shores, species characterized by different tolerance to physical stress (e.g. heat and desiccation) and competitive ability segregate at different heights above mean low water level. For example, the barnacle, *Balanus balanoides* (hereafter referred to with the current name, *Semibalanus balanoides*), can exclude competitively inferior barnacles such as *Chthamalus stellatus* from the lower

shore, but not from higher elevations, where physical stress exceeds its tolerance limits (Connell 1961). A trade-off between stress tolerance and competitive ability, a common feature of species' life traits (Grime 1977; Liancourt, Callaway & Michalet 2005; Gross *et al.* 2010), results in the dominance of space by *S. balanoides* and *C. stellatus* at low and high levels on the shore, respectively. Amelioration of physical conditions by a hypothetical canopy-forming macroalga could favour the expansion of *S. balanoides* (Bertness *et al.* 1999; the competitive species; red line in Fig. 1) towards upper levels on the shore. In contrast, the canopy-forming algae would have little, if any, beneficial effect on the stress-tolerant species, *C. stellatus* (black line in Fig. 1). The presence of a canopy-former would, thus, broaden the fundamental niche of *S. balanoides* while causing no major changes in that of *C. stellatus*. The result would be increased overlap between the potential geographic niches of the two species (Fig. 1h), and an increase in the spatial extent of competition, ultimately reducing the realized niche of the stress-tolerant *C. stellatus*. An untested prediction of this idea is that the relative niche sizes of stress-tolerant and intolerant species should shift as canopy algal cover changes, as, for example, along productivity gradients (Menge & Menge 2013).

At the community level, generalized expansion of species' fundamental niche may ultimately enhance average niche overlapping (Fig. 1g). Thus, trade-off between fundamental niche expansion and increased overlap among competitors and predators would determine the intensity of interactions within the associated community and, as consequence, the net effect of the foundation species on species' realized niches and realized species diversity. The presence of a foundation species would facilitate an associated species when positive effects from niche expansion exceed negative effects of increased niche overlapping (blue and red lines in Fig. 1). In other cases, niche broadening may be not sufficient to compensate for increased overlapping (black line in Fig. 1). Under these circumstances, the two species would only continue to coexist locally if they were also differentiated in some other important niche dimension or if the foundation species is sufficiently patchy or creates new microenvironments that increase environmental heterogeneity and provide spatial refuges for the inferior competitors (Fig. 2).

Indeed, a cornerstone of niche theory is that heterogeneity of environmental conditions (i.e. creation of microhabitats) enables expression of species' differences and promotes coexistence on larger scales (Chesson 2000a,b). For instance, by reducing light levels, macroalgal canopies allow erect species to escape competitive exclusion by algal turf species that monopolize open space but have higher light requirements (Bulleri *et al.* 2002). Likewise, even moderate variations in soil water status due to heterogeneous microtopography can promote the coexistence of crop species (Brooker *et al.* 2015). Seascapes that include variable densities of canopy formers will allow the persistence of both filamentous and erect macroalgae, that is via

Fig. 2. Environmental scenarios in open vs. canopy-dominated rocky intertidal areas. Mean environmental severity is generally lower underneath macroalgal canopies (b, c) than open substrates (a). Environmental conditions in the open can be slightly heterogeneous due to variation in substrate topography, angle of the rock, etc. Underneath canopies, conditions can be homogeneous (b) or, alternatively, vary (c) as a consequence of small-scale variation in features of macroalgal canopies (plant density or morphology and size, as illustrated in c).



increased environmental heterogeneity. Potential enhancement of environmental heterogeneity by foundation species is acknowledged as a key mechanism fostering species coexistence and diversity at the scale of the landscape (Callaway 2007), while local effects have been largely overlooked. So far, the emphasis of positive effects of habitat-formers on associated species has been almost exclusively on their role in mitigating adverse environmental conditions (i.e. provision of more benign environments). We know little of how habitat-formers modify small-scale variability (spatial, temporal or both) of relevant abiotic variables within their biogenic matrix, including non-resource (temperature, desiccation, hydrodynamic forces, sediment deposition, wind) or resource (light, primary space) characteristics of the environment.

