Geographically variable biotic interactions and implications for species ranges

Running title: Geographic variation in biotic interactions

Abstract:

Understanding how biotic interactions affect species’ geographic ranges, biodiversity patterns, and ecological responses to environmental change is one of the most pressing challenges in macroecology. Extensive efforts are underway to detect signals of biotic interactions in macroecological data. However, efforts are limited by bias in the taxa and spatial scale for which occurrence data are available, and by difficulty in ascribing causality to co-occurrence patterns. Moreover, we are not necessarily looking in the right places: analyses are largely ad hoc, depending on data availability, rather than focusing on regions, taxa, ecosystems, or interaction types where biotic interactions might affect species’ geographic ranges most strongly.

We suggest that macroecology would benefit from recognising that abiotic conditions alter two key components of biotic interaction strength: frequency and intensity. We outline how and why variation in biotic interaction strength occurs, explore the implications for species’ geographic ranges, and discuss the challenges inherent in quantifying these effects. In addition, we explore the role of behavioural flexibility in mediating biotic interactions to potentially mitigate impacts of environmental change. We argue that macroecology should take advantage of “independent” data on the strength of biotic interactions measured by those in other disciplines to capture a far wider array of taxa, locations and interaction types than are typically studied in macroecology. Data on biotic interactions are readily available from community, disease, microbial, and parasite ecology, evolution, palaeontology, invasion biology, and agriculture, but most are yet to be exploited within macroecology. Inter-disciplinary synthesis of these data would pave the way towards inclusion of geographically variable biotic interactions within macroecological models. We believe that taking the steps we outline would improve forecasts of changes in species’ geographic ranges and increase
fundamental understanding of the processes that underpin patterns of species diversity and
distribution.

Keywords

Encounter rate, climate envelope model, latitudinal biodiversity gradient, niche, species distribution
model, stress gradient hypothesis, competition, trophic interaction, facilitation, mutualism.
Introduction

Evolutionary history, environmental conditions and dispersal ability set the playing field for species’ geographic ranges, abundances, and macroecological patterns (Hampe, 2011; Keith et al., 2013; Estrada et al., 2015; Dallas et al., 2017). However, interspecific biotic interactions (hereafter, BIs) are recognised increasingly as key factors affecting the extent and occupancy of species’ geographic ranges (Wisz et al., 2012; Pigot & Tobias, 2013), species abundances (Keane & Crawley, 2002), and species diversity gradients (Whittaker et al., 2001; Louthan et al., 2015). Competition and trophic interactions that have a negative effect (e.g., predation, parasitism, herbivory are negative for the consumed species) can decrease abundance, potentially to the point of excluding populations and limiting ranges (Soberón, 2007; Holt & Barfield, 2009). Facilitation, mutualism, and trophic interactions with a positive effect (i.e. for the consumer) can extend ranges into locations that are otherwise unsuitable (Karvonen et al., 2012; Afkhami et al., 2014; Crotty & Bertness, 2015).

However, as environmental change and biological invasions reshuffle species’ geographic ranges, it is unclear how, and to what extent, biotic interactions influence range shifts and consequent changes in diversity. To improve fundamental understanding and predict, and potentially mitigate, the effects of environmental change on biodiversity, it is therefore imperative that we seek to resolve the role for biotic interactions in species’ geographic ranges and macroecological patterns.

Advances in this area have so far focused primarily on how to make best use of co-occurrence data as proxies for interactions in biogeographical models (e.g. Species Distribution Models, SDMs), and more recently on incorporating BI data derived from small scale experiments (Jabot & Bascompte, 2012; Staniczenko et al., 2017). Although this approach can yield important new insight (Pollock et al., 2014; Morueta-Holme et al., 2016), distribution data are too sparse to study co-occurrences of species involved in the majority of BIs, for example disease, invertebrate herbivory, pollination, or below-ground microbial mutualisms. Moreover, co-occurrences can spark spurious claims for evidence of biotic interactions (Dormann et al., 2018; Montesinos-Navarro et al., 2018). To some
extent, these attempts and criticisms rehash the decades-old dispute between Diamond (1975) and Connor and Simberloff (1979) on whether a lack of co-occurrence between species was sufficient to infer competitive exclusion (Connor et al., 2013). We clearly need to revise our approach if we are to exit the biotic interactions “groundhog day” that has plagued macroecology since before the inception of Global Ecology & Biogeography.

