OIKOS

Forum

Positive species interactions shape species' range limits

Pauline Stephan, Bernat Bramon Mora and Jake M. Alexander

P. Stephan (https://orcid.org/0000-0002-5218-3852) ✉ (stephanp@student.ethz.ch), B. B. Mora (https://orcid.org/0000-0003-4735-567X) and J. M. Alexander (https://orcid.org/0000-0003-2226-7913), Dept of Environmental Systems Science, ETH Zürich, Zürich, Switzerland.

The relationship between niche and distribution, and especially the role of biotic interactions in shaping species' geographic distributions, has gained increasing interest in the last two decades. Most ecological research has focused on negative species interactions, especially competition, predation and parasitism. Yet the relevance of positive interactions – mutualisms and commensalisms – have been brought to the fore in recent years by an increasing number of empirical studies exploring their impact on range limits. Based on a review of 73 studies from a Web of Science search, we found strong evidence that positive interactions can influence the extent of species' geographic or ecological ranges through a diversity of mechanisms. More specifically, we found that while obligate interactions, and especially obligate mutualisms, tend to constrain the ranges of one or both partners, facultative positive interactions tend to widen ranges. Nonetheless, there was more variation in effects of facultative interactions on range limits, pointing to important context-dependencies. Therefore, we propose that conceptual development in this field will come from studying ecological interactions in the context of networks of many species across environmental gradients, since pairwise interactions alone might overlook the indirect and environmentally-contingent effects that species have on each other in communities of many interacting species. Finally, our study also revealed key data gaps that limit our current understanding of the pervasiveness of effects that positive interactions have on species' ranges, highlighting potential avenues for future theoretical and experimental work.

Keywords: commensalism, facilitation, interaction networks, mutualism, niche limits, positive species interactions, range limits, symbiosis.

Introduction

Understanding the mechanims shaping species' geographic range limits constitutes one of ecology's great challenges (Grinnell 1917, Elton 1927, Hutchinson 1957). Despite considerable progress, one critical aspect remains poorly understood: the extent to which species' ranges and their responses to environmental changes are governed by species' interactions (Wisz et al. 2013, Singer et al. 2013, Alexander et al. 2016, Godsoe et al. 2017). Many ecologists have studied how interactions such as competition, predation and parasitism can constrain species' ranges (Antonovics 1976, Bruno et al. 2003, Soberón 2007). These interactions have been shown to set abrupt

NSO
NORDIC SOCIETY OIKOS

species boundaries along smooth environmental gradients, both in theoretical and empirical studies (Gross and Price 2000, Briers 2003, Sexton et al. 2009, Cahill et al. 2014), but the overwhelming majority of this work has focussed on the ways negative interactions – i.e. those detrimental to at least one partner (Fig. 1C–E) – can shape species' distributions. In contrast, much less is known about how and when positive interactions could help define range limits.

Positive interactions can be divided into two broad groups, mutualisms and commensalisms, which in turn can be either obligate or facultative (Fig. 1). Mutualism generally refers to any mutually beneficial association between different kinds of organisms (e.g. pollination, endosymbiosis, seed dispersal). Commensalism is, on the other hand, a relationship between two species in which one obtains benefits from the other without damaging or benefiting it (e.g. nurse plants, nesting associations; but see section 'Context-dependency

of interactions' for further discussion of potential reciprocal effects). An obligate mutualism or commensalism describes an association where one or both species depend on the interaction for persistence, whereas facultative mutualists or commensalists do not have this dependency (Bruno et al. 2003).

Ecological theory provides expectations regarding the prevalence of positive interactions across environmental gradients. Most notably, the stress gradient hypothesis predicts the frequency of positive interactions to increase in harsh environments such as salt marshes, deserts or alpine ecosystems (Bertness and Callaway 1994, Louthan et al. 2015), and has been tested and received support in both plant (Brooker and Callaway 2009) and animal (Fugère et al. 2012, Barrio et al. 2013, Dangles et al. 2018) communities (see Anthelme et al. 2014 for a review). While the stress gradient hypothesis makes no explicit predictions about how positive interactions might shape distribution limits, it follows that
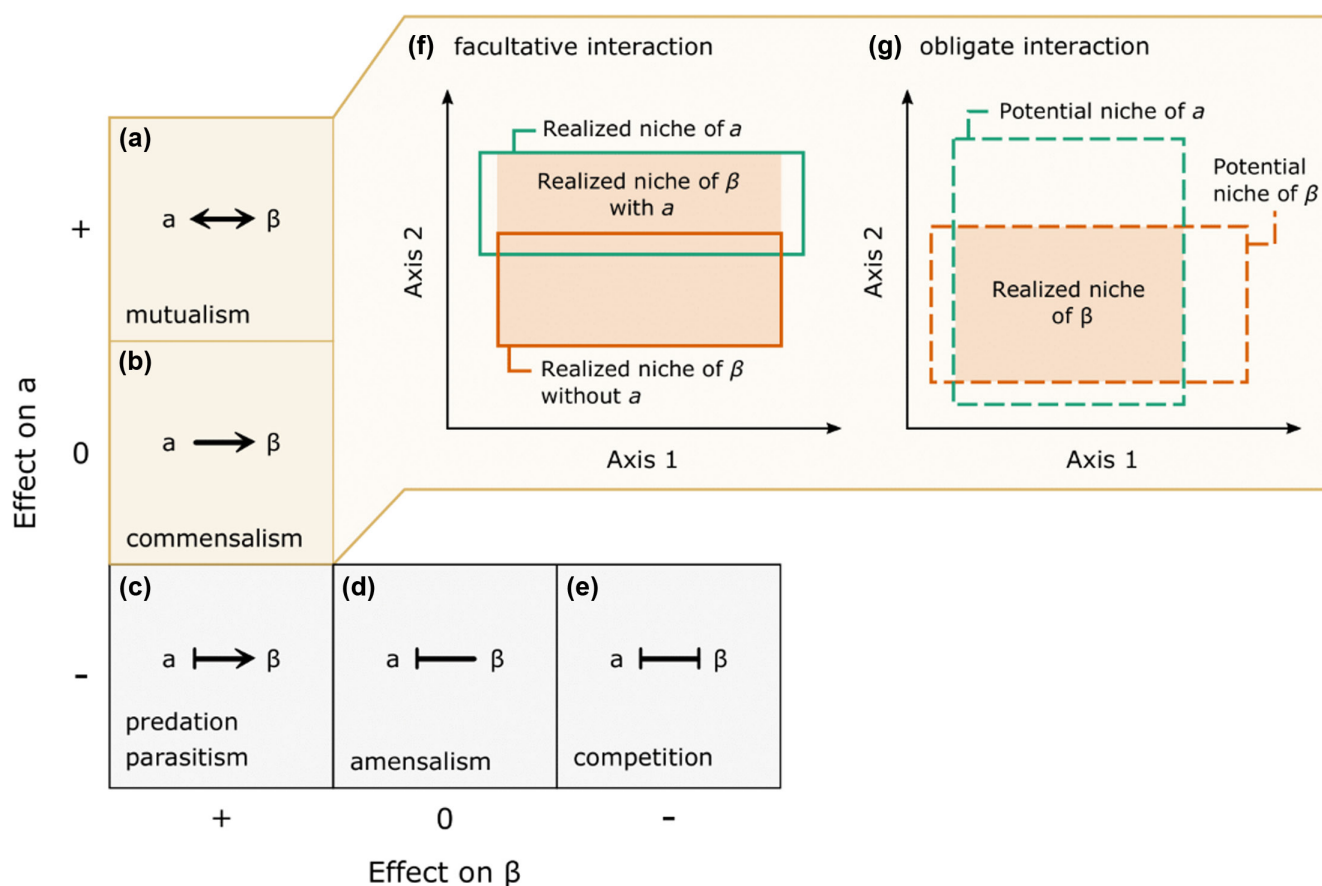

Figure 1. A conceptual illustration of possible interaction types, and how positive species' interactions may influence a species' niche. We choose to define a species' potential niche as the range of environments it could occupy if biotic interactions were not limiting. Following Jackson and Overpeck (2000), we define a species' realized niche as the projection of the actual geographical distribution back into niche space – i.e. accounting for both biotic interactions and dispersal limitation. Panels (A)-(E) classify all possible interaction types between two species a and β based on the effect that the interaction has on each species. Panels (A) and (B) characterize mutualistic and commensalistic interactions, respectively, which are the main focus of this review study. We consider these interactions to be facilitative, as they do not have a priori direct negative consequences for either interacting partner. Panels (C), (D) and (E) characterize predation and parasitism, amensalism and competition, which we exclude from our literature review. Panels (F) and (G) present the effect that facultative and obligate positive interactions would theoretically have on a and β's realized niches. In this illustration, species β is the focal species; in (F), species a allows species β to expand its realized niche, while in (G), species a constrains species β's realized niche.

these could enable species to persist in otherwise unsuitable habitats (He and Bertness 2014). Positive interactions are, however, not exclusive to environments where conditions are considered to be stressful, and so are likely to impact distribution limits across species' ranges.