At a local scale, we can envision two scenarios of change in mean severity and heterogeneity of environmental conditions in the absence vs. the presence of a foundation species (Fig. 2). On intertidal rocky shores and in forests, environmental conditions generally become less stressful when moving from open space to beneath a canopy-forming plant or macroalga (i.e. from scenario a to b or c). Heterogeneity of environmental conditions could remain unaltered or, indeed, be reduced (Fig. 2, scenario b). For example, substrates underneath dense canopies of intertidal algae or oak trees are generally cool and moist (Bertness & Leonard 1997; Angelini & Silliman 2014) and small-scale variations (centimetre to 10s of centimetre) in these features depicted in Fig 2a could be rendered biologically irrelevant. Hence, the habitat provided in scenario b, while perhaps suitable for a greater number of species, might offer few opportunities for niche segregation, at least with respect to thermal and desiccation stress. In this case, generalized niche broadening might be expected to increase niche overlapping, implying intense competition, with important implications on species coexistence, sink and source dynamics and ecosystem functioning at local scale.

In contrast, when the amelioration of mean environmental severity is also associated with an increase in heterogeneity of environmental conditions (i.e. from scenario a to c), niche segregation could be promoted and result in reduced niche overlap. Such heterogeneity does not have to occur along all of the multiple axes that compose the niche (sum-

marized as cumulative severity in Fig. 2). Heterogeneity along some axes might be sufficient to promote niche segregation and increased coexistence. For instance, on intertidal rocky shores, small-scale variation in the topography of the substratum or inclination of the substratum, as well as spatial or seasonal changes in the architecture of macroalgal habitat-formers (loss of secondary fronds, variation in the size of thalli, etc.), may well result in a mosaic of environmental microhabitats in space and time. Likewise, trees can generate a variety of microenvironments underneath their canopy (Weltzin & Coughenour 1990). If facilitation broadens niche overlap by reducing mean environmental severity, the net local effect on diversity might depend upon the extent to which heterogeneity is increased or differentiation on other niche axes occurs.

Such heterogeneity could be generated at small or larger scales by the presence of multiple facilitators. The co-occurrence (e.g. Spanish moss on live oaks and mussel mounds in saltmarshes) of facilitators that differ to some extent in the way they modify the environment would produce distinctive micro-habitats, increasing opportunities for niche partitioning among associated species and likely increase both diversity and abundance of co-occurring species. Angelini & Silliman (2014) have conceptualized this in the Foundation Species Biodiversity Hypothesis and suggested that enrichment of abundance and diversity of organisms is highest in areas where overlapping foundation species generate complimentary vs. redundant habitat types. For instance, on Mediterranean shores, canopy-forming seaweeds such as *Cystoseira* spp. can form distinct patches or mixed stands (Benedetti-Cecchi *et al.* 2001). Different *Cystoseira* species vary in architecture and their effect on the environment and thus likely host different understory assemblages. Similarly, different genetic varieties of cottonwood trees support distinctive communities of associated insects and microbes (Whitham *et al.* 2006) that, at the landscape scale, should result in a more diverse-associated community.

Niche overlapping and species coexistence

Species coexistence is predicted to occur when stabilizing niche differences exceed average fitness differences among

species (Chesson 2000a; Adler, HilleRisLambers & Levine 2007; Mayfield & Levine 2010). Stabilizing niche differences, arising from variability in species physiology, phenology and resource requirements, often cause intraspecific competition to be stronger than interspecific competition. This mechanism, by favouring the demographic expansion of species occurring at low abundance, promotes coexistence (negative frequency dependence; Adler, HilleRisLambers & Levine 2007). In contrast, average fitness differences, reflecting variability in competitive ability, promote the predominance of one competitor over another regardless of its abundance and can cause competitive exclusion in the absence of niche differences (Adler, HilleRisLambers & Levine 2007; Mayfield & Levine 2010). Coexistence is, thus, dependent on the relative strength of these two forces (Chesson 2000a; Adler, HilleRisLambers & Levine 2007; Mayfield & Levine 2010). Within this framework, species can coexist despite occupying relatively similar niches when differences in relative competitive ability are small. When differences in competitive ability increase, coexistence requires large niche differences (Mayfield & Levine 2010).