We believe one promising approach that has received too little attention is to study how and why the strength of BIs and effects on species’ ranges vary geographically, and the subsequent implications for macroecological patterns (Whittaker et al., 2001; Chamberlain et al., 2014; Louthan et al., 2015). The occurrence or outcome of a BI can depend on environmental conditions, time period, or life-history stage (Pariaud et al., 2009; Valiente-Banuet & Verdu, 2013; Chamberlain et al., 2014; Tikhonov et al., 2017; Dormann et al., 2018; Rogers et al., 2018). However, we focus on environmental effects on BIs since environmental gradients will often lead to predictable patterns in BI strength across species’ ranges. Furthermore, focusing on geographic variation generally, rather than on particular environmental conditions or range margins (e.g. Solíveres et al., 2014; Louthan et al., 2015), liberates us to scrutinise BI effects on species’ entire range extents, as well as their abundances and range occupancies.

We propose that macroecology should invest extensive effort in understanding to what extent, how and why different environmental conditions influence BIs. Specifically, we explore how and why abiotic factors can cause both the frequency and intensity of BIs between two species to vary across space and time. We discuss the relevance of BI strength for fundamental biogeography, and for macroecological patterns under environmental change. We develop our ideas by considering pairwise interactions between ‘focal’ and ‘interactor’ species (fig. 1), and discuss how the ideas can be scaled up to apply to ecological communities. Although we recognise the significant challenges inherent in this research area, we hope that our ideas spur the development of new questions, new analyses and more focused data collection to further reveal the influence of BIs in macroecology.
Components of biotic interaction strength

BI strength can be characterised as the effect of one ‘interactor’ species on the growth rate of a ‘focal’ species’ population at a given location, which results ultimately in altered abundance or occurrence (fig. 1). BI strength can vary across abiotic gradients, and thus species’ ranges, in a predictable way. As we expand on below, the variation could be due to a direct effect of abiotic conditions on the interactor, or the interaction could be modified by the position in the abiotic niche of the focal species. To standardise measurement of BI strength across taxa and BI types (e.g., competition, mutualism, trophic) we suggest that strength can considered to be a function of two components: (1) frequency, the rate of interaction events experienced; and (2) intensity, the effect on lifetime reproductive output of individuals involved in the BI. For an additional consideration of these effects and excellent examples, we refer the reader to Louthan et al. (2015). Deconstructing BI strength into these components can provide insight additional insight because their relative contributions could lead to different implications for species’ geographic ranges (fig. 2). For example, for an interaction of the same overall strength, high frequency coupled with low intensity could maintain coexistence, whereas the converse - low frequency with high intensity - could reinforce competitive exclusion (e.g., allopatric sister species; fig. 2).

1. Frequency. For a BI to occur, two individuals must encounter one another in the same place and time (Gurarie & Ovaskainen, 2013; Poisot et al., 2015; CaraDonna et al., 2017), but this simple starting point has been largely overlooked. One of the clearest mediators of encounter rate, and thus interaction strength, is density of the interacting species’ populations (Wootton & Emmerson, 2005). For example, mammalian top predators suppress mesopredators more strongly at the centre of the top predators’ geographic ranges where the predators are more abundant (fig. 2, Newsome et al., 2017). On longer time scales, species diversity and abundance correlate with increased predation of marine metazoans throughout the Phanerozoic (Huntley & Kowalewski, 2007). Implications of varying density across abiotic gradients are addressed thoroughly by Louthan et al. (2015). However,
one point we wish to add is that, not only does density influence BIs, but BIs can influence density 
(Poisot et al., 2014). Although we cannot eliminate this complexity, we must remain mindful of 
circularity when considering the effect of density on BI frequency.

