



26 fundamental understanding of the processes that underpin patterns of species diversity and  
27 distribution.

28

29 **Keywords**

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

## 32 **Introduction**

33 Evolutionary history, environmental conditions and dispersal ability set the playing field for species'  
34 geographic ranges, abundances, and macroecological patterns (Hampe, 2011; Keith *et al.*, 2013;  
35 Estrada *et al.*, 2015; Dallas *et al.*, 2017). However, interspecific biotic interactions (hereafter, BIs) are  
36 recognised increasingly as key factors affecting the extent and occupancy of species' geographic  
37 ranges (Wisz *et al.*, 2012; Pigot & Tobias, 2013), species abundances (Keane & Crawley, 2002), and  
38 species diversity gradients (Whittaker *et al.*, 2001; Louthan *et al.*, 2015). Competition and trophic  
39 interactions that have a negative effect (e.g., predation, parasitism, herbivory are negative for the  
40 consumed species) can decrease abundance, potentially to the point of excluding populations and  
41 limiting ranges (Soberón, 2007; Holt & Barfield, 2009). Facilitation, mutualism, and trophic  
42 interactions with a positive effect (i.e. for the consumer) can extend ranges into locations that are  
43 otherwise unsuitable (Karvonen *et al.*, 2012; Afkhami *et al.*, 2014; Crotty & Bertness, 2015).  
44 However, as environmental change and biological invasions reshuffle species' geographic ranges, it is  
45 unclear how, and to what extent, biotic interactions influence range shifts and consequent changes  
46 in diversity. To improve fundamental understanding and predict, and potentially mitigate, the effects  
47 of environmental change on biodiversity, it is therefore imperative that we seek to resolve the role  
48 for biotic interactions in species' geographic ranges and macroecological patterns.

49 Advances in this area have so far focused primarily on how to make best use of co-occurrence data  
50 as proxies for interactions in biogeographical models (e.g. Species Distribution Models, SDMs), and  
51 more recently on incorporating BI data derived from small scale experiments (Jabot & Bascompte,  
52 2012; Staniczenko *et al.*, 2017). Although this approach can yield important new insight (Pollock *et al.*,  
53 2014; Morueta-Holme *et al.*, 2016), distribution data are too sparse to study co-occurrences of  
54 species involved in the majority of BIs, for example disease, invertebrate herbivory, pollination, or  
55 below-ground microbial mutualisms. Moreover, co-occurrences can spark spurious claims for  
56 evidence of biotic interactions (Dormann *et al.*, 2018; Montesinos-Navarro *et al.*, 2018). To some

57 extent, these attempts and criticisms rehash the decades-old dispute between Diamond (1975) and  
58 Connor and Simberloff (1979) on whether a lack of co-occurrence between species was sufficient to  
59 infer competitive exclusion (Connor *et al.*, 2013). We clearly need to revise our approach if we are to  
60 exit the biotic interactions “groundhog day” that has plagued macroecology since before the  
61 inception of *Global Ecology & Biogeography*.

62 We believe one promising approach that has received too little attention is to study how and why  
63 the strength of BIs and effects on species’ ranges vary geographically, and the subsequent  
64 implications for macroecological patterns (Whittaker *et al.*, 2001; Chamberlain *et al.*, 2014; Louthan  
65 *et al.*, 2015). The occurrence or outcome of a BI can depend on environmental conditions, time  
66 period, or life-history stage (Pariaud *et al.*, 2009; Valiente-Banuet & Verdu, 2013; Chamberlain *et al.*,  
67 2014; Tikhonov *et al.*, 2017; Dormann *et al.*, 2018; Rogers *et al.*, 2018). However, we focus on  
68 environmental effects on BIs since environmental gradients will often lead to predictable patterns in  
69 BI strength across species’ ranges. Furthermore, focusing on geographic variation generally, rather  
70 than on particular environmental conditions or range margins (e.g. Soliveres *et al.*, 2014; Louthan *et al.*,  
71 2015), liberates us to scrutinise BI effects on species’ entire range extents, as well as their  
72 abundances and range occupancies.