By broadening niches and increasing overlap, facilitation may weaken the strength of stabilizing niche differences. Whether this results in exclusion of one of the species, however, depend both on the environmental heterogeneity and differences in competitive ability among species in the presence of the facilitator. For two species with small differences in competitive ability, greater niche overlapping due to facilitation (i.e. reduced niche differences) might not cause competitive exclusion (Fig. 3a,b). Such competitive exclusion will be more likely with greater differences in competitive ability (Fig. 3c,d). Finally, relatively small increases in niche overlapping might be sufficient for exclusion to occur when species markedly differ in competitive ability (Fig. 3e,f). In summary, the net outcome of facilitation on species coexistence rests, therefore, on the extent to which increased niche overlapping (i.e. extended distribution of stress-sensitive species) can be compensated for by reductions in fitness differences.

Theoretical and empirical work has shown trade-offs between species competitive ability and stress tolerance (Grime 1977; Liancourt, Callaway & Michalet 2005; Gross *et al.* 2010). Species exhibiting greater expansion of their niche due to facilitation are likely characterized by traits conferring greater competitive ability relative to stress-tolerant species (Choler, Michalet & Callaway 2001; Liancourt, Callaway & Michalet 2005). Under these circumstances, enhanced niche overlapping could cause increased interactions among species with large differences in fitness, leading to competitive exclusion of stress-tolerant species if the stress amelioration is sufficiently large that stress intolerant species do not suffer a reduction in fitness in the facilitated environment.

Reports of increased biodiversity in the presence of macroalgal canopies on intertidal rocky shores (Chapman 1995; Benedetti-Cecchi *et al.* 2001; Schiel & Lilley 2007) or cushion plants in Alpine environments (Cavieres *et al.*

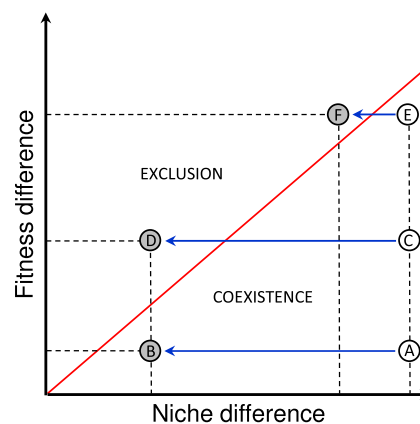


Fig. 3. The effect of facilitation-caused niche broadening on species coexistence. Coexistence depends on stabilizing niche differences exceeding the difference in competitive ability between species (fitness). Following Mayfield & Levine (2010), coexistence is predicted below the 1 : 1 line that describes where growth rates of a species when rare are zero. Facilitation (blue arrow) can reduce niche differences (i.e. increase overlapping) via niche broadening. When considering two species that both benefit from the same facilitator, enhanced niche overlapping is less likely to cause competitive exclusion when fitness differences are small (a, b) than when they are large (c, d). Indeed, when interacting species are characterized by large differences in competitive ability, even subtle increases in niche overlap might be sufficient to cause competitive exclusion (e, f).

2014) suggest, however, that niche differentiation may limit niche overlapping due to facilitation. For instance, underneath macroalgal canopies, small-scale (i.e. centimetre) variation in a number of physical factors, including temperature, desiccation, water flow, light, substratum topography and sediment deposition, may allow coexistence of species characterized by marked differences in competitive ability. Alternatively, facilitation may equalize fitness among species making competitive exclusion beneath a canopy less likely, and allowing local diversity to be maintained by influx of propagules coupled with slow rates of exclusion. Understanding how landscape scale processes (dispersal) interact with local processes (species interactions) remains a major challenge for understanding diversity maintenance at broader scales.