Encounter rate can also be influenced by abiotic context. Effects of temperature on encounter rate 
are particularly interesting because temperature is often cited as one of the most important abiotic 
factors affecting species’ ranges and shows strong geographic gradients. Temperature can affect 
encounter rate directly by altering physiological performance or tolerance. For example, ectothermic 
individuals move faster at higher temperatures due to increased metabolic rates (Biro et al., 2010; 
Öhlund et al., 2015), increasing encounter rates through Brownian motion alone (Vahl et al., 2005). 
Yet these effects are not restricted to ectotherms. In endotherms, the effects on physiological 
tolerance can lead to behaviourally-mediated changes in encounter rates as temperatures alter daily 
activity budgets, and consequently, alter available net energy. For example, across three sites in 
Africa, wild dog hunting activity was restricted by high temperatures due to the danger of over-
heating, which led to lower daily prey encounter rates (Woodroffe et al., 2017, fig. 3).

An additional mediator of encounter rate is structural complexity, which could be abiotic (i.e., 
topographic) or biotic (e.g., vegetation), but in either case has been included in SDMs as an 
‘environmental’ factor (St-Louis et al., 2009). Structural complexity can alter encounter rates by 
changing the distance between individuals required for awareness of each other’s presence (Michel 
& Adams, 2009; Karkarey et al., 2017). For example, aquatic insect predators changed predation 
strategy in response to structural vegetation complexity because high complexity interfered with 
vision (Michel & Adams, 2009). Similarly, open habitats allow individuals to be aware of each other’s 
presence over long distances, which can enable individuals to avoid or engage in an interaction.

Cheetahs that hear calls from lion and hyena competitors on open plains avoid encounters by 
retreating before the other individual becomes aware of their presence (Durant, 2000), coral reef 
damselfish use structural refuges to avoid encounters with predators (Beukers & Jones, 1997), and
following coral mortality, predatory groupers respond to reduced structural complexity by altering foraging strategies to maintain prey encounter rate (Karkarey et al., 2017). When asking whether structural complexity and behaviour affect population dynamics or range occupancy, one must also consider different perceptions of complexity across organisms – what is complex for an insect might be simple for a large mammal (Nash et al., 2013). This point is particularly relevant for trophic interactions where focal and interactor species are often of very different body size. Although little evidence exists as yet for structural complexity mediating BIs and thus species’ ranges, we believe it is worth exploring in the context of ongoing anthropogenic habitat modification (Møller et al., 2013; Karkarey et al., 2017). Consideration should also be given to whether there is a parallel for encounter rate between sessile species, for example distance over which allelopathic chemicals can act.

2. Intensity. Abiotic factors can affect intensity by affecting both the interactor and the focal species.

a) Effect of interactor (“effect per interactor” in Louthan et al., 2015). Abiotic conditions can alter the behaviour, physiology and population growth rate of the interactor. For example, particular temperatures can select for stronger interactions in microbial and insect parasites (e.g. aggressiveness, spore production, virulence, Thomas & Blanford, 2003; Laine, 2007; Pariaud et al., 2009), and influence swimming speeds of pike predating brown trout (Öhlund et al., 2015). In addition, abiotic effects on the focal species can mediate the effect of the interactor. Optimum nitrogen conditions for plants increases infection efficiency and spore production of their biotrophic pathogens (Pariaud et al., 2009). Favourable abiotic conditions can also increase crop productivity, which in turn increases the number of herbivores plants can host (Foster et al., 1992) and the vigour of their pathogens (Hersh et al., 2012).

