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

3 Running title: Geographic variation in biotic interactions

## 4 Abstract:

5 Understanding how biotic interactions affect species' geographic ranges, biodiversity patterns, and

6 ecological responses to environmental change is one of the most pressing challenges in

7 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 We suggest that macroecology would benefit from recognising that abiotic conditions alter two key

14 components of biotic interaction strength: frequency and intensity. We outline how and why

15 variation in biotic interaction strength occurs, explore the implications for species' geographic

16 ranges, and discuss the challenges inherent in quantifying these effects. In addition, we explore the

17 role of behavioural flexibility in mediating biotic interactions to potentially mitigate impacts of

18 environmental change.  We argue that macroecology should take advantage of "independent" data

19 on the strength of biotic interactions measured by those in other disciplines to capture a far wider

20 array of taxa, locations and interaction types than are typically studied in macroecology. Data on

21 biotic interactions are readily available from community, disease, microbial, and parasite ecology,

22 evolution, palaeontology, invasion biology, and agriculture, but most are yet to be exploited within

23 macroecology. Inter-disciplinary synthesis of these data would pave the way towards inclusion of

24 geographically variable biotic interactions within macroecological models. We believe that taking the

25 steps we outline would improve forecasts of changes in species' geographic ranges and increase

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.

## 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 can considered to be a function of two components: (1) *frequency*, the rate of interaction events experienced; and (2) *intensity*, the effect on lifetime reproductive output of individuals involved in the BI. For an additional consideration of these effects and excellent examples, we refer the reader to Louthan *et al.* (2015). Deconstructing BI strength into these components can provide insight additional insight because their relative contributions could lead to different implications for species' geographic ranges (fig. 2). For example, for an interaction of the same overall strength, high frequency coupled with low intensity could maintain coexistence, whereas the converse - low frequency with high intensity - could reinforce competitive exclusion (e.g., allopatric sister species; fig. 2).

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

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.

## 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

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

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

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.

## References

391  Afkhami, M.E., McIntyre, P.J. & Strauss, S.Y. (2014) Mutualist-mediated effects on species' range
392      limits across large geographic scales. *Ecology Letters*, **17**, 1265-1273.
393  Alba, C. & Hufbauer, R. (2012) Exploring the potential for climatic factors, herbivory, and co-
394      occurring vegetation to shape performance in native and introduced populations of
395      Verbascum thapsus. *Biological Invasions*, **14**, 2505-2518.
396  Allesina, S. & Levine, J.M. (2011) A competitive network theory of species diversity. *Proceedings of
397      the National Academy of Sciences*, **108**, 5638-5642.
398  Álvarez-Loayza, P., White, J.F., Jr., Torres, M.S., Balslev, H., Kristiansen, T., Svenning, J.-C. & Gil, N.
399      (2011) Light Converts Endosymbiotic Fungus to Pathogen, Influencing Seedling Survival and
400      Niche-Space Filling of a Common Tropical Tree, Iriartea deltoidea. *PLOS ONE*, **6**, e16386.
401  Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Marquet, P.A., Valladares, F. & Chown, S.L. (2013) Heat
402      freezes niche evolution. *Ecology Letters*, **16**, 1206-1219.
403  Baffoe, K.O., Dalin, P., Nordlander, G. & Stenberg, J.A. (2012) Importance of temperature for the
404      performance and biocontrol efficiency of the parasitoid Perilitus brevicollis (Hymenoptera:
405      Braconidae) on Salix. *BioControl*, **57**, 611-618.
406  Benítez, M.-S., Hersh, M.H., Vilgalys, R. & Clark, J.S. (2013) Pathogen regulation of plant diversity via
407      effective specialization. *Trends in Ecology & Evolution*, **28**, 705-711.
408  Beukers, J.S. & Jones, G.P. (1997) Habitat complexity modifies the impact of piscivores on a coral
409      reef fish population. *Oecologia*, **114**, 50-59.