All types of positive interaction might decisively impact the range limits of species along gradients, in both geographic and environmental niche space (Fig. 1). Furthermore, positive interactions could affect the rate and ultimate extent of range expansion in response to changing environmental conditions, such as those caused by climate change or encountered during biological invasions (HilleRisLambers et al. 2013, Svenning et al. 2014). That said, we might expect the direction of these effects to vary across interaction types, due to their different effects on species' realized niches (Fig. 1). Facultative commensalisms and mutualisms should be more likely to expand a species' realized niche, and hence geographic range or range expansion (Fig. 1F), by supplementing resources or ameliorating unfavourable environmental conditions at the range edge (Bruno et al. 2003, Afkhami et al. 2014). A well-known example of this phenomenon is displayed by alpine cushion plants, which provide favourable sites for the establishment of plants that are less tolerant of conditions at higher elevations (Cavieres et al. 2014). In contrast, obligate commensalisms and mutualisms might be more likely to constrain the distribution of partner species and hinder range expansion, whenever the species have non-identical environmental tolerances (Mestre et al. 2020) (Fig. 1G). For instance, a plant species that depends on one or a few pollinators for its reproduction cannot persist if these are absent, even in those places where the abiotic conditions are favourable to the plant's growth (Pauw and Bond 2011, Moeller et al. 2012, Harrower and Gilbert 2018). Similarly, animal commensalists that depend on using nests constructed by other species are naturally constrained by the distribution of their hosts (Quinn and Ueta 2008, Pendleton et al. 2012, Gray et al. 2018).

Here, we review empirical studies explicitly addressing the link between range limits and positive species interactions. More specifically, we assess how much evidence there is that positive interactions play a significant role in defining range limits or impact range expansion processes, and we address the extent to which the effects of positive interactions vary across interaction types. Inspired by previous theory on this topic (Bruno et al. 2003, Sexton et al. 2009, HilleRisLambers et al. 2013, Bulleri et al. 2016, Mestre et al. 2020), we hypothesise that while 1) facultative interactions tend to extend species' ranges (Fig. 1F, 2) obligate interactions generally constrain ranges (Fig. 1G). We find abundant evidence that obligate and facultative interactions shape species' range limits; however, we also observe several discrepancies that span study systems and interaction types. To explore these discrepancies, we then discuss how the effects of pairwise interactions, which are the focus of most studies, will extrapolate to systems of many interacting species. In particular, we outline the ways in which the structure and distribution of positive interactions in complex ecological communities might determine their effects in setting species' range limits across environmental gradients.

Literature review

We performed a literature survey with Web of Science using the search terms "('positive interaction'' OR 'facilitati'' OR 'mutuali'' OR 'commensal'' OR 'symbio'') AND ('range limit'' OR 'range edge'' OR 'range margin'' OR 'distribution* limit'' OR 'geographi* range'' OR 'niche limit'' OR 'niche edge*'' OR 'niche margin'' OR 'niche width')", searching all articles published until the end of January 2021. In total, we screened the 502 titles and abstracts retrieved by this search to select only empirical studies focussing on the link between positive interactions and species distribution or niche limits (n = 73 studies). We consider possible bias due to this choice of search terms in 'Data gaps', including the potential exclusion of studies only using system-specific terminology. We explicitly excluded human commensals (Schrey et al. 2014) and studies documenting indirect positive interactions, such as apparent competition, but revisit these cases in 'From positive interactions to networks of interactions' below. For each of the 73 retained studies, we recorded the geographic location of the field study (or species' origin for laboratory studies) as well as the identities of the species involved (Fig. 2). We classified each study by interaction type as an obligate or facultative mutualism or commensalism, while recognizing that interaction strengths and directions can vary across time and space (Dowie et al. 2016; 'The distribution of positive interactions'). We recorded whether or not each study supported the hypothesis that positive interactions contribute to defining range limits (Table 1). We also noted whether these effects on range limits were shown to be negative (constraining niche breadth) or positive (expanding niche breadth).

More than half (n = 40) of the final 73 studies were published in the last six years. They cover a broad range of interactions, from fish algal-cultivation (Hata et al. 2010) to bird protective nesting associations (Quinn and Ueta 2008), Pyrenean tree facilitation (Ameztegui and Coll 2013) and insect gut symbioses (Zhang et al. 2019). Overall, 56 studies (77%) supported the hypothesis that positive interactions significantly impacted the realized niche or geographic range of species, while 17 did not. Four studies indicated only partial support: one study focussing on mycorrhizal interactions at the leading and trailing range edges of tree species (Lankau et al. 2015); one focussing on the interaction between different orchid species and their pollinators (Pauw and Bond 2011); and two studies on ant–fungus cultivation (Mueller et al. 2011a, Luiso et al. 2020). The extent to which positive interactions influenced range limits varied with the interaction type and was strongest for obligate mutualisms and obligate commensalisms (Fig. 3). As a broad generalization, we found that obligate positive interactions, whether mutualistic or commensal, tended to constrain ranges, while facultative interactions extended them (Fig. 3). Nonetheless,
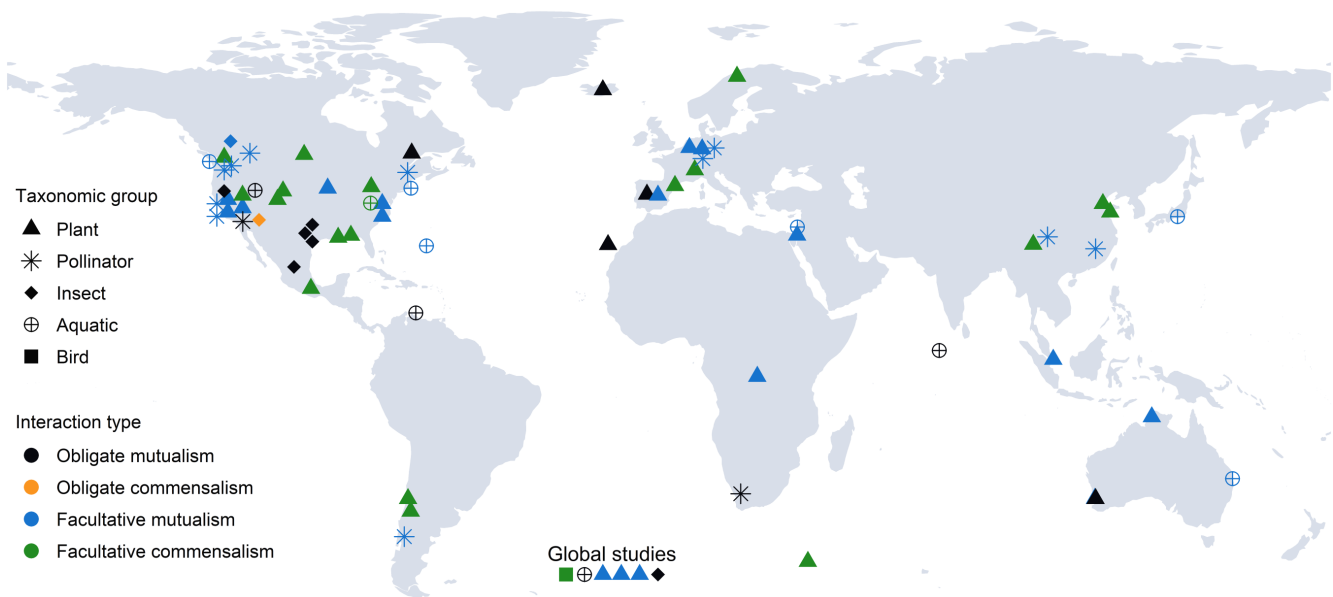
Figure 2. Locations of study sites or population sampling sites for the studies retrieved by our literature search, classified by positive interaction type. For studies with multiple sampling sites, the most sampled one is mapped. Studies labelled as 'aquatic' include mollusc–algae, fish–algae, fish–fish, coral–endosymbionts, and shrimp–gut symbiont interactions. For further details on the effects of the interactions on range limits see Table 1.

evidence for links between interactions and ranges was less consistent for facultative interactions, and especially mutualistic ones, suggesting greater context-dependency. In the next section, we provide an overview, with illustrative examples, of some mechanisms through which positive interactions affect range limits.

Obligate interactions tend to constrain ranges

The strong biotic interactions connecting obligate partners imply that their range dynamics are intimately linked; therefore, one species' environmental tolerance will define that of the other (e.g. symbionts) (Mestre et al. 2020). Our literature review retrieved several examples of such constraints acting on at least one of the obligate partners, with only 4/18 studies failing to find evidence of obligate interactions shaping range limits (Fig. 3, Table 1). More than three-quarters of the remaining studies (11/14) indicated that obligate mutualists and commensalists, such as pollinators, gut symbionts or others, tended to constrain, rather than expand, the ecological range of their partner species on one or more niche axes (Fig. 3, Table 1). A particularly clear illustration of this mechanism is provided by Nougué et al. (2015). The authors investigated the brine shrimp's observed salinity range as a function of its gut symbionts *Salinivibrio* spp., which the shrimp requires to digest algae. The bacteria's survival dropped with decreasing salt content, yet its host's survival did not drop when fed on yeast. When fed on algae and reinoculated with the bacterial strains, juvenile shrimps also exhibited lower salinity ranges, supporting the hypothesis

that the symbiont's environmental niche constrains that of its host. Our literature search retrieved only a single study of an obligate commensalism, but this also indicated that the ecological range of the commensalist can be constrained by that of its benefactor (Quinn and Ueta 2008, Pendleton et al. 2012). In this example, Gray et al. (2018), despite intensive sampling over a significant portion of the geographic range of an ant host, never found its commensalist ant species in independent nests.

While the majority of studies retrieved by our literature search provide clear evidence that obligate interactions constrain range limits, three studies provided contrasting evidence (Mueller et al. 2011a, Pauw and Bond 2011, Luiso et al. 2020). In all cases, the authors described key eco-evolutionary mechanisms that are critical to overcome the constraining effect of the interaction. Pauw and Bond (2011) showed how orchids require the ability to asexually reproduce in order to escape the constraining effect of the interactions with their pollinators. Likewise, studying the interaction between leaf-cutter ants and their cultivated fungi, Mueller et al. (2011a) and Luiso et al. (2020) also presented evidence of an obligate mutualist that is able to overcome the range limits imposed by its host. The authors hypothesized that the fungi are able to use airborne spore dispersal or unknown vectors and survive independently of their former cultivators, before engaging in novel interactions with endemic species. More generally, range expansions can result from a symbiont switching to a new host or a host acquiring a new symbiont, for example following evolutionary (e.g. for corals – Leydet and Hellberg 2016, for lichens – Dal Grande et al. 2018) or environmental – Tye Pettay et al. 2015) changes (Mestre et al. 2020).