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

## 82 **Components of biotic interaction strength**

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

98 **1. Frequency.** For a BI to occur, two individuals must encounter one another in the same place and  
99 time (Gurarie & Ovaskainen, 2013; Poisot *et al.*, 2015; CaraDonna *et al.*, 2017), but this simple  
100 starting point has been largely overlooked. One of the clearest mediators of encounter rate, and  
101 thus interaction strength, is density of the interacting species’ populations (Wootton & Emmerson,  
102 2005). For example, mammalian top predators suppress mesopredators more strongly at the centre  
103 of the top predators’ geographic ranges where the predators are more abundant (fig. 2, Newsome *et al.*,  
104 2017). On longer time scales, species diversity and abundance correlate with increased predation  
105 of marine metazoans throughout the Phanerozoic (Huntley & Kowalewski, 2007). Implications of  
106 varying density across abiotic gradients are addressed thoroughly by Louthan *et al.* (2015). However,

107 one point we wish to add is that, not only does density influence BIs, but BIs can influence density  
108 (Poisot *et al.*, 2014). Although we cannot eliminate this complexity, we must remain mindful of  
109 circularity when considering the effect of density on BI frequency.

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

121 An additional mediator of encounter rate is structural complexity, which could be abiotic (i.e.,  
122 topographic) or biotic (e.g., vegetation), but in either case has been included in SDMs as an  
123 'environmental' factor (St-Louis *et al.*, 2009). Structural complexity can alter encounter rates by  
124 changing the distance between individuals required for awareness of each other's presence (Michel  
125 & Adams, 2009; Karkarey *et al.*, 2017). For example, aquatic insect predators changed predation  
126 strategy in response to structural vegetation complexity because high complexity interfered with  
127 vision (Michel & Adams, 2009). Similarly, open habitats allow individuals to be aware of each other's  
128 presence over long distances, which can enable individuals to avoid or engage in an interaction.  
129 Cheetahs that hear calls from lion and hyena competitors on open plains avoid encounters by  
130 retreating before the other individual becomes aware of their presence (Durant, 2000), coral reef  
131 damselfish use structural refuges to avoid encounters with predators (Beukers & Jones, 1997), and

132 following coral mortality, predatory groupers respond to reduced structural complexity by altering  
133 foraging strategies to maintain prey encounter rate (Karkarey *et al.*, 2017). When asking whether  
134 structural complexity and behaviour affect population dynamics or range occupancy, one must also  
135 consider different perceptions of complexity across organisms – what is complex for an insect might  
136 be simple for a large mammal (Nash *et al.*, 2013). This point is particularly relevant for trophic  
137 interactions where focal and interactor species are often of very different body size. Although little  
138 evidence exists as yet for structural complexity mediating BIs and thus species' ranges, we believe it  
139 is worth exploring in the context of ongoing anthropogenic habitat modification (Møller *et al.*, 2013;  
140 Karkarey *et al.*, 2017). Consideration should also be given to whether there is a parallel for  
141 encounter rate between sessile species, for example distance over which allelopathic chemicals can  
142 act.

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

144 **a) Effect of interactor** ("effect per interactor" in Louthan *et al.*, 2015). Abiotic conditions can alter  
145 the behaviour, physiology and population growth rate of the interactor. For example, particular  
146 temperatures can select for stronger interactions in microbial and insect parasites (e.g.  
147 aggressiveness, spore production, virulence, Thomas & Blanford, 2003; Laine, 2007; Pariaud *et al.*,  
148 2009), and influence swimming speeds of pike predating brown trout (Öhlund *et al.*, 2015). In  
149 addition, abiotic effects on the focal species can mediate the effect of the interactor. Optimum  
150 nitrogen conditions for plants increases infection efficiency and spore production of their biotrophic  
151 pathogens (Pariaud *et al.*, 2009). Favourable abiotic conditions can also increase crop productivity,  
152 which in turn increases the number of herbivores plants can host (Foster *et al.*, 1992) and the vigour  
153 of their pathogens (Hersh *et al.*, 2012).