For example, environmental heterogeneity at larger spatial scales can determine local coexistence by influencing source-sink dynamics (Chesson 2000b). Local coexistence in the presence of a foundation species might rely on the subsidy of propagules from areas in which fitness is greater. Species fitness is likely to vary when examined at the scale of the landscape that can be viewed as a mosaic of environmental conditions. On rocky shores, key physical factors can vary at scales of 10s of centimetre to metre, not only according to tidal height, but also as a consequence of variations in wave exposure, topography and inclination of the substratum (Helmuth & Denny 2003). Broad dispersal may offset negative effects of generalized facilitation niche-broadening for stress-tolerant species, but the extent to which these individuals remain demographically relevant is not clear.

Facilitation and climate change

Climate envelope models assume species response to climate changes to be exclusively based on their limits of physiological tolerance and attempt to predict their distribution by identifying suitable environmental conditions (Guisan & Zimmermann 2000). The key role of biotic interactions in shaping species' response to climate changes has been emphasized by recent studies (Van der Putten, Macel & Visser 2010; HilleRisLambers *et al.* 2013; Michalet *et al.* 2014). Yet, the potential influence of positive interactions (e.g. mutualism and facilitation) has seldom been taken into account in attempts to forecast climate-driven variations in species distributions at geographical scales (but see Kiers *et al.* 2010 and Anthelme, Cavieres & Dangles 2014). For instance, on evolutionary time-scales, plant species in the North American southwest that evolved in the mesic Tertiary period persist in the drier Quaternary by associating with more recently evolved, drought tolerant species, on which they largely depend for successful germination and establishment (Valiente-Banuet *et al.* 2006). Similarly, at global scales, alpine plants appear to rely on facilitation as a buffer against harsh environmental conditions to persist at high elevation (Cavieres *et al.* 2014). Facilitation by nurse plants is predicted to play a crucial role in structuring alpine plant biodiversity under future climate scenarios, by regulating both vertical and local shifts in plant distribution (Anthelme, Cavieres & Dangles 2014). More intimate associations also appear to play a role in the sensitivity of species to climate change. The symbiotic algae on which tropical corals depend vary in thermal tolerance in ways that alter host susceptibility to thermal stress (Baker, Glynn & Riegl 2008). Similarly, mutualistic fungal endophytes expand the geographical distribution of their grass host, *Bromus laevipes*, towards drier regions, suggesting that positive species interactions may enhance resilience to global climate change (Afkhani, McIntyre & Strauss 2014).

In response to increasingly harsh environmental conditions, populations could increase reliance on positive associations for persistence or respond evolutionarily to selection for stress tolerance, or some combination of the two. Research in both terrestrial and aquatic systems suggests that facilitation may collapse or switch back to competition once critical thresholds of environmental severity or disturbance intensity are exceeded (Maestre & Cortina 2004; Brooker *et al.* 2006; Le Bagousse-Pinguet, Gross & Straile 2012). Indeed, if climatic conditions exceed thresholds for the facilitator itself, the result could be cascading extinctions beyond that expected by the direct effects of temperature change *per se* (Thomsen *et al.* 2010). Within areas where facilitators still occur, the extent to which facilitated species can seek refuge with facilitators depends on the degree of niche overlap and differences in competitive ability among potential beneficiaries. If species become reliant on facilitators in a larger portion of their geographic range, understanding the opportunities for niche differentiation within facilitated habitats will become

critical for species' persistence. In the absence of such opportunities, an increasing proportion of viable habitat may function as sinks for propagules produced in more benign habitats across heterogeneous landscapes. The sort of habitat heterogeneity created when different facilitators co-occur may reduce chances of competitive exclusion due to excessive niche overlapping.