Table 1. Studies retrieved by the Web of Science search, grouped into specific positive interaction types and indicating whether the interaction constrains, widens or has no effect on species range (geographic or realized niche) limits.

	Specific interaction type	Effect on range limits	References
Obligate mutualism	Corals and endosymbionts	constraining	Bongaerts et al. 2015
	Cultivation	constraining	Mueller et al. 2011a, Bracewell and Six 2014
		no significant effect	Mueller et al. 2011b, Luiso et al. 2020
		widening	Hata et al. 2010
	Gut symbiosis	constraining	Nougué et al. 2015, Zhang et al. 2019
	Habitat provisioning	widening	Litsios et al. 2014
	Lichens	constraining	Fernández-Mendoza et al. 2011, Dal Grande et al. 2018
		no significant effect	Lu et al. 2018
	Plant and specific mycorrhiza	constraining	Swarts et al. 2010
	Pollination	constraining	Pauw and Bond 2011, Harrower and Gilbert 2018
	Protection from predation	widening	Forister et al. 2011
	Seed dispersal	constraining	Pérez-Méndez et al. 2015
Facultative mutualism	Beetle and fungal symbionts	widening	Roe et al. 2011
	Bioluminescence symbiosis	constraining	Urbanczyk et al. 2012
	Grass and fungal endophyte	widening	Afkhami et al. 2014
	Legume and rhizobia	constraining	Stanton-Geddes and Anderson 2011, Harrison et al. 2018, Lopez et al. 2020
		widening	Parker et al. 2007, Bamba et al. 2016
	Phytoendosymbiosis	constraining	Dimond et al. 2013
		widening	Verde and McCloskey 2002, Loh et al. 2006, Leydet and Hellberg 2016
	Plant and endophytic leaf bacteria	no significant effect	Verstraete et al. 2013
	Plant and mycorrhiza	widening	Menzel et al. 2017, Gerz et al. 2018
	Pollination	constraining	Chalcoff et al. 2012, Moeller et al. 2012, Lachmuth et al. 2018, Benning and Moeller 2019, Bontrager et al. 2019
		no significant effect	Zhang et al. 2014, Hargreaves et al. 2015, Theobald et al. 2016, Rivest and Vellend 2018, Corli and Sheppard 2019
	Pollination and seed dispersal	no significant effect	Wang et al. 2018
	Protection from predation (algae – fish)	widening	Lapointe et al. 2014
	Seed dispersal	constraining	Ben Zvi et al. 2020
		no significant effect	Jordano 1993
		widening	Vittoz et al. 2009, Gómez and Verdú 2012
	Plant and mycorrhiza	constraining	Lankau et al. 2015, Lankau and Keymer 2016, Karst et al. 2018
	Plant and mycorrhiza	no significant effect	Davis et al. 2015
Obligate commensalisms	Nesting association	constraining	Pendleton et al. 2012, Gray et al. 2018
		widening	Quinn and Ueta 2008
Facultative commensalism	Grassland plant-plant facilitation (drought stress)	no significant effect	Martorell et al. 2015
	Nurse plant	no significant effect	Ameztegui and Coll 2013, Drezner 2019, Pickens et al. 2019, Villellas et al. 2019
		widening	Brittingham and Walker 2000, Dona and Galen 2007, Cavieres et al. 2008, Peña-Gómez and Bustamante 2012, Gao et al. 2014, Chhin and Wang 2016, Loudermilk et al. 2016, Ettinger and HilleRisLambers 2017, Raath-Krüger et al. 2019, Chen et al. 2020, Jabis et al. 2020
	Protection from predation (shrub – crab)	widening	He and Cui 2015

Facultative interactions tend to extend ranges

Support for the role of facultative mutualisms and commensalisms – i.e. interactions with partner species that are not essential for growth and survival – in shaping range limits was more heterogeneous than for obligate mutualists. The hypothesis that positive interactions contribute to setting range limits or affect range expansion was supported by 12/37 studies dealing with facultative mutualisms, and 14/20 studies of facultative commensalisms (Fig. 3, Table 1). These results suggest a greater context-dependency for the impact of facultative interactions on geographic or environmental niche limits. Where studies implicated interactions as affecting range limits, they tended, as we hypothesised, to expand rather than constrain range limits (Fig. 3, Table 1).
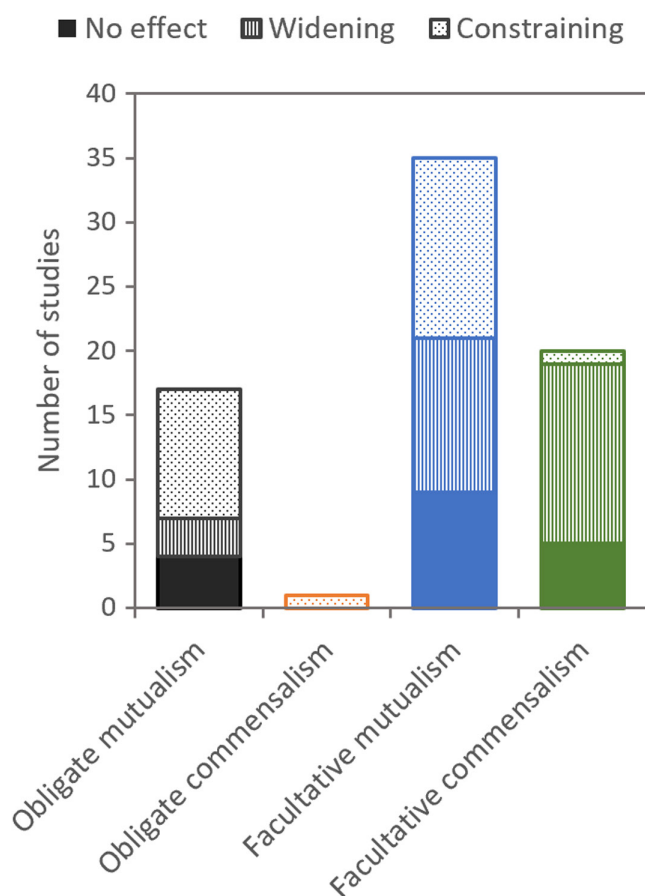
5

Figure 3. Studies retrieved by the Web of Science search, grouped according to interaction type and whether they support the hypothesis that the interaction impacts species range (geographic or realized niche) limits; for studies supporting this hypothesis, the impact can either widen (hatched) or constrain (dotted) the range limit.

The remaining studies often concluded that abiotic factors were the primary drivers of the focal species' range limits (Hargreaves et al. 2015, Theobald et al. 2016). Noticeably, pollination was a facultative interaction with a particularly high proportion of studies demonstrating constraining effects (Chalcoff et al. 2012), perhaps because the specificity of plant–pollinator interactions can be particularly variable in time and space (Dupont et al. 2009, CaraDonna et al. 2017, Fortuna et al. 2020). The studies we reviewed indicated that, although they differed in levels of support, both facultative mutualisms and commensalisms can influence a species' range through a similar set of mechanisms, primarily through transport of propagules, ameliorating environmental conditions, or resource/habitat provisioning.

Transport

Interactions promoting dispersal can be mutualistic (e.g. in cases of active dispersal by an animal that also derives benefit from this service in the form of resources; Gómez and Verdú 2012, Ben Zvi et al. 2020) or commensal (e.g. in cases of

passive dispersal agents such as 'hitch-hiking'; Vittoz et al. 2009). Although both interactions can help species overcome potential dispersal limitations and thereby expand their ranges to novel environments (Bruno et al. 2003), this will crucially depend on the behaviour of the dispersal agent and might only be expected to play a role when environments (or behaviours) change. For example, while bears are helping cherry to track changing climate by dispersing seeds to higher elevations (Naoe et al. 2016), the range limit of Swiss stone pine is prevented from expanding into suitable environments above timberline as a result of the behaviour of its primary disperser, the spotted nutcracker (Neuschulz et al. 2018).

Despite not being considered in this review, the most dramatic example of commensalism driving range expansion is undoubtedly the global spread of non-native species, which are transported to new regions by people (although arguably the negative effect on people that some invasive species can have brings the classification of this interaction type into question). Around 4% of the global vascular flora has been introduced outside of regions where it evolved (Van Kleunen et al. 2015), and some of these species extend not only their geographic range but also their niche limits in their non-native range (Liu et al. 2020). Human-mediated dispersal can also play out at a more local level, as shown by Peña-Gómez and Bustamante (2012), who describe how a multitrophic positive interaction promotes the range expansion of the invasive *Eschscholzia californica* in the Andes; domestic cattle enable *E. californica* to move from areas of suitable habitat at lower elevation to the cushion plant zone by means of passive seed transport.

Habitat suitability and resource provisioning

Positive interactions can influence range limits by improving environmental conditions of species in different ways. This can operate directly via resource provisioning, promoting environmental tolerance, and/or via providing favourable local conditions for an organism to live within an otherwise hostile environment. Typical examples include effects of nurse plants (Jabis et al. 2020), or plant associations with rhizobia (Bamba et al. 2016) and mycorrhizal fungi (Menzel et al. 2017). In all cases, benefits of the interaction may flow to only one or to both interacting partners. In this way, positive interactions can expand a species' realized niche, potentially even into environments that it would be physiologically unable to tolerate in the absence of any biotic interactions (Svenning et al. 2014). For example, Afkhami et al. (2014) showed that by ameliorating drought-stress, a facultative mutualistic fungal endophyte allowed the grass *Bromus laevipes* to expand its geographic range by 20% into drier regions. Similarly, Lapointe et al. (2014) showed analogous effects for pelagic *Sargassum*, a species of algae that provides refuge from predation to numerous juvenile fish. The authors hypothesize that these algae can expand their niches to oligotrophic oceanic gyres – also referred to as biological deserts – by deriving nutrients from excretions of the juvenile fish they harbour. As environments change, interactions like these

can help species to track changes by expanding their ranges, as well as buffer range contraction at the trailing edge. For example, Lankau et al. (2015) found that while fungal mutualists didn't impact the expansion rate of temperate tree species in response to past and current climates at their leading range edges, they consistently facilitated their persistence at the trailing edge by inducing tolerance of the novel climate.