154 **b) Response of focal species** ("effect per encounter" in Louthan *et al.*, 2015). The degree to which a  
155 given interaction affects the population growth rate, and subsequent abundance or occurrence of  
156 the focal species can vary across its abiotic niche because the species' ability to moderate the

157 interaction varies with abiotic conditions. This variation could be due to abiotic limitations or trade-  
158 offs for the focal species. For example host immune systems are often more active at higher  
159 temperatures, reducing bacterial proliferation (Lazzaro *et al.*, 2008), and temperature can alter the  
160 accuracy of marmalade hoverfly defence mimicry of wasps due to thermoregulation constraints on  
161 the amount of black or yellow pigment (Marriott & J. Holloway, 1998). Alternatively, focal species  
162 can allocate resources differently in response to abiotic factors that regulate the interaction. For  
163 instance, facultative mycorrhizal plant species can regulate the level of mycorrhization under  
164 different soil nutrient conditions (Johnson *et al.*, 2008; Grman, 2012). Similarly, populations facing  
165 more challenging environmental conditions towards the edge of their abiotic niche could have less  
166 resource to invest in defence (suggested by the results of Pennings *et al.*, 2007) so experience a  
167 more negative response per encounter in that region.

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



179 **Variation in biotic interaction strength and implications for species'**  
180 **geographic ranges**

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

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

197 Endophytic fungi are found frequently to affect plant demographic processes both positively and  
198 negatively, and to have varying interaction strengths across abiotic gradients (David *et al.*, 2018). For  
199 example, *Discula quercina* colonised *Quercus cerris* trees in Mediterranean oak forests in the early  
200 1990s and remained largely quiescent. However, at times of drought, the fungus becomes an  
201 aggressive coloniser, killing its host (Fig. 1 E-H, Moricca & Ragazzi, 2011; and see Hersh *et al.*, 2012  
202 for further examples). A very different effect results from the interaction between the mutualistic  
203 fungal endophyte and its grass host *Bromus laevipes*. The endophyte ameliorates the plant's drought

204 stress, extending the grass' geographic range into thousands of square kilometres, which experience  
205 drier conditions than the grass could otherwise tolerate (fig. 1 I-L, Afkhami *et al.*, 2014).

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

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

225 This last example highlights a major constraint on identifying the effects of BIs on species'  
226 geographic ranges: spatial variation in BI strength can correspond to abiotic factors that do not have  
227 systematic geographic gradients. For example, light affects forest plant susceptibility to pathogenic  
228 fungi (effect for focal species, García-Guzmán *et al.*, 2017) and fungal pathogenicity or mutualism

229 (effect of interactor, *Álvarez-Loayza et al.*, 2011). The lack of a geographic gradient in light gaps  
230 means these effects will depress or enhance plant abundance or occurrence heterogeneously across  
231 species' ranges (*Nielsen et al.*, 2005; *VanDerWal et al.*, 2009).

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

245 In contrast to examples in fig. 1, strong BI effects can occur at the centre of the abiotic niche and  
246 weak effects at the edges (e.g. *Foster et al.*, 1992; *Pariaud et al.*, 2009; *Hersh et al.*, 2012; *Newsome*  
247 *et al.*, 2017). In this case BIs do not restrict species' geographic ranges within the abiotic range limits  
248 (fig. 3 E-G). However, the pattern of BI strength can depress abundance and population growth rates  
249 within the species' range (a pattern noted by *VanDerWal et al.*, 2009; *Dallas et al.*, 2017). This could  
250 lead to unexpected consequences for species' current strongholds if BI strength changes at locations  
251 with peak abiotic favourability due, for example, to idiosyncratic species movement in response to  
252 climate change (*Keith et al.*, 2011).

253 Whilst many BI effects on ranges are due to steady changes in interaction strength through space  
254 (fig. 1, 3), range limits could result from abrupt exclusion by another species, as is observed for  
255 hedgehogs in Europe and allopatric sister species (Wisz *et al.*, 2012; Pigot & Tobias, 2013). In this  
256 situation, interaction strength could increase very sharply at a range margin, which could be difficult  
257 to detect. However, by considering the components of BI strength, we can clarify that the frequency  
258 of interactions is low whilst the intensity is high, leading to greater understanding of the process  
259 underlying 'checkerboard' species ranges (fig. 2).

