

1 **Geographically variable biotic interactions and implications for species** 2 **ranges**

3 Running title: Geographic variation in biotic interactions

4 **Abstract:**

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

13 **Unpicking biotic interactions:** We suggest that macroecology would benefit from recognising that
14 abiotic conditions alter two key components of biotic interaction strength: frequency and intensity.
15 We outline how and why variation in biotic interaction strength occurs, explore the implications for
16 species' geographic ranges, and discuss the challenges inherent in quantifying these effects. In
17 addition, we explore the role of behavioural flexibility in mediating biotic interactions to potentially
18 mitigate impacts of environmental change.

19 **New data:** We argue that macroecology should take advantage of “independent” data on the
20 strength of biotic interactions measured by other disciplines, in order to capture a far wider array of
21 taxa, locations and interaction types than are typically studied in macroecology. Data on biotic
22 interactions are readily available from community, disease, microbial, and parasite ecology,
23 evolution, palaeontology, invasion biology, and agriculture, but most are yet to be exploited within
24 macroecology.

25 **Integrating biotic interaction strength data into macroecology:** Harmonising data across inter-
26 disciplinary sources, taxa, and interaction types could be achieved by breaking down interactions
27 into elements that contribute to frequency and intensity. This would allow quantitative BI data to be
28 incorporated directly into models of species distributions and macroecological patterns.

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 is a function of two components: (1)
90 *frequency*, the rate of interaction events experienced; and (2) *intensity*, the effect on lifetime
91 reproductive output of individuals involved in the BI. For an additional consideration of these effects
92 and excellent examples, we refer the reader to Louthan *et al.* (2015). Deconstructing BI strength into
93 these components can provide insight additional insight because their relative contributions could
94 lead to different implications for species’ geographic ranges (fig. 2). For example, for an interaction
95 of the same overall strength, high frequency coupled with low intensity could maintain coexistence,
96 whereas the converse - low frequency with high intensity - could reinforce competitive exclusion
97 (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*
104 *al.*, 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 such as plants, for example distance over which allelopathic
142 chemicals can 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*
291 *al.*, 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