One of the most well-known and most studied examples of within-trophic level commensalisms are nurse plants, which can facilitate the establishment and performance of both native and non-native species in harsh environments like deserts (Brittingham and Walker 2000) or at high elevations (Cavieres et al. 2008). Indeed, we found this to be the most studied interaction (15/19 studies of facultative commensalisms; Table 1). As a typical example, Dona and Galen (2007) demonstrate how alpine willow shrubs enhance the montane fireweed's *Chamerion angustifolium* over-winter survival, thus permitting its persistence at higher elevation. Despite nurse plants dominating the examples we found of within-trophic level commensalisms, other systems are also represented in our review as well. Another interesting case of commensalism influencing ranges through a form of resource provisioning is commensal nesting associations, in which one species occupies the nests vacated by another. Pendleton et al. (2012) reviewed commensal nesting in 11 species of fresh-water fishes from the genus *Nocomis*, while Quinn and Ueta (2008) reviewed 62 studies of bird nesting associations. Similar to what has been observed for obligate interactions, both reviews document significant distribution overlaps in cases of a strong dependence of the species benefitting from the association on the nest providing species. They thus also describe how range shifts in response to environmental changes can be frequently linked in these cases, with the range expansion of the bird species benefitting from the nesting association lagging behind that of its host.

Mitigation of consumer pressure

Interacting species can provide benefits to each other through protection from consumers, including predators and parasites, which can in turn influence their range limits. This might occur across trophic levels, as in the case of the shrub *Tamarix chinensis*, which allows the crab *Helice tientsinensis* to expand its upper intertidal distribution by sheltering it from predators and desiccation (He and Cui 2015). Similarly, it can also occur within trophic levels, as in some of the already mentioned bird nesting associations, where commensalists benefit primarily from reduced predation rates and, in some cases, from lower parasitism and higher mating success (Quinn and Ueta 2008). Although interactions like these are likely to be common, very few were retrieved by our search, perhaps because many act indirectly (see next section for further information) or have been less frequently investigated explicitly in the context of species' range limits. Mutualists might also promote range expansion by protecting a host against pathogens. For instance leaf endophytes have been implicated in the invasion success of the reed *Phragmites*

australis (Fischer and Rodriguez 2013), potentially promoting growth and disease resistance.

From positive interactions to networks of interactions

As our review shows, there is abundant evidence that positive interactions shape species' ranges in a diversity of ecosystems and through a diversity of mechanisms. However, it also revealed discrepancies regarding the direction and significance of the effects that positive interactions have on species' range limits (Fig. 3), indicating that these effects might often be context-dependent and challenging to disentangle within communities of many species. Indeed, the interaction between a pair of species, which constitute the majority of studies reviewed here, can be altered by the presence or absence of a third species (Levine et al. 2017, Losapio et al. 2019). For example, Aguilera and colleagues (Aguilera and Navarrete 2007, Aguilera et al. 2015) explored the impact of two molluscan grazers on algal succession in intertidal rocky systems of the Chilean coast, finding that the molluscs (*Chiton granosus* and *Scurria viridula*) cleared intertidal space and allowed the competitively inferior algal species *Mazzaella laminarioides* to establish. Similarly, Vittoz et al. (2009) describe how cattle grazing facilitates the persistence of alpine plants at lower elevations by reducing competitive pressure from lower elevation plant species. In this context, therefore, indirect positive interactions can expand a species' realized niche and geographical distribution by alleviating the negative effect of interactions with antagonists (e.g. through apparent competition, Holt and Bonsall 2017). While effects of indirect interactions are likely to be pervasive, they are not necessarily investigated explicitly in the context of range limits.

More generally, species are embedded in complex networks of interactions, linked together in non-random ways that may directly or indirectly influence their range limits (Bascompte and Jordano 2007). Therefore, their coexistence, and range limits, cannot be fully understood solely in terms of pairwise interactions but rather after accounting for the entire structure of the complex interaction networks that they form (Levine et al. 2017). In the following sections, we identify three key challenges that must be addressed to fully untangle the role of positive interactions in setting range limits: first, we must shed light on the context-dependent nature of the effects that biotic interactions have in shaping species' ranges; second, we need a well-resolved picture of the distribution of positive interactions for any given species across space and time; and third, we need a clear understanding of how the structure of networks of positive interactions will affect species' range limits.

Context-dependency of interactions

While biotic interactions have traditionally been classified as falling into distinct categories like those depicted in Fig. 1, in

reality any given interaction between two or more species can span a continuum from positive to negative effects depending on environmental context (Leung and Poulin 2008), including abiotic conditions (Chamberlain et al. 2014), community composition (Lankau 2012) or population density (Schöb et al. 2014, Filazzola et al. 2020). For example, client fish can benefit from services provided by cleaning fish in areas where ectoparasite loads are high (mutualism), but suffer from scale and mucus removal by cleaning fish (parasitism) where ectoparasite loads are low (Cheney and Côté 2005). Also, the benefits that plants derive from mycorrhizal fungi can be altered by the presence or absence of particular plant competitors (Lankau 2012). True commensal interactions are likely to be rare (Leung and Poulin 2008), with effects of commensals on their hosts changing over space or time. In particular, effects of commensals on their hosts can be density-dependent, with minimal measurable effects at low density and increasingly negative effects at high density, as has been show several times in nurse plants (Rodríguez-Buriticá and Miriti 2009, Schöb et al. 2014, Michalet et al. 2016, Filazzola et al. 2020). Indeed, such feedbacks will help to stabilize the population dynamics of species that are interacting in this way (Hart and Marshall 2013). Therefore, to achieve a more complete picture of how range limits are influenced by species interactions, we need conceptual frameworks and empirical approaches that embrace the full spectrum of interaction types and intensities, and their simultaneous effects on population dynamics.

The distribution of positive interactions

The influence of positive interactions on species' distributions might also change along an environmental gradient. For example, the extent to which mutualistic interactions are obligate or facultative along a particular gradient will be context-dependent (Chamberlain et al. 2014). A plant species could strongly rely on the services provided by a single pollinator in a given location while also being found in environments where several of its pollinators can coexist (Trøjelsgaard et al. 2015). Therefore, the mutualistic interaction between any two species could strongly contribute to setting their range limits in one location, while the same type of interaction expands or becomes a poor predictor of distribution limits in another location. This is important because the degree of specialization of species along environmental gradients will mediate the extent to which positive interactions affect their range limits (Chomicki et al. 2019).

There is a growing literature investigating the structure of ecological communities along environmental gradients (Tylianakis and Morris 2017, Pellissier et al. 2018). Likewise, the increasing amount of ecological data on species' occurrences (Wüest et al. 2020) allow us to infer the degree of overlap between species' distributions and the distributions of their interacting partners (Lefebvre et al. 2018). However, combining these two sources of information to understand the distribution of positive interactions along environmental gradients is not an easy task. Methodological challenges aside, the presence or absence of positive interactions might be subject to many sources of variation (Fortuna et al. 2020). Among them, positive interactions might respond differently to multiple environmental drivers (Tylianakis et al. 2008), and different types of mutualistic relationships have been shown to present high levels of within and across-season temporal variability (Díaz-Castelazo et al. 2010, Ramos-Robles et al. 2016, CaraDonna et al. 2017). That said, some work on plant–pollinator interactions has revealed that the level of specialization of species is somewhat predictable along temporal and environmental axes (Schleuning et al. 2012, Benadi et al. 2014, Bramon Mora et al. 2020). For e.g. the level of specialization of plant–pollinator communities in alpine grasslands has been shown to decrease with elevation, and change in predictable ways following extreme climatic events (Hoiss et al. 2015). This is important because such information could help us to understand where and how exactly species' ranges might be more strongly shaped by their interacting partners (Fig. 4). Generalizing this across species, interaction types and environmental gradients becomes then a critical step moving forward.