## 260 **Quantifying biotic interaction effects on geographic ranges**

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

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

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

275 BI strength along abiotic gradients has been quantified to different extents across taxonomic groups.  
276 Perhaps the most comprehensive data are available for terrestrial plants, and intertidal

277 invertebrates - particularly for competition, pollination, herbivory, facilitation and mutualism - as  
278 these taxa are classic systems used to understand effects of BIs on abundance, diversity,  
279 distributional ranges. Some obligate trophic interactions have been quantified, often for charismatic  
280 species e.g., butterflies and their host-plant use (Pateman *et al.*, 2012), pollinators (Burkle & Alarcón,  
281 2011), and Iberian lynx and rabbits (Fordham *et al.*, 2013). The frequency component of BI strength  
282 has received disproportionate research attention, for example, number of parasites per individual  
283 and amount of herbivory damage are often used as to indicate the degree of regulation by enemies  
284 (Dostál *et al.*, 2013). Intensity is more commonly quantified in laboratory studies on model  
285 organisms, which has limited taxonomic scope. Laboratory studies also tend to focus on the effect of  
286 a single abiotic factor, often temperature or moisture, despite the fact that in nature, multiple  
287 abiotic factors vary simultaneously. In contrast, field experiments or observations capture the effect  
288 of multiple factors simultaneously, which can make it hard to disentangle the different abiotic  
289 effects. Also in the field, BI strength is often measured indirectly by proxies such as resistance  
290 (Álvarez-Loayza *et al.*, 2011), anti-predator behaviour (Díaz *et al.*, 2013), and palatability (Pennings *et al.*,  
291 2007), rather than an outcome directly relevant to species' ranges such as individual  
292 reproductive output or population growth rate.

293 Synthesising data on BI strength will enable us to pool the advantages, and mitigate the  
294 disadvantages, of both methods to identify taxa, interaction types, geographic locations, abiotic  
295 conditions, and ecosystems where BIs strongly affect species' ranges. This will inform expectations  
296 about where and when BIs might underlie macroecological patterns. Quantitative BI data could also  
297 be incorporated directly into models to improve measurements of species' niches and forecasts of  
298 geographic ranges. For example, patterns of BI strength could be used in SDMs to account for biotic  
299 effects on occupancy or abundance. SDMs could then measure species associations with abiotic  
300 factors more accurately (similar to efforts to account for recorder effort) and better forecast effects  
301 of changes in abiotic conditions or the distributions of interactors. In many cases, quantifying biotic  
302 effects in this way will require more data than can be obtained from existing research. Thus, we

303 recommend the macroecological community invests in collecting new “for-purpose” data on BI  
304 strength, using existing data and theory to target systems where BI strength is likely to be important.

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

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

316 We have so far dealt with pairwise interactions only, but the link between BI strength and range  
317 limitation could be extended to interactions between multiple species. Data on pairwise species  
318 interactions is likely to be able to ‘scale up’ to inform the effects of the wider ecological community  
319 on a species’ range if that species has particularly strong interactions with one or a few other  
320 species. This may be the case for species that interact with keystone predators such as lynx, wolf,  
321 and sea stars, or foundational prey species such as mussels (Melis *et al.*, 2009; Pasanen-Mortensen  
322 *et al.*, 2013; Wallingford & Sorte, in review). Furthermore, naturalised species that undergo enemy  
323 release reveal that a few specialist enemies tend to have a larger effect than a large number of  
324 generalist enemies (Keane & Crawley, 2002; Alba & Hufbauer, 2012). We also see evidence from  
325 agricultural ecology where a single biocontrol species can reduce herbivory of an invasive pest (and  
326 this effect varies with temperature, Baffoe *et al.*, 2012).