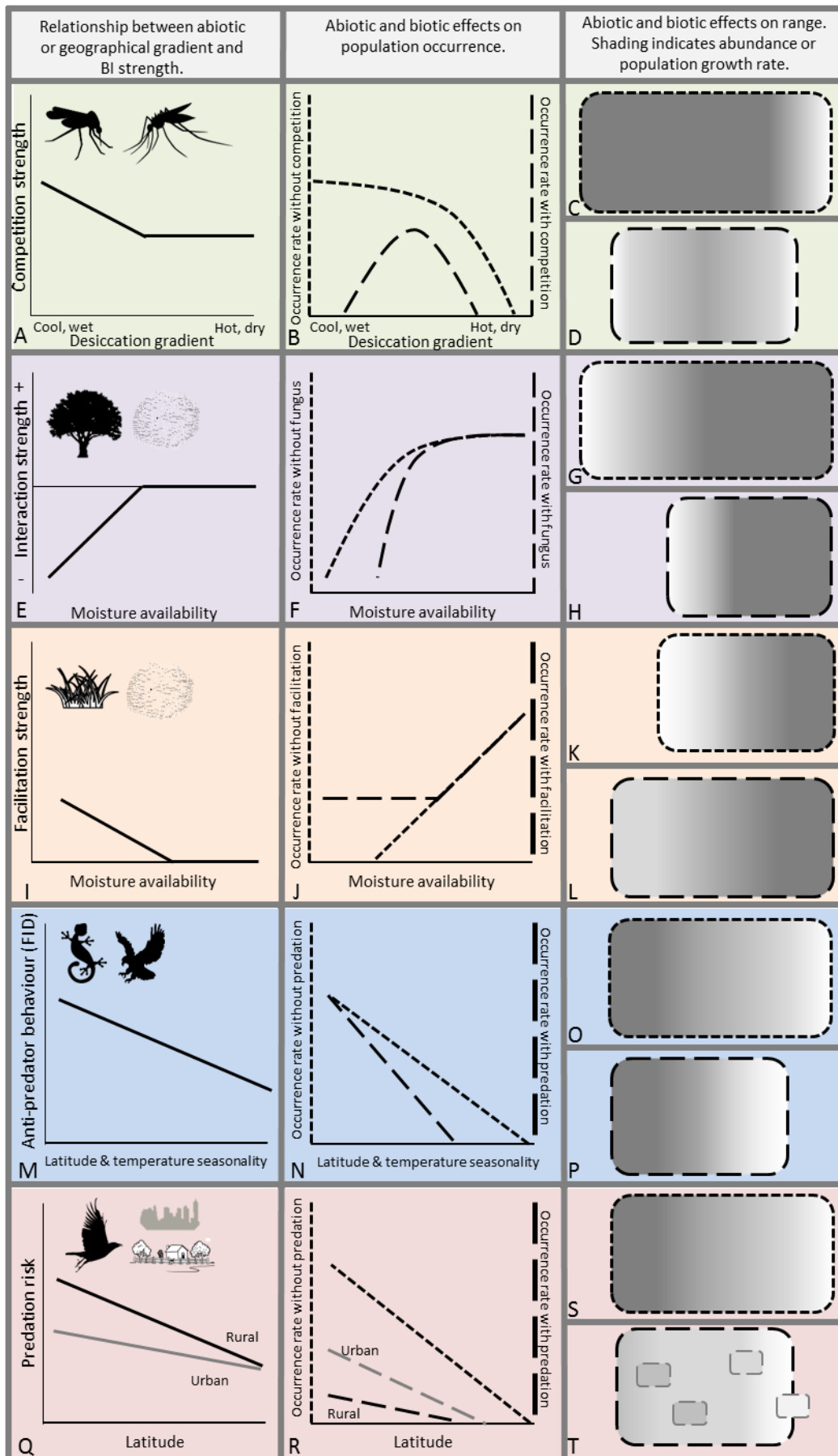
637 **Data Accessibility Statement**

638 No empirical data were used in this paper.

639 **Biosketch**

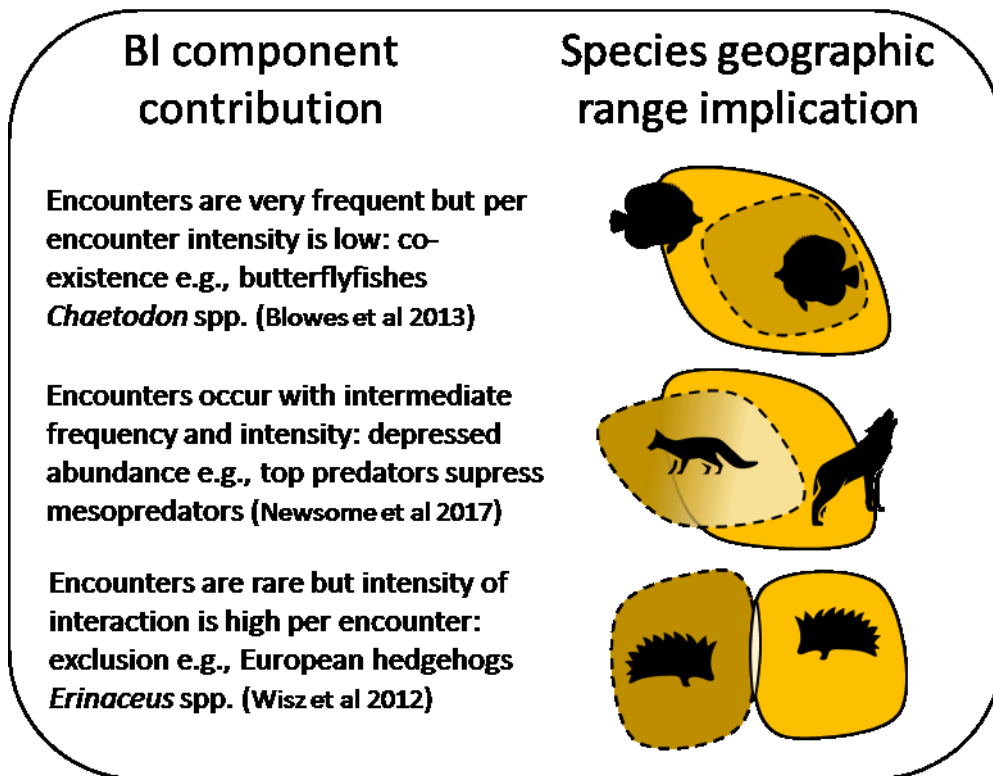
640 RE aims to disentangle the effects of abiotic and biotic drivers of species' distributions, asking how
641 this information can be used to improve biodiversity models, and forecasts of climate change and
642 biological invasions. She works with a multitude of ecosystems, taxa, and geographic regions, 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