A complete mapping of a species' positive and negative interactions could reveal the locations where interactions most strongly affect its distribution. Indeed, using species distribution models, there is the potential to test the extent to which positive interactions will constrain or expand the range limits of a focal species by controlling for its degree of specialization across locations. There are several limitations to the ability of these models to describe species' fundamental niches, as many studies have questioned their potential to untangle and resolve the effects positive and negative interactions have on species' distributions (Hortal et al. 2012, Norberg et al. 2019). Nonetheless, researchers are already using similar models to try to understand the role that species' interactions have on shaping their entire distributions (e.g., using joint species distribution models; Pollock et al. 2014, Ovaskainen et al. 2016), but these rarely account for the context-dependency of species' interactions (Raath et al. 2018, Arumoogum et al. 2019). This might have led to contrasting observations in the literature. For example Filazzola et al. (2018) saw improvements in the prediction of a Mojave plant distribution when including the occurrence of facilitating shrubs as an explanatory variable (Meier et al. 2010, Pellissier et al. 2010, Arumoogum et al. 2019, Thompson et al. 2020). Others have concluded that positive interactions have limited roles in shaping range limits (Giannini et al. 2013, Copenhaver-Parry and Bell 2018). For example Giannini et al. (2013) found that information regarding the pollinators of a particular plant resulted in limited improvements in the predictions of its distribution. Overall, it is clear that the context-dependency of interactions might play a major role in shaping species' distributions, and understanding temporal and spatial variation in the impact of positive interactions on range limits remains a major challenge.
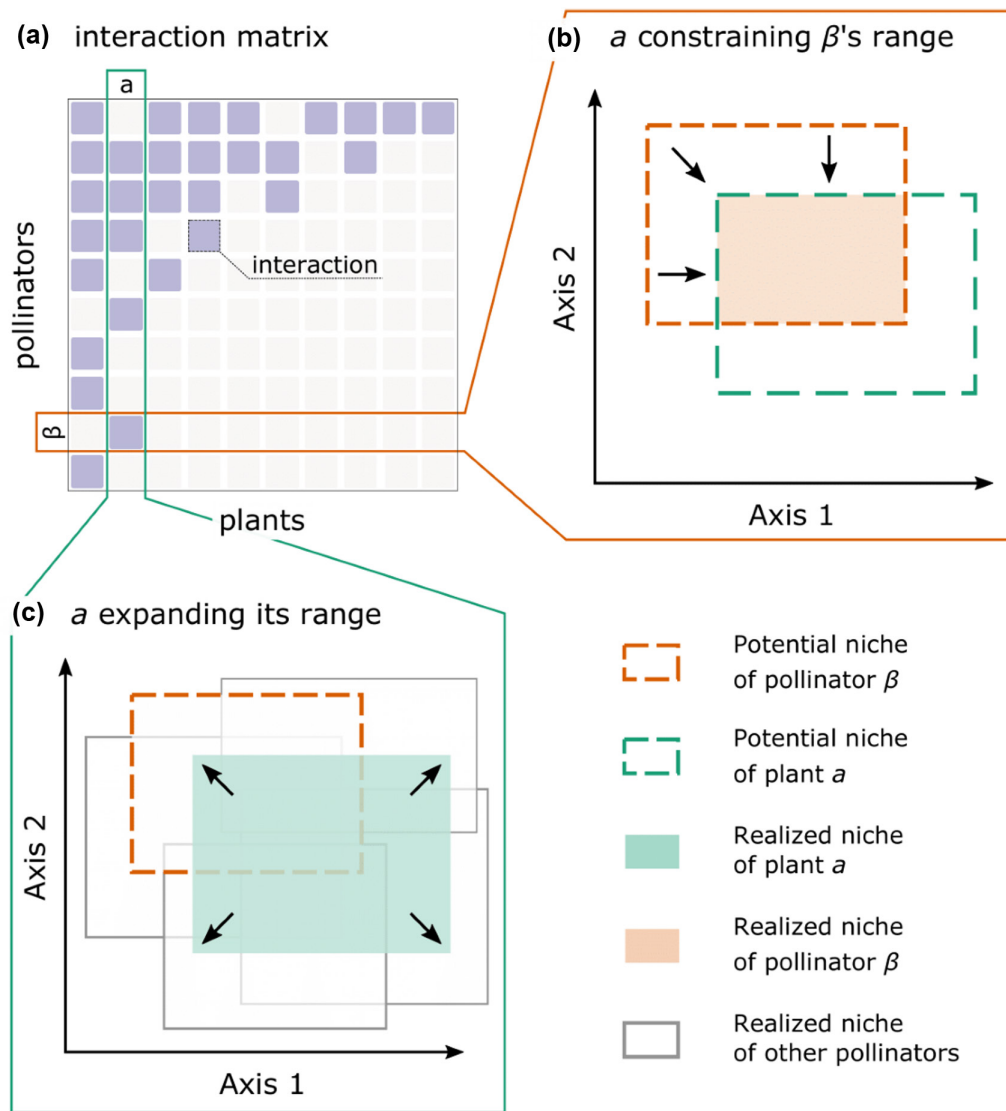
Figure 4. Potential effects of network structure on species' realized niches. (A) Interaction network between plants and pollinators presenting a nested structure, where the interacting partners of specialist species are generally proper subsets of those that interact with the most generalist species. Every purple and grey square represents the presence and absence of an interaction between any given two species, respectively. In this network, we highlighted the interactions of plant *a* and pollinator *β*. (B) Pollinator *β* only interacts with a single plant *a*; therefore, the distribution of this specialist pollinator could be strongly constrained by the presence and absence of *a* across environmental gradients (axes 1 and 2). The regions delimited by the dashed lines represent the potential niche of both species (Fig. 1). The shaded region represents the realized niche of species *β*. The arrows describe the direction of the effects the interaction between *a* and *β* have on *β*'s range limits. (C) Plant *a* interacts with several species that could potentially help it to expand its range limits. The regions delimited by continuous lines represent the realized niche of some of the pollinators interacting with *a*. The region delimited by a dashed line represents the potential niche of species *β*. The shaded region represents the realized niche of species *a*. The arrows indicated the direction of the effects the different interactions have on species *a*.

Effects of network structure on species' range limits

Beyond the variable nature of ecological interactions, the structure of mutualistic and commensal systems could play an important role in predicting changes in species' ranges. A large body of research has focused on uncovering nonrandom patterns underlying mutualistic networks. In general, these communities seem to present a nested structure (Bascompte et al. 2003), where specialist species tend to interact with generalist species (Fig. 4A). While such a network structure has crucial implications from a coexistence perspective, as it reduces effective interspecific competition (Bastolla et al. 2009), it could also have implications for predicting species' ranges (Chomicki et al. 2019). In particular, given the asymmetric relationship between specialist and

generalist species in nested networks, the effects of mutualistic interactions on species' ranges might in turn be asymmetric (Fig. 4). For instance a specialist pollinator's range limits could be strongly constrained by a given plant (Fig. 4B), but that plant could have a diverse set of interacting partners that expand its limits (Fig. 4C). That is, the mutualistic interaction between two species could have opposing effects on their ranges, potentially presenting additional feedback effects on each other. This could result in a stabilizing effect for species' range limits, as nested structures have been theoretically shown to promote community robustness to environmental perturbations (Baumgartner 2020); it could also lead to competitive interactions among specialist species that interact with the same generalist, potentially constraining the distributions of these specialist species (Cai et al. 2020). Furthermore, the asymmetric nature of the influence that positive interactions have on the distribution of both interacting partners could shed some light on the mechanisms underlying range expansion rates and biological invasion (Cagua et al. 2019).

Other structural patterns could also be relevant in predicting species' ranges. One such pattern is modularity – a property describing the extent to which networks are divided into densely connected groups of species (Jordano 1987). Communities such as plant–pollinator, seed–dispersal or host–parasitoid systems are often modular (Olesen et al. 2007, Fortuna et al. 2010, Schleuning et al. 2014). At local scales, these modules are likely to reflect eco-evolutionary pressures shaping who interacts with whom (Donatti et al. 2011, Ballarin et al. 2020); however, habitat filtering can also cluster species with similar habitat requirements, leading to modular structures at larger scales. Indeed, dynamical models accounting for niche relationships and distributions of species uncovered a naturally emerging modular structure in mutualistic systems, one in which each module presented in turn an internal nested structure (Cai et al. 2020). Under this perspective, network modules could perhaps define a better scale at which to test the effects of positive interactions on species' range limits. While this scale might not have the resolution needed to fully understand species' distributions, network modules could potentially become useful predictors of species' range limits by providing a general picture of who interacts with whom across space (Cai et al. 2020) and time (Morente-López et al. 2018).

Data gaps

Given the diversity of ways in which species interactions can affect range limits, there are certainly other examples that were not picked-up by our review. The aim of this review, however, was not to provide a comprehensive list of articles on a particular topic, but to have instead a representative sample that provided the basis for a qualitative analysis of the ways in which positive interactions affect range limits. Nonetheless, we expect some bias resulting from the choice of search terms in our literature survey. Similarly, we cannot exclude a possible detection bias in the literature favouring study systems where positive interactions are known to be important, or

studies reporting significant associations between biotic interactions and range limits. Finally, a mapping of the locations and taxonomic groups used across studies allowed us to shed light on additional geographic and taxonomic biases (Fig. 2).

Reporting bias
The number of articles annually published that could be relevant for this review is rapidly growing. Consequently, this review required us to narrow the search of articles to a strict list of keywords, potentially missing relevant articles, study systems and topics. First and foremost, our review is exclusively centered around positive interactions (Fig. 1), excluding interactions such as parasitism, herbivory and competition. This is important because while some of these interactions could lead to indirect positive effects, these were not the main focus of our study, and they have already been the target of other reviews (Wootton 1994, Holt and Bonsall 2017, Levine et al. 2017). Second, other much broader terms could have been accounted for in our literature survey, providing this review with a potentially broader scope. We could have included terms such as 'propagule pressure' or 'range expansion', which would have targeted work from the invasion literature. While this would have resulted in potentially hundreds of articles that tangentially linked positive interactions and species' range limits, our focus was instead on articles that explicitly made such a connection. Finally, terminology often differs across study systems, which might result in relevant articles being missed by our survey; we could have included terms targeting specific interaction types, such as seed-dispersal interactions (Neuschulz et al. 2018). However, we decided to use general search terms to avoid making the literature survey too wide.

Detection, geographic and taxonomic biases
We found a strong geographic bias towards North America in studies of the effects of positive interactions on species' distribution – a common problem in ecological field studies (Culumber et al. 2019) – with studies from the tropics, polar regions and deserts being particularly underrepresented. This is especially surprising, at least for the latter environments, where the stress gradient hypothesis predicts higher levels of positive species interactions (He et al. 2013). From an organismal perspective, our review revealed a pronounced plant bias. These organisms are sessile and are thus amenable to experimentation. Likewise, ant species have also been a disproportionately studied taxonomic group. A likely reason for this is that they are spatially constrained within nest networks and therefore convenient to sample; but they also engage in fascinating interactions with their abiotic and biotic environment that has long captured scientific and public interest. Lastly, even though intertidal ecosystems were among the first study systems focused on the link between biotic interactions and range limits (Paine 1969), and despite calls for additional facilitation research on marine systems (Bulleri 2009), aquatic ecosystems were clearly underrepresented in our review (11/73 studies, Silknetter et al. 2020).