b) Response of focal species (“effect per encounter” in Louthan et al., 2015). The degree to which a given interaction affects the population growth rate, and subsequent abundance or occurrence of the focal species can vary across its abiotic niche because the species’ ability to moderate the
interaction varies with abiotic conditions. This variation could be due to abiotic limitations or trade-offs for the focal species. For example host immune systems are often more active at higher temperatures, reducing bacterial proliferation (Lazzaro et al., 2008), and temperature can alter the accuracy of marmalade hoverfly defence mimicry of wasps due to thermoregulation constraints on the amount of black or yellow pigment (Marriott & J. Holloway, 1998). Alternatively, focal species can allocate resources differently in response to abiotic factors that regulate the interaction. For instance, facultative mycorrhizal plant species can regulate the level of mycorrhization under different soil nutrient conditions (Johnson et al., 2008; Grman, 2012). Similarly, populations facing more challenging environmental conditions towards the edge of their abiotic niche could have less resource to invest in defence (suggested by the results of Pennings et al., 2007) so experience a more negative response per encounter in that region.

The components of BI strength outlined above could act in synergy or opposition, generating different species’ range patterns. For example, Katz and Ibáñez (2017) found little spatial variation in the frequency of foliar pathogen damage of Quercus velutina (effect of interactor), but strong variation in tree population dynamics (response) and hence high (intensity), whereas the situation was reversed for Liriodendron tulipifera. Pike speed (effect) when attacking brown trout increased with temperature but trout escape speed did not, leading to increased encounter rates (frequency), and ultimately increased catch rates, at high temperatures (Öhlund et al., 2015). Bacterial infection in waterfleas was most frequent at intermediate temperatures, but host mortality (response) was greatest at high temperatures (Vale et al., 2008). Breaking down BIs into the components we describe paves the way for a framework that could standardise BI strength between taxa and interaction types, and ultimately aid macroecological analysis of BI strength.
Variation in biotic interaction strength and implications for species’ geographic ranges

Variation in BI strength along abiotic gradients will often cause species’ ranges and abundances to differ from those expected based on abiotic tolerances alone. To demonstrate this effect, we present examples where geographic variation in BI strength could, or has been observed to, alter species’ ranges (fig. 1).

*Anopheles albopictus* mosquitos are stronger competitors than *A. aegypti* at temperatures below ~24°C. However, at higher temperatures and low humidity, *A. albopictus* eggs desiccate more readily than *A. aegypti* eggs (Juliano *et al.*, 2002; Lounibos *et al.*, 2002). Therefore, reduced frequency of the interaction in dry conditions above ~24°C means that populations of *A. albopictus* no longer outcompete *A. aegypti* (Fig. 1 A-D). This temperature-dependent competition strength affects the range of *A. aegypti*: an invasion of *A. albopictus* excluded *A. aegypti* from parts of the south-eastern US where it previously thrived. Modelling *A. aegypti*’s geographic range using a classic climatic SDM, would therefore underestimate thermal tolerance at low and intermediate temperatures. This would cause substantial errors when trying to project *A. aegypti*’s range in the absence of the competitor, or in understanding the consequences of competitor removal. We note that even in the absence of a geographic gradient in BI strength, BI effects need only be additive to abiotic effects to limit species’ ranges (right hand of graph in fig. 1B).

Endophytic fungi are found frequently to affect plant demographic processes both positively and negatively, and to have varying interaction strengths across abiotic gradients (David *et al.*, 2018). For example, *Discula quercina* colonised *Quercus cerris* trees in Mediterranean oak forests in the early 1990s and remained largely quiescent. However, at times of drought, the fungus becomes an aggressive coloniser, killing its host (Fig. 1 E-H, Moricca & Ragazzi, 2011; and see Hersh *et al.*, 2012 for further examples). A very different effect results from the interaction between the mutualistic fungal endophyte and its grass host *Bromus laevipes*. The endophyte ameliorates the plant’s drought
stress, extending the grass’ geographic range into thousands of square kilometres, which experience
drier conditions than the grass could otherwise tolerate (fig. 1 I-L, Afkhami et al., 2014).