410 Biro, P.A., Beckmann, C. & Stamps, J.A. (2010) Small within-day increases in temperature affects
411      boldness and alters personality in coral reef fish. *Proceedings of the Royal Society B:*
412      *Biological Sciences*, **277**, 71-77.
413 Blowes, S.A., Pratchett, M.S. & Connolly, S.R. (2013) Heterospecific aggression and dominance in a
414      guild of coral-feeding fishes: the roles of dietary ecology and phylogeny. *Am Nat*, **182**, 157-
415      68.
416 Bowker, M.A., Soliveres, S. & Maestre, F.T. (2010) Competition increases with abiotic stress and
417      regulates the diversity of biological soil crusts. *Journal of Ecology*, **98**, 551-560.
418 Burkle, L.A. & Alarcón, R. (2011) The future of plant–pollinator diversity: Understanding interaction
419      networks across time, space, and global change. *American Journal of Botany*, **98**, 528-538.
420 CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M. &
421      Sanders, N.J. (2017) Interaction rewiring and the rapid turnover of plant–pollinator
422      networks. *Ecology Letters*, **20**, 385-394.
423 Chamberlain, S.A., Bronstein, J.L. & Rudgers, J.A. (2014) How context dependent are species
424      interactions? *Ecology Letters*, **17**, 881-890.
425 Connor, E.F. & Simberloff, D. (1979) The Assembly of Species Communities: Chance or Competition?
426      *Ecology*, **60**, 1132-1140.
427 Connor, E.F., Collins, M.D. & Simberloff, D. (2013) The checkered history of checkerboard
428      distributions. *Ecology*, **94**, 2403-2414.
429 Crotty, S.M. & Bertness, M.D. (2015) Positive interactions expand habitat use and the realized niches
430      of sympatric species. *Ecology*,
431 Dallas, T., Decker, R.R. & Hastings, A. (2017) Species are not most abundant in the centre of their
432      geographic range or climatic niche. *Ecology Letters*, **20**, 1526-1533.
433 David, A.S., Thapa-Magar, K.B. & Afkhami, M.E. (2018) Microbial mitigation–exacerbation
434      continuum: a novel framework for microbiome effects on hosts in the face of stress. *Ecology*,
435      **99**, 517-523.
436 Diamond, J.M. (1975) Assembly of species communities. *Ecology and evolution of communities* (ed.
437      by M.L. Cody and J.M. Diamond), pp. 342-444. Belknap Press.
438 Díaz, M., Møller, A.P., Flensted-Jensen, E., Grim, T., Ibáñez-Álamo, J.D., Jokimäki, J., Markó, G. &
439      Tryjanowski, P. (2013) The Geography of Fear: A Latitudinal Gradient in Anti-Predator Escape
440      Distances of Birds across Europe. *PLOS ONE*, **8**, e64634.
441 Díaz, M., Cuervo, J.J., Grim, T., Flensted-Jensen, E., Ibáñez-Álamo, J.D., Jokimäki, J., Markó, G.,
442      Tryjanowski, P. & Møller, A.P. (2015) Interactive effects of fearfulness and geographical
443      location on bird population trends. *Behavioral Ecology*, **26**, 716-721.
444 Dormann, C.F., Bobrowski, M., Dehling, D.M., Harris, D.J., Hartig, F., Lischke, H., Moretti, M.D., Pagel,
445      J., Pinkert, S., Schleuning, M., Schmidt, S.I., Sheppard, C.S., Steinbauer, M.J., Zeuss, D. &
446      Kraan, C. (2018) Biotic interactions in species distribution modelling: 10 questions to guide
447      interpretation and avoid false conclusions. *Global Ecology and Biogeography*, **0**, 1-13.
448 Dostál, P., Allan, E., Dawson, W., van Kleunen, M., Bartish, I. & Fischer, M. (2013) Enemy damage of
449      exotic plant species is similar to that of natives and increases with productivity. *Journal of*
450      *Ecology*, **101**, 388-399.
451 Durant, S.M. (2000) Living with the enemy: avoidance of hyenas and lions by cheetahs in the
452      Serengeti. *Behavioral Ecology*, **11**, 624-632.
453 Estrada, A., Meireles, C., Morales-Castilla, I., Poschlod, P., Vieites, D., Araújo, M.B. & Early, R. (2015)
454      Species' intrinsic traits inform their range limitations and vulnerability under environmental
455      change. *Global Ecology and Biogeography*, **24**, 849-858.
456 Fordham, D.A., Akcakaya, H.R., Brook, B.W., Rodriguez, A., Alves, P.C., Civantos, E., Trivino, M.,
457      Watts, M.J. & Araujo, M.B. (2013) Adapted conservation measures are required to save the
458      Iberian lynx in a changing climate. *Nature Clim. Change*, **3**, 899-903.