As one route to addressing these knowledge and data gaps, we believe that there is great potential for simple, distributed

experiments to provide spatial replication (Callaway et al. 2002) or to test the importance of particular interactions across latitudinal or other gradients (Hargreaves et al. 2019). Transplant experiments across range limits that manipulate the presence/absence, or ideally abundance, of partners are one of the most direct ways to test how biotic interactions influence range limits (Westoby et al. 2018) but were only adopted in 9 of the 73 studies that we reviewed. Transplant experiments are most convenient with sessile organisms (e.g. plants or marine invertebrates, Hargreaves et al. 2015, Hart et al. 2018), but caging more mobile organisms is also possible in some cases.

Conclusions

Overall, our review indicates that it will often be necessary to account for positive interactions to understand a species' geographic range limits or predict its response to environmental changes. Interestingly, the literature indicates that these effects aren't only important in environmentally stressful environments, but also at range limits characterized by biotic stresses like competition or predation (Crotty and Bertness 2015). This suggests that the historical focus on the role of negative interactions may have stifled a more holistic view of how biotic interactions influence species range limits (Bruno et al. 2003). The challenge now is to understand how positive and negative interactions within complex communities act together to shape patterns of distributions, and ultimately to develop modelling frameworks that can account for these effects when predicting species ranges.

Author contributions

Pauline Stephan: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Investigation (lead); Methodology (equal); Project administration (lead); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Bernat Bramon Mora**: Conceptualization (equal); Visualization (equal); Writing – review and editing (equal). **Jake M. Alexander**: Conceptualization (equal); Methodology (equal); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

References

Afkhami, M. E. et al. 2014. Mutualist-mediated effects on species' range limits across large geographic scales. – Ecol. Lett. 17: 1265–1273.

Aguilera, M. A. and Navarrete, S. A. 2007. Effects of *Chiton granosus* (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. – J. Exp. Mar. Bio. Ecol. 349: 84–98.

Aguilera, M. A. et al. 2015. Facilitative effect of a generalist herbivore on the recovery of a perennial alga: consequences for persistence at the edge of their geographic range. – PLoS One 10: e0148303.

Alexander, J. M. et al. 2016. When climate reshuffles competitors: a call for experimental macroecology. – Trends Ecol. Evol. 31: 831–841.

Ameztegui, A. and Coll, L. 2013. Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients. – For. Ecol. Manage. 303: 25–34.

Anthelme, F. et al. 2014. Facilitation among plants in alpine environments in the face of climate change. – Front. Plant Sci. 5: 1–15.

Antonovics, J. 1976. The nature of limits to natural selection. – Ann. Mo. Bot. Gard. 63: 224–247.

Arumoogum, N. et al. 2019. The relative influence of abiotic and biotic factors on suitable habitat of Old World fruit bats under current and future climate scenarios. – Mamm. Biol. 98: 188–200.

Ballarin, C. S. et al. 2020. The resource-mediated modular structure of a non-symbiotic ant–plant mutualism. – Ecol. Entomol. 45: 121–129.

Bamba, M. et al. 2016. Wide distribution range of rhizobial symbionts associated with pantropical sea-dispersed legumes. – Antonie van Leeuwenhoek. 109: 1605–1614.

Barrio, I. C. et al. 2013. Extending the stress-gradient hypothesis – is competition among animals less common in harsh environments? – Oikos 122: 516–523.

Bascompte, J. and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. – Annu. Rev. Ecol. Evol. Syst. 38: 567–593.

Bascompte, J. et al. 2003. The nested assembly of plant–animal mutualistic networks. – Proc. Natl Acad. Sci. USA 100: 9383–9387.

Bastolla, U. et al. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. – Nature 458: 1018–1020.

Baumgartner, M. T. 2020. Connectance and nestedness as stabilizing factors in response to pulse disturbances in adaptive antagonistic networks. – J. Theor. Biol. 486: 110073.

Ben Zvi, G. et al. 2020. Reduced dispersal at nonexpanding range margins: a matter of disperser identity. – Ecol. Evol. 10: 4665–4676.

Benadi, G. et al. 2014. Specialization and phenological synchrony of plant-pollinator interactions along an altitudinal gradient. – J. Anim. Ecol. 83: 639–650.

Benning, J. W. and Moeller, D. A. 2019. Maladaptation beyond a geographic range limit driven by antagonistic and mutualistic biotic interactions across an abiotic gradient. – Evolution 73: 2044–2059.

Bertness, M. D. and Callaway, R. 1994. Positive interactions in communities. – Trends Ecol. Evol. 9: 191–193.

Bongaerts, P. et al. 2015. Deep down on a Caribbean reef: lower mesophotic depths harbor a specialized coral-endosymbiont community. – Sci. Rep. 5: 7652.

Bontrager, M. et al. 2019. Geographic variation in reproductive assurance of *Clarkia pulchella*. – Oecologia 190: 59–67.

Bracewell, R. R. and Six, D. L. 2014. Broadscale specificity in a bark beetle–fungal symbiosis: a spatio–temporal analysis of the

mycangial fungi of the western pine beetle. – Microb. Ecol. 68: 859–870.

Bramon Mora, B. et al. 2020. Untangling the seasonal dynamics of plant–pollinator communities. – Nat. Commun. 11: 4086.

Briers, R. A. 2003. Range limits and parasite prevalence in a fresh-water snail. – Proc. R. Soc. B 270 Supplement 2: 178–180.

Brittingham, S. and Walker, L. R. 2000. Facilitation of *Yucca brevifolia* recruitment by Mojave Desert shrubs. – W. N. Am. Nat. 60: 374–383.

Brooker, R. W. and Callaway, R. M. 2009. Facilitation in the conceptual melting pot. – J. Ecol. 97: 1117–1120.

Bruno, J. F. et al. 2003. Inclusion of facilitation into ecological theory. – Trends Ecol. Evol. 18: 119–125.

Bulleri, F. 2009. Facilitation research in marine systems: state of the art, emerging patterns and insights for future developments. – J. Ecol. 97: 1121–1130.

Bulleri, F. et al. 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. - Funct. Ecol. 30: 70–78.

Cagua, E. F. et al. 2019. Keystoneness, centrality, and the structural controllability of ecological networks. – J. Ecol. 107: 1779–1790.

Cahill, A. E. et al. 2014. Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. – J. Biogeogr. 41: 429–442.

Cai, W. et al. 2020. Mutualistic networks emerging from adaptive niche-based interactions. – Nat. Commun. 11: 5470.

Callaway, R. M. et al. 2002. Positive interactions among alpine plants increase with stress. – Nature 417: 844–848.

CaraDonna, P. J. et al. 2017. Interaction rewiring and the rapid turnover of plant–pollinator networks. – Ecol. Lett. 20: 385–394.

Cavieres, L. A. et al. 2008. Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? – Funct. Ecol. 22: 148–156.

Cavieres, L. A. et al. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. – Ecol. Lett. 17: 193–202.

Chalcoff, V. R. et al. 2012. Erosion of a pollination mutualism along an environmental gradient in a south Andean treelet, *Embothrium coccineum* (Proteaceae). – Oikos 121: 471–480.

Chamberlain, S. A. et al. 2014. How context dependent are species interactions? – Ecol. Lett. 17: 881–890.

Chen, J. et al. 2020. Shrub facilitation promotes selective tree establishment beyond the climatic treeline. – Sci. Total Environ. 708: 134618.

Cheney, K. L. and Côté, I. M. 2005. Mutualism or parasitism? The variable outcome of cleaning symbioses. – Biol. Lett. 1: 162–165.

Chhin, S. and Wang, G. G. 2016. Climatic sensitivity of a mixed forest association of white spruce and trembling aspen at their southern range limit. – Forests 7: 1–12.

Chomicki, G. et al. 2019. The impact of mutualisms on species richness. – Trends Ecol. Evol. 34: 698–711.

Copenhaver-Parry, P. E. and Bell, D. M. 2018. Species interactions weakly modify climate-induced tree co-occurrence patterns. – J. Veg. Sci. 29: 52–61.

Corli, A. and Sheppard, C. S. 2019. Effects of residence time, auto-fertility and pollinator dependence on reproductive output and spread of alien and native Asteraceae. – Plants 8: 108.

Crotty, S. M. and Bertness, M. D. 2015. Positive interactions expand habitat use and the realized niches of sympatric species. – Ecology 96: 2575–2582.

Culumber, Z. W. et al. 2019. Widespread biases in ecological and evolutionary studies. – Bioscience 69: 631–640.

Dal Grande, F. et al. 2018. Environment and host identity structure communities of green algal symbionts in lichens. - New Phytol. 217: 277–289.

Dangles, O. et al. 2018. Facilitation costs and benefits function simultaneously on stress gradients for animals. – Proc. R. Soc. B 285: 20180983.

Davis, B. J. et al. 2015. Continent-wide distribution in mycorrhizal fungi: implications for the biogeography of specialized orchids. – Ann. Bot. 116: 413–421.

Díaz-Castelazo, C. et al. 2010. Changes of a mutualistic network over time: reanalysis over a 10-year period. – Ecology 91: 793–801.

Dimond, J. L. et al. 2013. A simple temperature-based model predicts the upper latitudinal limit of the temperate coral *Astrangia poculata*. – Coral Reefs 32: 401–409.

Dona, A. J. and Galen, C. 2007. Nurse effects of alpine willows (*Salix*) enhance over-winter survival at the upper range limit of fireweed, *Chamerion angustifolium*. – Arct. Antarct. Alp. Res. 39: 57–64.

