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.

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

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*

71   *al.*, 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.

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 is 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,

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.

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).

A. 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

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).

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.

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.

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.

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

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.

A — Competition strength / Cool, wet — Hot, dry / Desiccation gradient

B — Occurrence rate without competition / Occurrence rate with competition / Cool, wet — Hot, dry / Desiccation gradient

C

D

E — Interaction strength (+ / −) / Moisture availability

F — Occurrence rate without fungus / Occurrence rate with fungus / Moisture availability

G

H

I — Facilitation strength / Moisture availability

J — Occurrence rate without facilitation / Occurrence rate with facilitation / Moisture availability

K

L

M — Anti-predator behaviour (FID) / Latitude & temperature seasonality

N — Occurrence rate without predation / Occurrence rate with predation / Latitude & temperature seasonality

O

P

Q — Predation risk / Rural / Urban / Latitude

R — Occurrence rate without predation / Urban / Rural / Occurrence rate with predation / Latitude

S

T

651

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.

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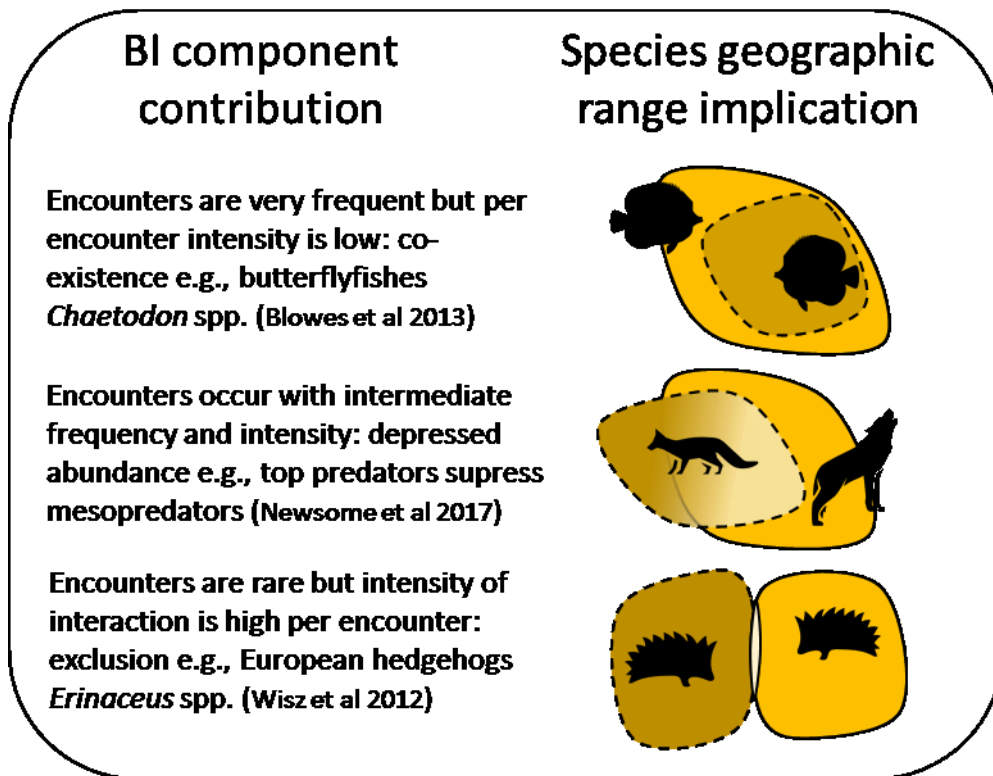
Figure 2. Effect of the relative contributions of frequency and intensity components of BI strength on

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.

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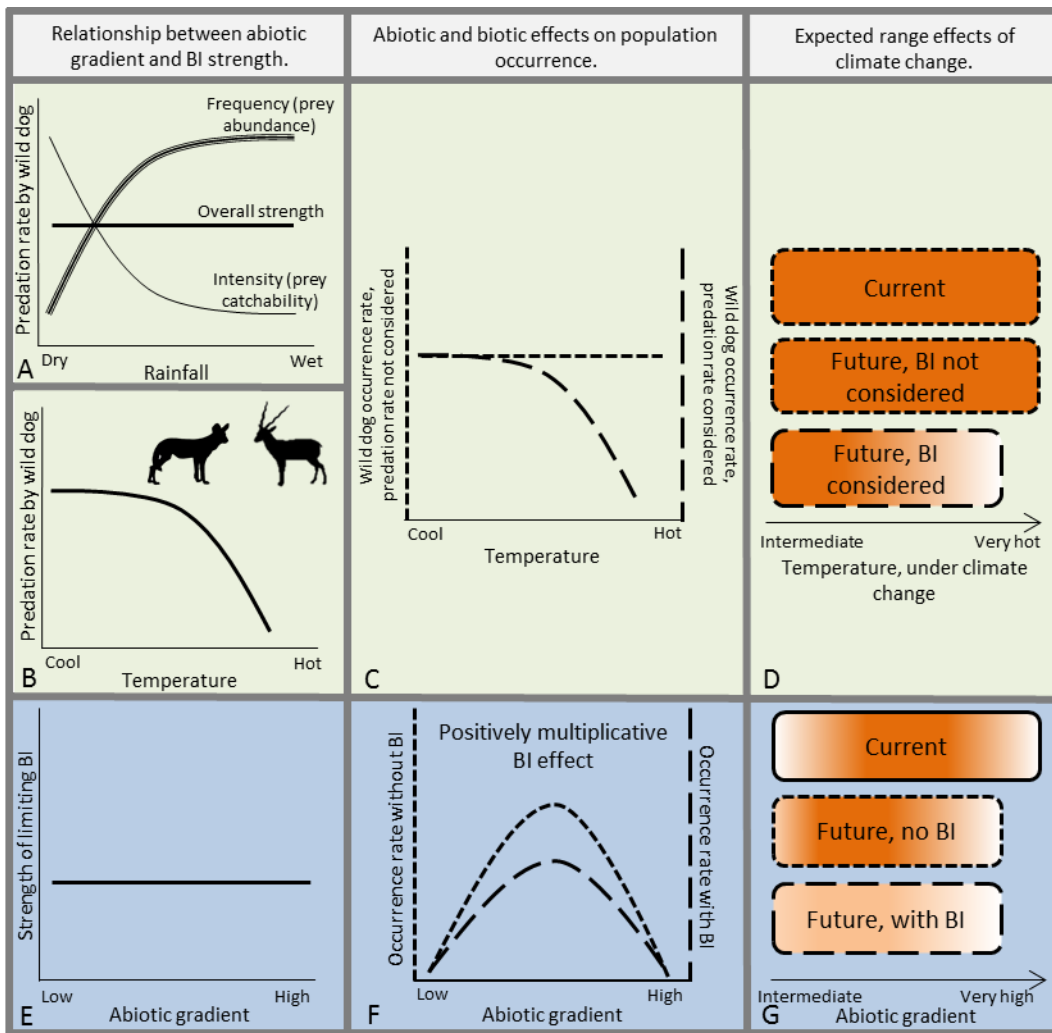
676

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.