459 Foster, M.A., Schultz, J.C. & Hunter, M.D. (1992) Modelling Gypsy Moth--Virus--Leaf Chemistry
460         Interactions: Implications of Plant Quality for Pest and Pathogen Dynamics. *Journal of Animal*
461         *Ecology*, **61**, 509-520.
462 García-Guzmán, G., Domínguez-Velázquez, F., Soto, J.M. & Heil, M. (2017) Light environment affects
463         the levels of resistance hormones in Syngonium podophyllum leaves and its attack by
464         herbivores and fungi. *Botanical Sciences*, **95**, 363-373.
465 Grman, E. (2012) Plant species differ in their ability to reduce allocation to non-beneficial arbuscular
466         mycorrhizal fungi. *Ecology*, **93**, 711-718.
467 Gurarie, E. & Ovaskainen, O. (2013) Towards a general formalization of encounter rates in ecology.
468         *Theoretical Ecology*, **6**, 189-202.
469 Hampe, A. (2011) Plants on the move: The role of seed dispersal and initial population establishment
470         for climate-driven range expansions. *Acta Oecologica*, **37**, 666-673.
471 He, Q., Bertness, M.D. & Altieri, A.H. (2013) Global shifts towards positive species interactions with
472         increasing environmental stress. *Ecology Letters*, **16**, 695-706.
473 Hersh, M.H., Vilgalys, R. & Clark, J.S. (2012) Evaluating the impacts of multiple generalist fungal
474         pathogens on temperate tree seedling survival. *Ecology*, **93**, 511-520.
475 Holt, R.D. & Barfield, M. (2009) Trophic interactions and range limits: the diverse roles of predation.
476         *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1435-1442.
477 Huntley, J.W. & Kowalewski, M. (2007) Strong coupling of predation intensity and diversity in the
478         Phanerozoic fossil record. *Proceedings of the National Academy of Sciences*, **104**, 15006-
479         15010.
480 Jabot, F. & Bascompte, J. (2012) Bitrophic interactions shape biodiversity in space. *Proceedings of*
481         *the National Academy of Sciences*, **109**, 4521-4526.
482 Johnson, N.C., Rowland, D.L., Corkidi, L. & Allen, E.B. (2008) Plant winners and losers during
483         grassland N-eutrophication differ in biomass allocation amd mycorrhizas. *Ecology*, **89**, 2868-
484         2878.
485 Juliano, S.A., O'Meara, G.F., Morrill, J.R. & Cutwa, M.M. (2002) Desiccation and thermal tolerance of
486         eggs and the coexistence of competing mosquitoes. *Oecologia*, **130**, 458-469.
487 Karkarey, R., Alcoverro, T., Kumar, S. & Arthur, R. (2017) Coping with catastrophe: foraging plasticity
488         enables a benthic predator to survive in rapidly degrading coral reefs. *Animal Behaviour*,
489         **131**, 13-22.
490 Karvonen, A., Rellstab, C., Louhi, K.R. & Jokela, J. (2012) Synchronous attack is advantageous: mixed
491         genotype infections lead to higher infection success in trematode parasites. *Proc Biol Sci*,
492         **279**, 171-6.
493 Katz, D.S.W. & Ibáñez, I. (2016) Biotic interactions with natural enemies do not affect potential range
494         expansion of three invasive plants in response to climate change. *Biological Invasions*, **18**,
495         3351-3363.
496 Katz, D.S.W. & Ibáñez, I. (2017) Differences in biotic interactions across range edges have only minor
497         effects on plant performance. *Journal of Ecology*, **105**, 321-331.
498 Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends*
499         *in Ecology and Evolution*, **17**, 164-170.
500 Keith, S.A. & Bull, J.W. (2017) Animal culture impacts species' capacity to realise climate-driven
501         range shifts. *Ecography*, **40**, 296-304.
502 Keith, S.A., Herbert, R.J.H., Norton, P.A., Hawkins, S.J. & Newton, A.C. (2011) Individualistic species
503         limitations of climate-induced range expansions generated by meso-scale dispersal barriers.
504         *Diversity and Distributions*, **17**, 275-286.
505 Keith, S.A., Baird, A.H., Hughes, T.P., Madin, J.S. & Connolly, S.R. (2013) Faunal breaks and species
506         composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat
507         distribution. *Proceedings of the Royal Society B: Biological Sciences*, **280**