Donatti, C. I. et al. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. – Ecol. Lett. 14: 773–781.

Dowie, N. J. et al. 2016. Variability of ecological and autotrophic host specificity in a mycoheterotrophic system: *Pterospora andromedea* and associated fungal and conifer hosts. – Fungal Ecol. 20: 97–107.

Drezner, T. D. 2019. Vegetation associations of the endangered *Opuntia cespitosa* (prickly pear, Cactaceae) and microsite variation in Point Pelee National Park, Ontario, Canada. – Phys. Geogr. 42: 126–142.

Dupont, Y. L. et al. 2009. Spatio–temporal variation in the structure of pollination networks. – Oikos 118: 1261–1269.

Elton, C. 1927. Animal ecology. – The Macmillan Company.

Ettinger, A. and HilleRisLambers, J. 2017. Competition and facilitation may lead to asymmetric range shift dynamics with climate change. – Global Change Biol. 23: 3921–3933.

Fernández-Mendoza, F. et al. 2011. Population structure of mycobionts and photobionts of the widespread lichen *Cetraria aculeata*. – Mol. Ecol. 20: 1208–1232.

Filazzola, A. et al. 2018. Modelling the niche space of desert annuals needs to include positive interactions. – Oikos 127: 264–273.

Filazzola, A. et al. 2020. Establishment of a desert foundation species is limited by exotic plants and light but not herbivory or water. – Appl. Veg. Sci. 23: 586–597.

Fischer, M. S. and Rodriguez, R. J. 2013. Fungal endophytes of invasive phagramites australis populations vary in species composition and fungicide susceptibility. – Symbiosis 61: 55–62.

Forister, M. L. et al. 2011. Ant association facilitates the evolution of diet breadth in a lycaenid butterfly. – Proc. R. Soc. B 278: 1539–1547.

Fortuna, M. A. et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? – J. Anim. Ecol. 79: 811–817.

Fortuna, M. A. et al. 2020. Partner fidelity and asymmetric specialization in ecological networks. – Am. Nat. 196: 382–389.

Fugère, V. et al. 2012. Testing the stress-gradient hypothesis with aquatic detritivorous invertebrates: insights for biodiversity-ecosystem functioning research. – Br. Ecol. Soc. 81: 1259–1267.

Gao, M. et al. 2014. Assembly of plant communities in coastal wetlands-the role of saltcedar *Tamarix chinensis* during early succession. – J. Plant Ecol. 8: 539–548.

Gerz, M. et al. 2018. Niche differentiation and expansion of plant species are associated with mycorrhizal symbiosis. – J. Ecol. 106: 254–264.

Giannini, T. C. et al. 2013. Improving species distribution models using biotic interactions: a case study of parasites, pollinators and plants. – Ecography 36: 649–656.

Godsoe, W. et al. 2017. Interspecific interactions and range limits: contrasts among interaction types. – Theor. Ecol. 10: 167–179.

Gómez, J. M. and Verdú, M. 2012. Mutualism with plants drives primate diversification. – Syst. Biol. 61: 567–577.

Gray, K. W. et al. 2018. The dacetine ant *Strumigenys arizonica*, an apparent obligate commensal of the fungus-growing ant *Trachymyrmex arizonensis* in southwestern North America. – Insectes Soc. 65: 401–410.

Grinnell, J. 1917. Field tests of theories concerning distributional control. – Am. Nat. 51: 115–128.

Gross, S. J. and Price, T. D. 2000. Determinants of the northern and southern range limits of a warbler. – J. Biogeogr. 27: 869–878.

Hargreaves, A. L. et al. 2015. High-elevation range limit of an annual herb is neither caused nor reinforced by declining pollinator service. – J. Ecol. 103: 572–584.

Hargreaves, A. L. et al. 2019. Seed predation increases from the Arctic to the Equator and from high to low elevations. – Sci. Adv. 5: eaau4403.

Harrison, T. L. et al. 2018. More partners, more ranges: generalist legumes spread more easily around the globe. – Biol. Lett. 14(11): 20180616.

Harrower, J. and Gilbert, G. S. 2018. Context-dependent mutualisms in the Joshua tree–yucca moth system shift along a climate gradient. – Ecosphere 9: e02439.

Hart, S. P. and Marshall, D. J. 2013. Environmental stress, facilitation, competition, and coexistence. – Ecology 94: 2719–2731.

Hart, S. P. et al. 2018. How to quantify competitive ability. – J. Ecol. 106: 1902–1909.

Hata, H. et al. 2010. Geographic variation in the damselfish-red alga cultivation mutualism in the Indo-West Pacific. – BMC Evol. Biol. 10: 185.

He, Q. and Bertness, M. D. 2014. Extreme stresses, niches, and positive species interactions along stress gradients. – Ecology 95: 1437–1443.

He, Q. and Cui, B. 2015. Multiple mechanisms sustain a plant-animal facilitation on a coastal ecotone. – Sci. Rep. 5: 8612.

He, Q. et al. 2013. Global shifts towards positive species interactions with increasing environmental stress. – Ecol. Lett. 16: 695–706.

HilleRisLambers, J. et al. 2013. How will biotic interactions influence climate change-induced range shifts? – Ann. N. Y. Acad. Sci. 1297: 112–125.

Hoiss, B. et al. 2015. Interactive effects of elevation, species richness and extreme climatic events on plant–pollinator networks. – Global Change Biol. 21: 4086–4097.

Holt, R. D. and Bonsall, M. B. 2017. Apparent competition. – Annu. Rev. Ecol. Evol. Syst. 48: 447–471.

Hortal, J. et al. 2012. Basic questions in biogeography and the (lack of) simplicity of species distributions: putting species distribution models in the right place. – Nat. Conserv. 10: 108–118.

Hutchinson, G. E. 1957. Concluding remarks. – Cold Spring Harb. Symp. Quant. Biol. 22: 415–427.

Jabis, M. D. et al. 2020. Colonisation of the alpine tundra by trees: Alpine neighbours assist late-seral but not early-seral conifer seedlings. – Plant Ecol. Divers. 13: 209–224.

Jackson, S. T. and Overpeck, J. T. 2000. Responses of plant populations and communities to environmental changes of the late quaternary. 26: 194–220.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries , and coevolution. – Am. Nat. 129: 657–677.

Jordano, P. 1993. Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. – Vegetatio 107: 85–104.

Karst, J. et al. 2018. Tree species with limited geographical ranges show extreme responses to ectomycorrhizas. – Global Ecol. Biogeogr. 27: 839–848.

Lachmuth, S. et al. 2018. Neighbourhood effects on plant reproduction: an experimental–analytical framework and its application to the invasive *Senecio inaequidens*. – J. Ecol. 106: 761–773.

Lankau, R. A. 2012. Coevolution between invasive and native plants driven by chemical competition and soil biota. – Proc. Natl Acad. Sci. USA 109: 11240–11245.

Lankau, R. A. and Keymer, D. P. 2016. Ectomycorrhizal fungal richness declines towards the host species' range edge. – Mol. Ecol. 25: 3224–3241.

Lankau, R. A. et al. 2015. Mycorrhizal strategies of tree species correlate with trailing range edge responses to current and past climate change. – Ecology 96: 1451–1458.

Lapointe, B. E. et al. 2014. Ryther revisited: nutrient excretions by fishes enhance productivity of pelagic sargassum in the western North Atlantic Ocean. – J. Exp. Mar. Biol. Ecol. 458: 46–56.

Lefebvre, V. et al. 2018. Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. – Sci. Rep. 8: 4706.

Leung, T. L. F. and Poulin, R. 2008. Parasistism, commensalism, and mutualism: exploring the many shades of symbioses. – Vie Milieu 58: 107–115.

Levine, J. M. et al. 2017. Beyond pairwise mechanisms of species coexistence in complex communities. – Nature 546: 56–64.

Leydet, K. P. and Hellberg, M. E. 2016. Discordant coral–symbiont structuring: factors shaping geographical variation of symbiodinium communities in a facultative zooxanthellate coral genus, *Oculina*. – Coral Reefs 35: 583–595.

Litsios, G. et al. 2014. Host specialist clownfishes are environmental niche generalists. – Proc. R. Soc. B 281: 20133220.

Liu, C. et al. 2020. Most invasive species largely conserve their climatic niche. – Proc. Natl Acad. Sci. USA 117: 23643–23651.

Loh, W. K. W. et al. 2006. Diversity of *Symbiodinium* dinoflagellate symbionts from the Indo-Pacific sea slug *Pteraeolidia ianthina* (Gastropoda: Mollusca). – Mar. Ecol. Prog. Ser. 320: 177–184.

Lopez, Z. C. et al. 2020. Microbial mutualist distribution limits spread of the invasive legume *Medicago polymorpha*. – Biol. Invas. 23: 843–856.

Losapio, G. et al. 2019. Plant interactions shape pollination networks via nonadditive effects. – Ecology 100(3): e02619.

Loudermilk, E. L. et al. 2016. The path back: oaks (*Quercus* spp.) facilitate longleaf pine (*Pinus palustris*) seedling establishment in xeric sites. – Ecosphere 7: e01361.

Louthan, A. M. et al. 2015. Where and when do species interactions set range limits? – Trends Ecol. Evol. 30: 780–792.

Lu, J. et al. 2018. Bioclimatic factors at an intrabiome scale are more limiting than cyanobiont availability for the lichen-forming genus *Peltigera*. – Am. J. Bot. 105: 1198–1211.

Luiso, J. et al. 2020. High diversity and multiple invasions to North America by fungi grown by the northern-most *Trachymyrmex* and *Mycetomoellerius* ant species. – Fungal Ecol. 44: 100878.

Martorell, C. et al. 2015. Co-existence in a species-rich grassland: competition, facilitation and niche structure over a soil depth gradient. – J. Veg. Sci. 26: 674–685.