327 Yet it is unclear how often a few BIs predominate. It is possible that bias in the literature leads us to  
328 believe this is more prevalent than it is because these clear interactions are prioritised for study (but  
329 see Allesina & Levine, 2011; Poisot *et al.*, 2015). Scaling up would also be relatively straightforward if  
330 species have many interactions that show a similar trend in strength across their abiotic niches or  
331 geographic ranges. For example, biotic resistance of communities to invasion tends to be higher in  
332 wetter and hotter environments (Stotz *et al.*, 2016), and the stress-gradient hypothesis suggests  
333 facilitation tends to be more important in harsh environments (e.g. deserts, salt marshes, intertidal  
334 zones, Soliveres *et al.*, 2014). This might be the case where a feature of the focal species underlies  
335 trends in BI strength for many of its interactors (e.g. aridity reduced the sensitivity of a savannah  
336 plant to competition, herbivory, and pollination Louthan *et al.*, 2018). Scaling up will be more  
337 difficult where multiple strong BIs occur, each showing a different relationship with the focal  
338 species' abiotic niche or geographic range. For example, species can "rewire" networks of  
339 interactions within a community (Poisot *et al.*, 2014; Tylianakis & Binzer, 2014; CaraDonna *et al.*,  
340 2017) and can form complex intransitive networks analogous to a game of rock-paper-scissors,  
341 where the co-existence of the community depends on multiple connected interactions (Allesina &  
342 Levine, 2011). Variation in BI strength means that environmental change could affect similar  
343 communities very differently between locations, with implications for biodiversity patterns and  
344 ecosystem services.

### 345 **Implications of flexibility in biotic interactions**

346 Flexibility in biotic interactions is particularly important under environmental change, which is  
347 reshuffling of species' ranges. When a focal species can modify the strength of BIs with existing  
348 interactors that species could persist in its current geographic range despite changing abiotic  
349 conditions (Keith & Bull, 2017). For example, fish and aquatic invertebrates can change predation  
350 strategies under different structural complexities (Michel & Adams, 2009; Karkarey *et al.*, 2017) and  
351 reef fish shift foraging strategy and reduce territorial aggression after mass coral bleaching to

352 maintain energy intake (Keith *et al.*, In revision). In communities where species composition is  
353 altered by environmental change, a species with flexible behaviour could have an advantage during  
354 encounters with novel species. For example, butterflies that switched to novel host plants colonised  
355 areas that were otherwise abiotically unsuitable (Pateman *et al.*, 2012). However, these types of  
356 behavioural change might be only a short-term buffer to environmental change, even creating  
357 ecological traps in the long-term as behavioural plasticity dampens the strength of natural selection  
358 (Schlaepfer *et al.*, 2002).

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

## 366 **Acknowledging complexity and moving forward**

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

374 An additional challenge is that, despite many convincing examples of BI effects on species' ranges, in  
375 other cases BI effects might be weak (Katz & Ibáñez, 2016; Katz & Ibáñez, 2017), vary with abiotic



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

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636

637 **Data Accessibility Statement**

638 No empirical data were used in this paper.

639 **Biosketch**

640 RE aims to disentangle the effects of abiotic and biotic drivers of species' distributions, asking how  
641 this information can be used to improve biodiversity models, and forecasts of climate change and  
642 biological invasions. She works with a multitude of ecosystems, taxa, and geographic regions, using  
643 field and computational studies. RE also seeks to apply fundamental biogeographic knowledge to  
644 conservation and crop pest management. SK seeks to understand how fundamental ecological  
645 patterns are generated and maintained by linking processes across spatial and temporal scales, from  
646 individual behaviour to global diversity dynamics. SK focuses on coral reefs as a model system yet  
647 will delve into whatever system is appropriate for a given question. SK's research uses a combination  
648 of empirical and theoretical approaches, combining fieldwork, advanced statistical analysis and  
649 simulation modelling.