Behaviour can mediate BI strength across abiotic conditions. For example, Flight Initiation Distance
(FID) of female lizards from predators decreases (i.e. is initiated when the predator gets closer) with
increased latitude and seasonal temperature fluctuations (Samia et al., 2015). Females must forage
for sufficient time to gain enough energy to produce eggs. Therefore in regions where short
summers constrain the amount of energy that can be gained from foraging, lizards continue to
forage when predators get closer compared to regions with longer summers. FID of male lizards is
constant with latitude, presumably because their reproductive investment is relatively cheap so they
do not need to forage at times of high predation risk (Samia et al., 2015). This suggests that
predation likelihood is constant with latitude, but female behaviour could increase encounter rate
with predators, increasing per capita predation rates and thus limit lizard ranges at high latitudes
(fig. 1 M-P).

As well as altering BI strength, anti-predator behaviour can vary geographically to maintain BI
strength. For example FID of prey bird species increases at lower latitudes, which suggests increased
risk because flight is energetically costly. Indeed, raptor density increases at low latitudes, which
would presumably increase predator-prey encounter rate and BI strength if FID did not alter (fig. 1
Q-T, Díaz et al., 2013). Therefore, this change in behaviour offsets the frequency change that would
otherwise occur due to different predator densities. Predator-prey interactions are also weaker in
urban than in rural environments (Díaz et al., 2013; Møller et al., 2013; Díaz et al., 2015), potentially
leading to increased prey population growth rate and range occupancy (fig. 1R, T).

This last example highlights a major constraint on identifying the effects of BIs on species’
geographic ranges: spatial variation in BI strength can correspond to abiotic factors that do not have
systematic geographic gradients. For example, light affects forest plant susceptibility to pathogenic
fungi (effect for focal species, García-Guzmán et al., 2017) and fungal pathogenicity or mutualism
The lack of a geographic gradient in light gaps means these effects will depress or enhance plant abundance or occurrence heterogeneously across species’ ranges (Nielsen et al., 2005; VanDerWal et al., 2009).

Another challenge arises when BI gradients are caused by multiple abiotic gradients and are mediated by the abiotic niche of both the interactor and focal species, making the mechanism underlying outcomes difficult to disentangle. For example, high rainfall is optimal for the ungulate prey (‘interactor’ species) of African wild dogs (Woodroffe et al., 2017). High rainfall, at an optimal position in the abiotic niche, can improve prey body condition, making prey harder to catch, which decreases encounter rate, and thus, frequency of interactions. High rainfall can also increase prey population growth rate, which increases density, and thus frequency of interactions. This can make a signal of rainfall hard to detect (fig. 3A). BI strength is also modulated by the wild dog (‘focal’ species) abiotic niche. Higher temperatures cause over-heating during hunting bouts, leading to lower encounter rates and decreased wild dog reproductive success (fig. 3B, C). By widely used standards, the wild dog should not be at risk from climate change, however temperature effects on hunting behaviour and energy intake suggests declines are indeed due to warming temperatures (fig. 3D, Woodroffe et al., 2017).

In contrast to examples in fig. 1, strong BI effects can occur at the centre of the abiotic niche and weak effects at the edges (e.g. Foster et al., 1992; Pariaud et al., 2009; Hersh et al., 2012; Newsome et al., 2017). In this case BIs do not restrict species’ geographic ranges within the abiotic range limits (fig. 3 E-G). However, the pattern of BI strength can depress abundance and population growth rates within the species’ range (a pattern noted by VanDerWal et al., 2009; Dallas et al., 2017). This could lead to unexpected consequences for species’ current strongholds if BI strength changes at locations with peak abiotic favourability due, for example, to idiosyncratic species movement in response to climate change (Keith et al., 2011).
Whilst many BI effects on ranges are due to steady changes in interaction strength through space (fig. 1, 3), range limits could result from abrupt exclusion by another species, as is observed for hedgehogs in Europe and allopatric sister species (Wisz et al., 2012; Pigot & Tobias, 2013). In this situation, interaction strength could increase very sharply at a range margin, which could be difficult to detect. However, by considering the components of BI strength, we can clarify that the frequency of interactions is low whilst the intensity is high, leading to greater understanding of the process underlying ‘checkerboard’ species ranges (fig. 2).