Some of the most dramatic effects of global warming are expected to occur in the form of extreme events, generated by climatic and non-climatic factors (Easterling *et al.* 2000). Heavy reliance on facilitators could be thus limited to periods of time over which one or a set of physical stressors exceed tolerance limits. For example, on intertidal rocky shores of Hong Kong, the association with the barnacle, *Tetraclita japonica*, allows the littorinid snails, *Echinolittorina malaccana* and *E. viduato*, to endure extreme desiccation and heat stress on open surfaces during summer low tides (Cartwright & Williams 2012). Reliance on barnacles is, however, relaxed during cooler winter conditions. In this case, foundation species represent temporary refuges from transitory adverse environmental conditions, suggesting temporal plasticity in niche breadth. Some degree of asynchronicity in niche expansion–contraction dynamics among species within a community, as a consequence of variations in their tolerance to multiple environmental stressors (see Harley 2008), would enhance temporal niche segregation (geographically, reduced chance of two or more species being restricted to the foundation species habitat at the same time). Within the limits set by species dispersal ability, foundation species may thus function as a source of propagules (e.g. seed banks) and allow the recolonization of open habitats after mass mortalities caused by extreme stress events.

In summary, tests of changes in fitness components (e.g. survival, growth, reproductive output) based on pairwise-species interactions may be insufficient to assess the potential of foundation species to mitigate climate-driven species loss or contractions, if multiple facilitated species exist. Taking into account indirect effects of facilitation will be thus crucial to enhance our understanding of the role of foundation species in mitigating global warming effects.

Implications for the relationship between biodiversity and ecosystem functioning

Increasing evidence supports the hypothesis that key functions of natural ecosystems, such as nutrient cycling, productivity, resistance to invasion, food web dynamics and temporal stability, are, to some extent, influenced by biodiversity (Tilman 1999; Loreau *et al.* 2001; Stachowicz, Bruno & Duffy 2007; Hensel & Silliman 2013). Biodiversity can promote ecosystem functioning via complementarity among species (e.g. in their use of resources) or by the sampling effect – a greater probability of including species with strong effects as diversity increases (reviewed in Stachowicz, Bruno & Duffy 2007; Cardinale, Palmer & Collins 2002). Thus, the effects of facilitation on diversity

discussed above may have considerable indirect effects on ecosystem functioning, in addition to the direct effects that foundation species often have on ecosystem function (Ellison *et al.* 2005; Crowe *et al.* 2013) by virtue of their high biomass and/or productivity.

Because facilitation can modify interactions among species, either by increasing niche overlap or altering environmental heterogeneity, facilitation can also modify the effects of other species interactions on ecosystem functioning in ways that change the fundamental shape of the relationship between diversity and functioning (Bruno, Stachowicz & Bertness 2003; Angelini *et al.* 2015). As one example where the role of facilitation was clearly identified, increased drought stress enhanced the role of species diversity on productivity in a community of bryophytes (Mulder, Uliassi & Doak 2001): there was no effect of diversity under benign conditions where competition prevails, but under simulated drought, diversity increased productivity thanks to the occurrence of facilitation. Similarly, species diversity of aquatic insects increased the topographic complexity of the stream bottom, altering boundary layer flow and increasing individual feeding rates leading to a positive effect of diversity on water filtration (Cardinale, Palmer & Collins 2002). Finally, the overlapping of foundation species of mussels and cordgrass in saltmarshes generates diversity aggregations that then result in enhancement of system multifunctionality that can increase disparate functions such as infiltration, decomposition and nursery provisioning by 2–10× (Angelini *et al.* 2015).

Facilitation can also reduce the importance of diversity, either by increasing performance differences among species (leading to sampling or strong identity effects) or by removing opportunities for niche partitioning (decreasing the strength of complementarity). For example, the effect of diversity on invasion is often mediated by resource use complementarity: diverse communities more consistently and completely use limiting resources, decreasing the probability of successful invasion (e.g. Stachowicz *et al.* 2002). However, if facilitators increase overlap among species, or increase the total amount of resource (space) available, the niche complementarity that links diversity to invasion resistance may weaken considerably. Indeed, native–invader diversity relationships shifted from negative to positive when comparing communities without vs. with a habitat forming species (Stachowicz & Byrnes 2006).