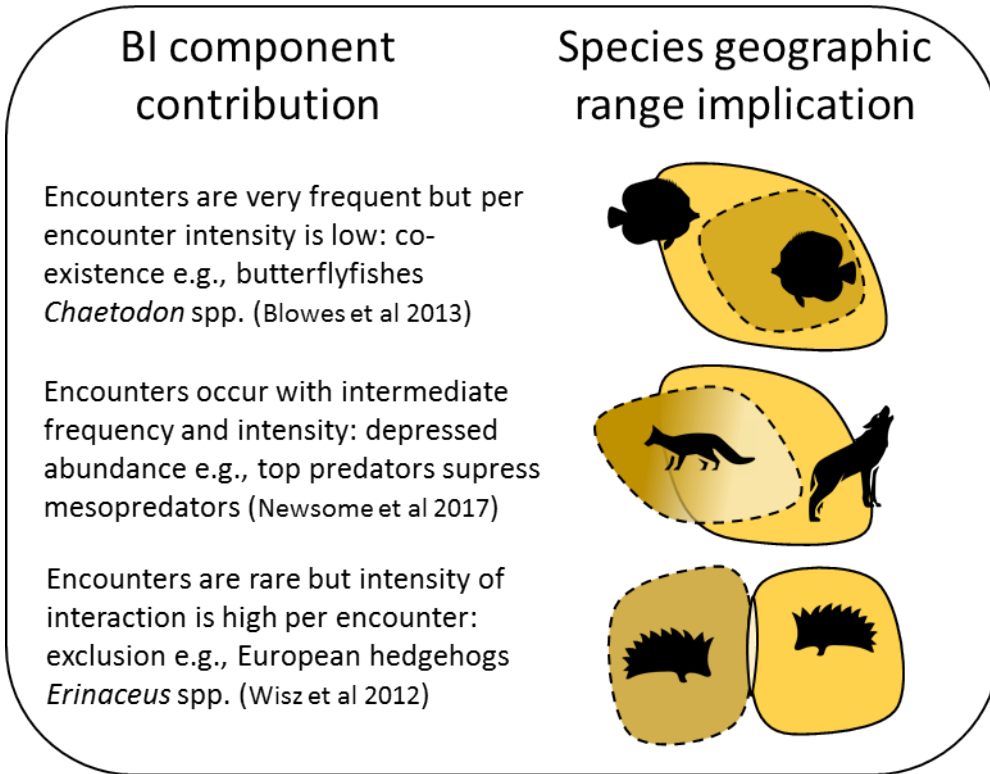
650

Relationship between abiotic or geographical gradient and BI strength.	Abiotic and biotic effects on population occurrence.	Abiotic and biotic effects on range. Shading indicates abundance or population growth rate.
<p><b>A</b></p>	<p><b>B</b></p>	<p><b>C</b></p> <p><b>D</b></p>
<p><b>E</b></p>	<p><b>F</b></p>	<p><b>G</b></p> <p><b>H</b></p>
<p><b>I</b></p>	<p><b>J</b></p>	<p><b>K</b></p> <p><b>L</b></p>
<p><b>M</b></p>	<p><b>N</b></p>	<p><b>O</b></p> <p><b>P</b></p>
<p><b>Q</b></p>	<p><b>R</b></p>	<p><b>S</b></p> <p><b>T</b></p>



652 **Figure 1.** Proposed relationships between abiotic or geographic gradients and the strength of  
653 interaction experienced by a focal species (see main text). The left-hand column indicates the  
654 strength of the biotic interaction (BI) named on the y-axis. The centre column indicates the focal  
655 species' frequency of occurrence at the given abiotic or geographic location, with (long-dashed line)  
656 and without (short-dashed line) the named BI. Frequency of occurrence (i.e. number of sites that are  
657 occupied) is the metric commonly used in biogeographical analyses of species' ranges and co-  
658 occurrences, under the assumption that more positive population trends and abundances lead to a  
659 larger number of populations surviving in more suitable locations. Here we assume that the effect of  
660 the BI is additive to the abiotic or geographical trend. The right hand column indicates the  
661 geographic range along the named abiotic or geographic gradient, both with (long-dashed outline)  
662 and without (short-dashed outline) the named BI, and shading indicates the abundance or  
663 population growth rate at a given location. In the bottom row (Q-T), grey lines/outlines illustrate the  
664 strength and effects of BI on occurrences and ranges in urban environments, and black lines in rural  
665 environments.