Quantifying biotic interaction effects on geographic ranges

The relationship between BI strength and abiotic factors is widely studied for a very diverse range of organisms. Three main approaches are used to measure interaction strength explicitly (i.e., excluding biogeographical analyses of species co-occurrences):

1. Manipulative field experiments, including transplant or common garden experiments, used typically for sessile species such as plants.
2. Field observational studies across abiotic gradients, often using latitudinal or altitudinal gradients, or environmental changes through time, used typically for well-known taxa such as plants and vertebrates.
3. Laboratory or controlled environment experiments used typically for invertebrate, microbe (analysed rarely in biogeography), or plant interactions on a single abiotic gradient.

This plethora of data awaits synthesis to study species’ geographic ranges. Collating interaction data will require inter-disciplinary effort, involving community, disease, microbial, and parasite ecology, evolution, palaeontology, invasion biology, and agriculture – we have used examples from all of these fields throughout the paper to illustrate their value and applicability.

BI strength along abiotic gradients has been quantified to different extents across taxonomic groups.

Perhaps the most comprehensive data are available for terrestrial plants, and intertidal
invertebrates - particularly for competition, pollination, herbivory, facilitation and mutualism - as these taxa are classic systems used to understand effects of BIs on abundance, diversity, distributional ranges. Some obligate trophic interactions have been quantified, often for charismatic species e.g., butterflies and their host-plant use (Pateman et al., 2012), pollinators (Burkle & Alarcón, 2011), and Iberian lynx and rabbits (Fordham et al., 2013). The frequency component of BI strength has received disproportionate research attention, for example, number of parasites per individual and amount of herbivory damage are often used as to indicate the degree of regulation by enemies (Dostál et al., 2013). Intensity is more commonly quantified in laboratory studies on model organisms, which has limited taxonomic scope. Laboratory studies also tend to focus on the effect of a single abiotic factor, often temperature or moisture, despite the fact that in nature, multiple abiotic factors vary simultaneously. In contrast, field experiments or observations capture the effect of multiple factors simultaneously, which can make it hard to disentangle the different abiotic effects. Also in the field, BI strength is often measured indirectly by proxies such as resistance (Álvarez-Loayza et al., 2011), anti-predator behaviour (Díaz et al., 2013), and palatability (Pennings et al., 2007)), rather than an outcome directly relevant to species’ ranges such as individual reproductive output or population growth rate.

Synthesising data on BI strength will enable us to pool the advantages, and mitigate the disadvantages, of both methods to identify taxa, interaction types, geographic locations, abiotic conditions, and ecosystems where BIs strongly affect species’ ranges. This will inform expectations about where and when BIs might underlie macroecological patterns. Quantitative BI data could also be incorporated directly into models to improve measurements of species’ niches and forecasts of geographic ranges. For example, patterns of BI strength could be used in SDMs to account for biotic effects on occupancy or abundance. SDMs could then measure species associations with abiotic factors more accurately (similar to efforts to account for recorder effort) and better forecast effects of changes in abiotic conditions or the distributions of interactors. In many cases, quantifying biotic effects in this way will require more data than can be obtained from existing research. Thus, we
recommend the macroecological community invests in collecting new “for-purpose” data on BI strength, using existing data and theory to target systems where BI strength is likely to be important.

**Scaling up from individual species to macroecological patterns**

The strength of some BIs has been analysed simultaneously for multiple species in relation to geographic or environmental gradients (Bowker *et al.*, 2010; Moles *et al.*, 2011; He *et al.*, 2013; Zhang *et al.*, 2016). However, it is difficult to draw conclusions about BI effects on ranges from these analyses because position on an abiotic gradient does not necessarily correspond to position within a species’ geographic range or abiotic niche. There is considerable variation in abiotic tolerance between species (Araújo *et al.*, 2013) so measuring BI strength for many species along an abiotic gradient could compare interactions at the range (or abiotic niche) margin for one species, but at the centre for another. Multi-species analyses would therefore benefit from considering the position of each species within their individual niche or range rather than simply its position along an abiotic gradient.