Alternatively, facilitation might cause increased niche similarity and reduced complementarity in one niche dimension, but allow the expression of differences in other niche dimensions. For example, the intertidal canopy-forming alga, *Hormosira banksii*, facilitates understory algae by reducing desiccation (Lilley & Schiel 2006). However, canopy density greatly alters the extent to which understory species' spectral niches are distinct (Tait, Hawes & Schiel 2014). In the absence of a dense canopy, light intensity is high, and understory algal diversity has no effect on photosynthetic rate or gross primary production. In the presence of dense canopy, photosynthesis

increases with understory diversity, as species with diverse light capturing pigments are complementary to one another. Presumably, this effect is minimal under higher light conditions in the low canopy cover because light is far from limiting. At this point, the extent to which facilitation will enhance vs. reduce the importance of complementarity is unknown.

A further gap in our understanding of the role of foundation species in regulating ecosystem functioning concerns the temporal stability of community properties. Community stability is sustained by several mechanisms, including: (i) asynchronous species dynamics, resulting from competitive interactions and/or different response to environmental stress, which generate negative species covariances; (ii) overyielding, that is greater increase in the average of an aggregate community property in respect to its variance; and (iii) statistical averaging of fluctuations of species within the community that results in greater community stability at increasing levels of species richness, also referred to as portfolio effects (Tilman 1999). Foundation species can alter the strength of some of these mechanisms. For instance, Bulleri *et al.* (2012) have shown that the removal of macroalgal canopies on southern European shores increased temporal variation (i.e. a measure of stability) in community cover, as a consequence of increased synchrony in species fluctuations. This suggests that macroalgal canopies, while mitigating the mean severity of environmental conditions (i.e. desiccation and heat), likely reduced their temporal and/or spatial heterogeneity, ultimately strengthening negative species interactions among understory species (i.e. increased niche overlapping). More generally, facilitators can be thought to influence species fluctuations and, hence community stability in contrasting ways: (i) direct decrease of asynchrony in species fluctuation via the buffering environmental extremes or (ii) indirect enhancement of asynchrony in species fluctuation via higher competition intensity due to greater niche overlapping. The balance between these two contrasting forces, plus background levels of severity and variability of environmental stress, may determine net foundation species effects on associated species fluctuation dynamics and, hence, the temporal stability of emergent community properties.

Conclusions

Through the lens of the niche concept, we have outlined several gaps in our knowledge of the role of facilitation in regulating species coexistence, biodiversity and ecosystem functioning and species' response to global climate changes. Two questions emerge as central to gain a mechanistic understanding of the effects of facilitation on species distribution and for their incorporation in well-established ecological theories: (i) how does niche-broadening via facilitation change the degree of niche overlapping within a community when considering multiple relevant niche axes? (ii) how does the presence of a foundation species influence

the biotic and abiotic heterogeneity on which niche partitioning ultimately depends?

Answers to these questions require that field studies and models explicitly incorporate both facilitation and environmental heterogeneity. In some cases, small-scale spatial and temporal variation in physical variables, such as temperature, desiccation, sediment deposition, soil nutrient and water content, and the flow of air or water can be easily quantified in the presence and absence of facilitators. However, the effects of any change in heterogeneity vs. changes in mean conditions on associated species diversity will be more challenging to disentangle. There will be situations where increasing overlap and lower diversity is the likely net result, and others where habitat modification by a foundation species will lead to increased heterogeneity and greater diversity. We do not yet have sufficient data to fully explain the factors that lead to these different outcomes. Large-scale correlative studies encompassing foundation species markedly differing in the way they influence environmental conditions (both in terms of mean and variability) may provide insight into the generality of the mechanisms underpinning their effects on associated species. At small spatial scales, countless studies manipulate the presence or density of facilitators, but factorial manipulations of both facilitator traits and relevant environmental heterogeneity might provide some insight. Finally, the removal of dominant understorey species may allow assessing their competitive effects on rare species and, more generally, to disentangle direct and indirect effects of foundation species on community diversity and assembly dynamics.

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Data accessibility

This manuscript does not use data.

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