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

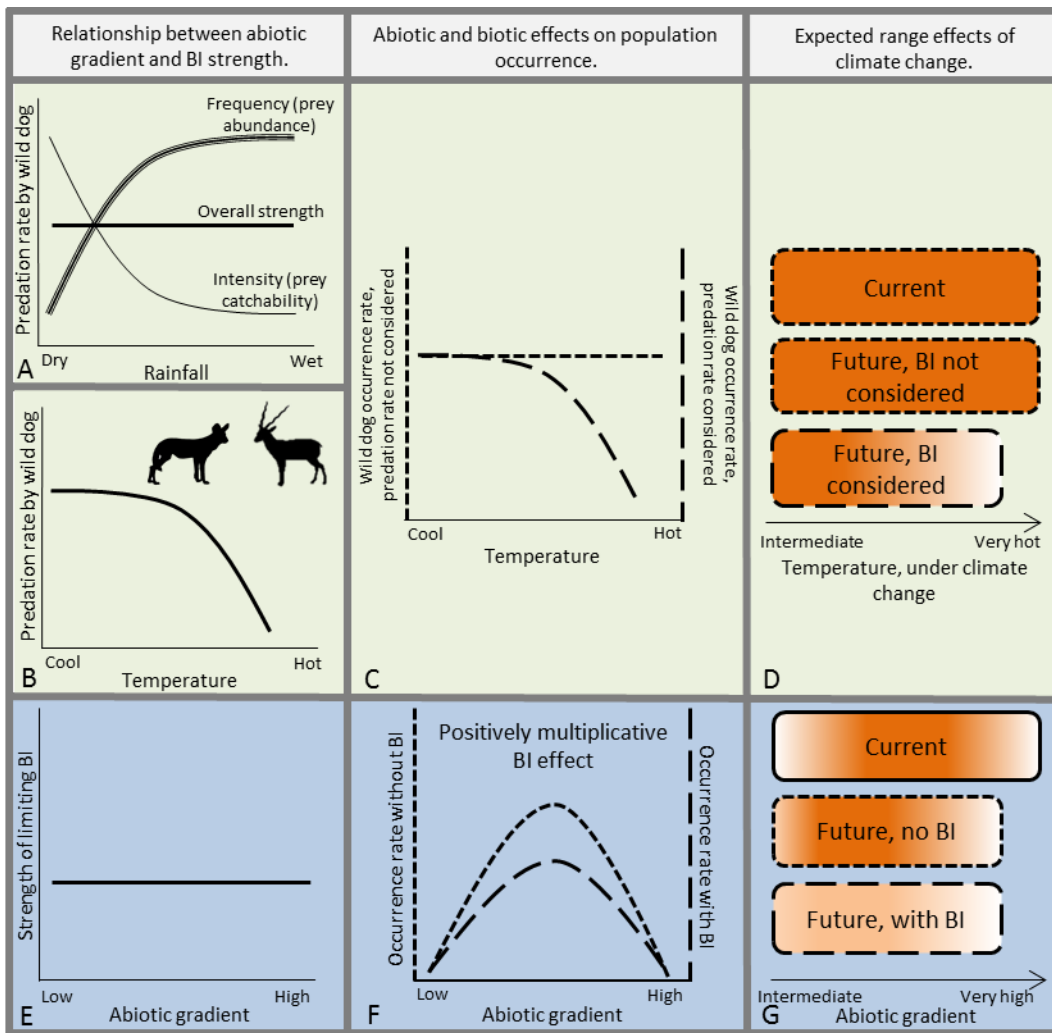


668

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.