We have so far dealt with pairwise interactions only, but the link between BI strength and range limitation could be extended to interactions between multiple species. Data on pairwise species interactions is likely to be able to ‘scale up’ to inform the effects of the wider ecological community on a species’ range if that species has particularly strong interactions with one or a few other species. This may be the case for species that interact with keystone predators such as lynx, wolf, and sea stars, or foundational prey species such as mussels (Melis *et al.*, 2009; Pasanen-Mortensen *et al.*, 2013; Wallingford & Sorte, in review). Furthermore, naturalised species that undergo enemy release reveal that a few specialist enemies tend to have a larger effect than a large number of generalist enemies (Keane & Crawley, 2002; Alba & Hufbauer, 2012). We also see evidence from agricultural ecology where a single biocontrol species can reduce herbivory of an invasive pest (and this effect varies with temperature, Baffoe *et al.*, 2012).
Yet it is unclear how often a few BIs predominate. It is possible that bias in the literature leads us to believe this is more prevalent than it is because these clear interactions are prioritised for study (but see Allesina & Levine, 2011; Poisot et al., 2015). Scaling up would also be relatively straightforward if species have many interactions that show a similar trend in strength across their abiotic niches or geographic ranges. For example, biotic resistance of communities to invasion tends to be higher in wetter and hotter environments (Stotz et al., 2016), and the stress-gradient hypothesis suggests facilitation tends to be more important in harsh environments (e.g. deserts, salt marshes, intertidal zones, Soliveres et al., 2014). This might be the case where a feature of the focal species underlies trends in BI strength for many of its interactors (e.g. aridity reduced the sensitivity of a savannah plant to competition, herbivory, and pollination Louthan et al., 2018). Scaling up will be more difficult where multiple strong BIs occur, each showing a different relationship with the focal species’ abiotic niche or geographic range. For example, species can “rewire” networks of interactions within a community (Poisot et al., 2014; Tylianakis & Binzer, 2014; CaraDonna et al., 2017) and can form complex intransitive networks analogous to a game of rock-paper-scissors, where the co-existence of the community depends on multiple connected interactions (Allesina & Levine, 2011). Variation in BI strength means that environmental change could affect similar communities very differently between locations, with implications for biodiversity patterns and ecosystem services.

**Implications of flexibility in biotic interactions**

Flexibility in biotic interactions is particularly important under environmental change, which is reshuffling of species’ ranges. When a focal species can modify the strength of BIs with existing interactors that species could persist in its current geographic range despite changing abiotic conditions (Keith & Bull, 2017). For example, fish and aquatic invertebrates can change predation strategies under different structural complexities (Michel & Adams, 2009; Karkarey et al., 2017) and reef fish shift foraging strategy and reduce territorial aggression after mass coral bleaching to
maintain energy intake (Keith et al., In revision). In communities where species composition is altered by environmental change, a species with flexible behaviour could have an advantage during encounters with novel species. For example, butterflies that switched to novel host plants colonised areas that were otherwise abiotically unsuitable (Pateman et al., 2012). However, these types of behavioural change might be only a short-term buffer to environmental change, even creating ecological traps in the long-term as behavioural plasticity dampens the strength of natural selection (Schlaepfer et al., 2002).

From a predictive perspective, flexibility in BIs makes it less likely that information on interactions in one region or time period can be extrapolated to other contexts. This strengthens the argument for quantifying BIs at multiple positions across a species’ abiotic niche and geographic range. It would be interesting to ask whether individuals of a given species are more or less flexible depending on abiotic conditions. If flexibility is low in an area of a species’ niche or range where BI strength is high, we could expect environmental changes that affect the BI to have particularly strong effects on species’ ranges.

Acknowledging complexity and moving forward

Synthesising the strength of BIs across many taxa and interaction types poses significant challenges. As we outline, different disciplines focus on different components of BI strength, abiotic gradients, spatial and temporal scales, and employ different metrics and methodologies. Despite this variety, synthesis of existing data will still result in substantial knowledge gaps for many of the world’s ecosystems. However, we believe that breaking down BI into components of frequency and intensity provides an initial framework to unite a large amount of disparate data and prioritise collection of new data.