Meier, E. S. et al. 2010. Biotic and abiotic variables show little redundancy in explaining tree species distributions. – Ecography 33: 1038–1048.

Menzel, A. et al. 2017. Mycorrhizal status helps explain invasion success of alien plant species. – Ecology 98: 92–102.

Mestre, A. et al. 2020. A niche perspective on the range expansion of symbionts. – Biol. Rev. 95: 491–516.

Michalet, R. et al. 2016. Beneficiary feedback effects on alpine cushion benefactors become more negative with increasing cover of graminoids and in dry conditions. – Funct. Ecol. 30: 79–87.

Moeller, D. A. et al. 2012. Reduced pollinator service and elevated pollen limitation at the geographic range limit of an annual plant. – Ecology 93: 1036–1048.

Morente-López, J. et al. 2018. Phenology drives species interactions and modularity in a plant - flower visitor network. – Sci. Rep. 8: 9386.

Mueller, U. G. et al. 2011a. Frontier mutualism: coevolutionary patterns at the northern range limit of the leaf-cutter ant–fungus symbiosis. – Proc. R. Soc. B 278: 3050–3059.

Mueller, U. G. et al. 2011b. Evolution of cold-tolerant fungal symbionts permits winter fungiculture by leafcutter ants at the northern frontier of a tropical ant–fungus symbiosis. – Proc. Natl Acad. Sci. USA 108: 4053–4056.

Naoe, S. et al. 2016. Mountain-climbing bears protect cherry species from global warming through vertical seed dispersal. – Curr. Biol. 26: 315–316.

Neuschulz, E. L. et al. 2018. Biotic interactions and seed deposition rather than abiotic factors determine recruitment at elevational range limits of an alpine tree. – J. Ecol. 106: 948–959.

Norberg, A. et al. 2019. A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. – Ecol. Monogr. 89: 1–24.

Nougué, O. et al. 2015. Niche limits of symbiotic gut microbiota constrain the salinity tolerance of brine shrimp. – Am. Nat. 186: 390–403.

Olesen, J. M. et al. 2007. The modularity of pollination networks. – Proc. Natl Acad. Sci. USA 104: 19891–19896.

Ovaskainen, O. et al. 2016. Uncovering hidden spatial structure in species communities with spatially explicit joint species distribution models. – Methods Ecol. Evol. 7: 428–436.

Paine, R. T. 1969. The *Pisaster–Tegula* interaction: prey patches , predator food preference , and intertidal community structure. – Ecology 50: 950–961.

Parker, M. A. et al. 2007. Nodule symbiosis of invasive *Mimosa pigra* in Australia and in ancestral habitats: a comparative analysis. – Biol. Invas. 9: 127–138.

Pauw, A. and Bond, W. J. 2011. Mutualisms matter: pollination rate limits the distribution of oil-secreting orchids. – Oikos 120: 1531–1538.

Pellissier, L. et al. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. – Ecography 33: 1004–1014.

Pellissier, L. et al. 2018. Comparing species interaction networks along environmental gradients. – Biol. Rev. 93: 785–800.

Peña-Gómez, F. T. and Bustamante, R. O. 2012. Life history variation and demography of the invasive plant *Eschscholzia californica* Cham. (Papaveraceae), in two altitudinal extremes, central Chile. – Gayana Bot. 69: 113–122.

Pendleton, R. M. et al. 2012. The strength of *Nocomis* nest association contributes to patterns of rarity and commonness among New River, Virginia Cyprinids. – Am. Midl. Nat. 168: 202–217.

Pérez-Méndez, N. et al. 2015. Downsized mutualisms: consequences of seed dispersers' body-size reduction for early plant recruitment. – Perspect. Plant Ecol. Evol. Syst. 17: 151–159.

Pickens, C. N. et al. 2019. Influence of salt marsh canopy on black mangrove (*Avicennia germinans*) survival and establishment at its northern latitudinal limit. – Hydrobiologia 826: 195–208.

Pollock, L. J. et al. 2014. Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). – Methods Ecol. Evol. 5: 397–406.

Quinn, J. L. and Ueta, M. 2008. Protective nesting associations in birds. – Ibis 150: 146–167.

Raath-Krüger, M. J. et al. 2019. Positive plant–plant interactions expand the upper distributional limits of some vascular plant species. – Ecosphere 10: e02820.

Raath, M. J. et al. 2018. Incorporating biotic interactions in the distribution models of African wild silk moths (*Gonometa* species, Lasiocampidae) using different representations of modelled host tree distributions. – Austral Ecol. 43: 316–327.

Ramos-Robles, M. et al. 2016. Temporal changes in the structure of a plant–frugivore network are influenced by bird migration and fruit availability. – PeerJ 2016: 1–21.

Rivest, S. and Velend, M. 2018. Herbivory and pollen limitation at the upper elevational range limit of two forest understory plants of eastern North America. – Ecol. Evol. 8: 892–903.

Rodríguez-Buriticá, S. and Miriti, M. N. 2009. Biting the hand that feeds: the invasive grass *Schismus barbatus* (Poaceae) is facilitated by, but reduces establishment of, the native shrub *Ambrosia dumosa* (Asteraceae). – J. Veg. Sci. 20: 241–250.

Roe, A. D. et al. 2011. Spatial community structure of mountain pine beetle fungal symbionts across a latitudinal gradient. – Microb. Ecol. 62: 347–360.

Schleuning, M. et al. 2012. Specialization of mutualistic interaction networks decreases toward tropical latitudes. – Curr. Biol. 22: 1925–1931.

Schleuning, M. et al. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. – Ecol. Lett. 17: 454–463.

Schöb, C. et al. 2014. Consequences of facilitation: one plant's benefit is another plant's cost. – Funct. Ecol. 28: 500–508.

Schrey, A. W. et al. 2014. Range expansion of house sparrows (*Passer domesticus*) in kenya: evidence of genetic admixture and human-mediated dispersal. – J. Hered. 105: 60–69.

Sexton, J. P. et al. 2009. Evolution and ecology of species range limits. – Annu. Rev. Ecol. Evol. Syst. 40: 415–436.

Silknetter, S. et al. 2020. Positive biotic interactions in freshwaters: a review and research directive. – Freshwater Biol. 65: 811–832.

Singer, A. et al. 2013. Interspecific interactions affect species and community responses to climate shifts. – Oikos 122: 358–366.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. – Ecol. Lett. 10: 1115–1123.

Stanton-Geddes, J. and Anderson, C. G. 2011. Does a facultative mutualism limit species range expansion? – Oecologia 167: 149–155.

Svenning, J. C. et al. 2014. The influence of interspecific interactions on species range expansion rates. – Ecography 37: 1198–1209.

Swarts, N. D. et al. 2010. Ecological specialization in mycorrhizal symbiosis leads to rarity in an endangered orchid. – Mol. Ecol. 19: 3226–3242.

Theobald, E. J. et al. 2016. Lilies at the limit: variation in plant–pollinator interactions across an elevational range. – Am. J. Bot. 103: 189–197.

Thompson, P. R. et al. 2020. Predictor species: improving assessments of rare species occurrence by modeling environmental co-responses. – Ecol. Evol. 10: 3293–3304.

Trøjelsgaard, K. et al. 2015. Geographical variation in mutualistic networks: Similarity, turnover and partner fidelity. – Proc. R. Soc. B 282: 1–9.

Tye Pettay, D. et al. 2015. Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella. – Proc. Natl Acad. Sci. USA 112: 7513–7518.

Tylianakis, J. M. and Morris, R. J. 2017. Ecological networks across environmental gradients. – Annu. Rev. Ecol. Evol. Syst. 48: 25–48.

Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. – Ecol. Lett. 11: 1351–1363.

Urbanczyk, H. et al. 2012. Limited geographic distribution of certain strains of the bioluminescent symbiont *Photobacterium leiognathi*. – FEMS Microbiol. Ecol. 81: 355–363.

Van Kleunen, M. et al. 2015. Global exchange and accumulation of non-native plants. – Nature 525: 100–103.

Verde, E. A. and McCloskey, L. R. 2002. A comparative analysis of the photobiology of zooxanthellae and zoochlorellae symbiotic with the temperate clonal anemone *Anthopleura elegantissima* (Brandt): II. Effect of light intensity. – Mar. Biol. 141: 225–239.

Verstraete, B. et al. 2013. Phylogenetic lineages in Vanguerieae (Rubiaceae) associated with *Burkholderia* bacteria in sub-Saharan Africa. – Am. J. Bot. 100: 2380–2387.

Villellas, J. et al. 2019. Geographic location, local environment, and individual size mediate the effects of climate warming and neighbors on a benefactor plant. – Oecologia 189: 243–253.

Vittoz, P. et al. 2009. Low impact of climate change on subalpine grasslands in the Swiss Northern Alps. – Global Change Biol. 15: 209–220.

Wang, R. et al. 2018. Weak genetic divergence suggests extensive gene flow at the northeastern range limit of a dioecious *Ficus* species. – Acta Oecol. 90: 12–17.

Westoby, M. et al. 2018. How species boundaries are determined : a response to Alexander et al . – Trends Ecol. Evol. 33: 713.

Wisz, M. S. et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. – Biol. Rev. 88: 15–30.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – Annu. Rev. Ecol. Syst. 25: 443–466.

Wüest, R. O. et al. 2020. Macroecology in the age of big data – where to go from here? – J. Biogeogr. 47: 1–12.

Zhang, L. S. et al. 2014. Living on the edge: fig tree phenology at the northern range limit of monoecious *Ficus* in China. – Acta Oecol. 57: 135–141.

Zhang, B. et al. 2019. Obligate bacterial endosymbionts limit thermal tolerance of insect host species. – Proc. Natl Acad. Sci. USA 116: 24712–24718.