666

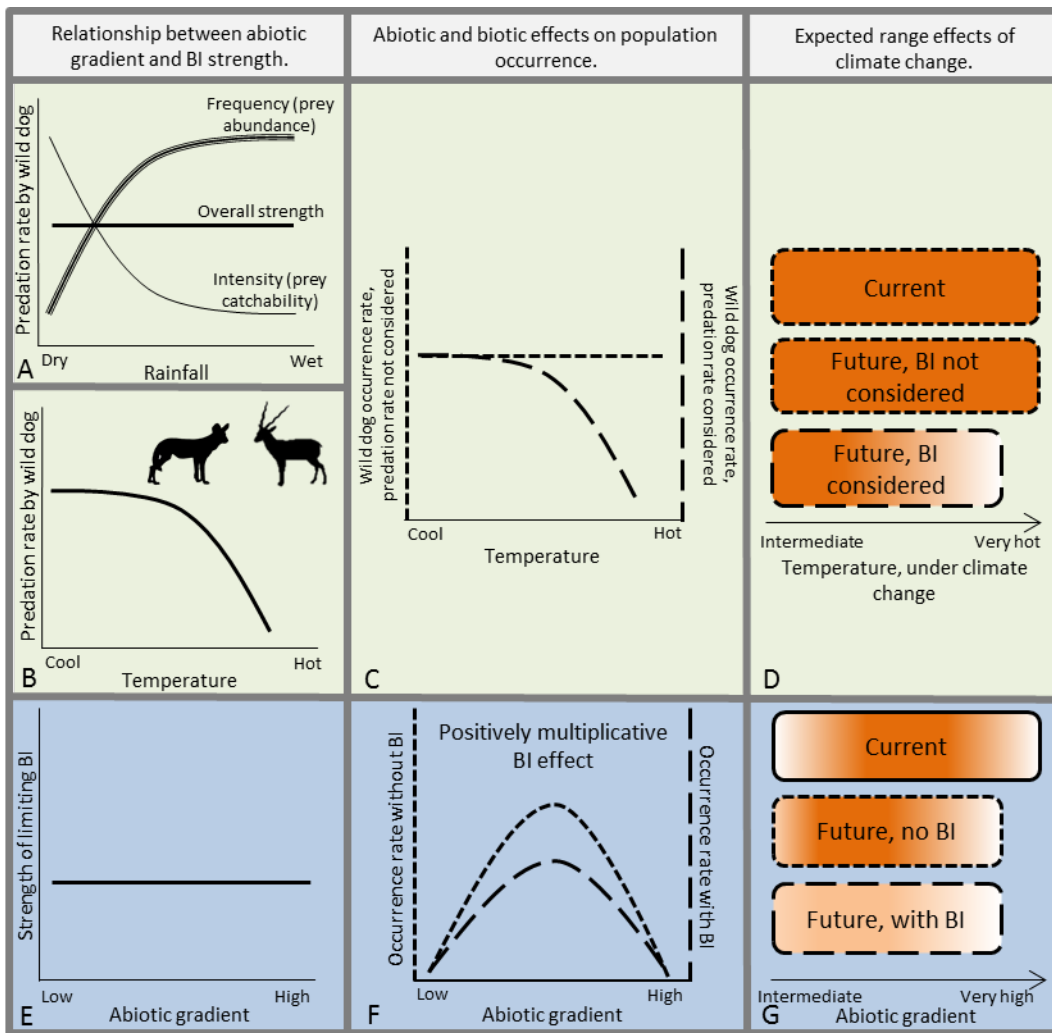


668

669 **Figure 2.** Effect of the relative contributions of frequency and intensity components of BI strength on  
670 pairwise competitive outcomes and their implications for species geographic ranges. Shading of the  
671 range schematics represents relative abundance. Icons are from the Noun Project: Hedgehog by  
672 Amie Murphy, Wolf by parkjisun, Fox by Andreas Reich, Mushroom toadstool by SBTS, Butterflyfish  
673 by Ed Harrison.

674

675



676

677 **Figure 3.** Biotic interactions (BIs) mediated by the abiotic niche of the interacting species. The left-  
 678 hand and centre columns follow Fig. 1, with the exception that in panel A, two components of BI  
 679 strength are shown, as well as overall BI strength. The right-hand column shows the impacts of  
 680 change in the abiotic environment on species' geographic ranges and abundances within areas that  
 681 the species currently occupies (i.e. species do not colonise new areas). Outlines correspond to  
 682 scenarios where BI strength is considered or not, and shading corresponds to expected abundance.