An additional challenge is that, despite many convincing examples of BI effects on species’ ranges, in other cases BI effects might be weak (Katz & Ibáñez, 2016; Katz & Ibáñez, 2017), vary with abiotic
factors that do not have a clear spatial gradient (García-Guzmán et al., 2017), be governed by multiple abiotic factors with conflicting effects, or components of BI strength could strengthen or weaken differently along the same abiotic gradient (Hersh et al., 2012; Benítez et al., 2013). As a result, some might argue that the effects of BIs are better included in macroecological models implicitly via the abiotic factors with which they correspond. However, excluding BIs, or assuming their implicit inclusion, can lead to serious error when using models to predict macroecological patterns in new time periods or places. Therefore, we believe the complexity of variation in BI strength underscores the need for macroecology to address this issue, yet urge careful prioritisation of data collection to ensure the task does not become intractable. More broadly, it is abundantly clear that variation in BI strength is integral to a fundamental understanding of species’ ranges and we should strive to understand how such variation contributes to macroecological patterns. To be successful in this endeavour, we must to look for willing collaborators across the field of ecology and beyond. Only then can we hope to understand the effects of BIs on past, present and future patterns of diversity and distribution in macroecology.

References


Data Accessibility Statement

No empirical data were used in this paper.

Biosketch

RE aims to disentangle the effects of abiotic and biotic drivers of species’ distributions, asking how this information can be used to improve biodiversity models, and forecasts of climate change and biological invasions. She works with a multitude of ecosystems, taxa, and geographic regions, using field and computational studies. RE also seeks to apply fundamental biogeographic knowledge to conservation and crop pest management. SK seeks to understand how fundamental ecological patterns are generated and maintained by linking processes across spatial and temporal scales, from individual behaviour to global diversity dynamics. SK focuses on coral reefs as a model system yet will delve into whatever system is appropriate for a given question. SK’s research uses a combination of empirical and theoretical approaches, combining fieldwork, advanced statistical analysis and simulation modelling.
Figure 1. Proposed relationships between abiotic or geographic gradients and the strength of interaction experienced by a focal species (see main text). The left-hand column indicates the strength of the biotic interaction (BI) named on the y-axis. The centre column indicates the focal species’ frequency of occurrence at the given abiotic or geographic location, with (long-dashed line) and without (short-dashed line) the named BI. Frequency of occurrence (i.e. number of sites that are occupied) is the metric commonly used in biogeographical analyses of species’ ranges and co-occurrences, under the assumption that more positive population trends and abundances lead to a larger number of populations surviving in more suitable locations. Here we assume that the effect of the BI is additive to the abiotic or geographical trend. The right hand column indicates the geographic range along the named abiotic or geographic gradient, both with (long-dashed outline) and without (short-dashed outline) the named BI, and shading indicates the abundance or population growth rate at a given location. In the bottom row (Q-T), grey lines/outlines illustrate the strength and effects of BI on occurrences and ranges in urban environments, and black lines in rural environments.
**Figure 2.** Effect of the relative contributions of frequency and intensity components of BI strength on pairwise competitive outcomes and their implications for species geographic ranges. Shading of the range schematics represents relative abundance. Icons are from the Noun Project: Hedgehog by Amie Murphy, Wolf by parkjisun, Fox by Andreas Reich, Mushroom toadstool by SBTS, Butterflyfish by Ed Harrison.
**Figure 3.** Biotic interactions (BIs) mediated by the abiotic niche of the interacting species. The left-hand and centre columns follow Fig. 1, with the exception that in panel A, two components of BI strength are shown, as well as overall BI strength. The right-hand column shows the impacts of change in the abiotic environment on species’ geographic ranges and abundances within areas that the species currently occupies (i.e. species do not colonise new areas). Outlines correspond to scenarios where BI strength is considered or not, and shading corresponds to expected abundance.