508 Keith, S.A., Baird, A.H., Hobbs, J.-P.A., Woolsey, E.S., Hoey, A.S., Fadli, N. & Sanders, N.J. (In revision)
509     Synchronous behavioural shifts in reef fishes linked to mass coral bleaching. *Nature Climate*
510     *Change*,

511 Laine, A.L. (2007) Pathogen fitness components and genotypes differ in their sensitivity to nutrient
512     and temperature variation in a wild plant–pathogen association. *Journal of Evolutionary*
513     *Biology*, **20**, 2371-2378.

514 Lazzaro, B.P., Flores, H.A., Lorigan, J.G. & Yourth, C.P. (2008) Genotype-by-Environment Interactions
515     and Adaptation to Local Temperature Affect Immunity and Fecundity in Drosophila
516     melanogaster. *PLOS Pathogens*, **4**, e1000025.

517 Lounibos, L.P., Suárez, S., Menéndez, Z., Nishimura, N., L Escher, R., M O'Connell, S. & R Rey, J.
518     (2002) *Does temperature affect the outcome of larval competition between Aedes aegypti*
519     *and Aedes albopictus?*

520 Louthan, A.M., Doak, D.F. & Angert, A.L. (2015) Where and When do Species Interactions Set Range
521     Limits? *Trends in Ecology & Evolution*, **30**, 780-792.

522 Louthan, A.M., Pringle, R.M., Goheen, J.R., Palmer, T.M., Morris, W.F. & Doak, D.F. (2018) Aridity
523     weakens population-level effects of multiple species interactions on Hibiscus meyeri.
524     *Proceedings of the National Academy of Sciences of the United States of America*, **115**, 543-
525     548.

526 Marriott, C.G. & J. Holloway, G. (1998) Colour Pattern Plasticity in the Hoverfly, Episyrphus balteatus:
527     The Critical Immature Stage and Reaction Norm on Developmental Temperature. *Journal of*
528     *Insect Physiology*, **44**, 113-119.

529 Melis, C., Jędrzejewska, B., Apollonio, M., Bartoń, K.A., Jędrzejewski, W., Linnell, J.D.C., Kojola, I.,
530     Kusak, J., Adamic, M., Ciuti, S., Delehan, I., Dykyy, I., Krapinec, K., Mattioli, L., Sagaydak, A.,
531     Samchuk, N., Schmidt, K., Shkvyrya, M., Sidorovich, V.E., Zawadzka, B. & Zhyla, S. (2009)
532     Predation has a greater impact in less productive environments: variation in roe deer,
533     Capreolus capreolus, population density across Europe. *Global Ecology and Biogeography*,
534     **18**, 724-734.

535 Michel, M.J. & Adams, M.M. (2009) Differential effects of structural complexity on predator foraging
536     behavior. *Behavioral Ecology*, **20**, 313-317.

537 Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R. & Foley, W.J. (2011) Assessing the evidence for
538     latitudinal gradients in plant defence and herbivory. *Functional Ecology*, **25**, 380-388.

539 Møller, A.P., Grim, T., Ibáñez-Álamo, J.D., Markó, G. & Tryjanowski, P. (2013) Change in flight
540     initiation distance between urban and rural habitats following a cold winter. *Behavioral*
541     *Ecology*, **24**, 1211-1217.

542 Montesinos-Navarro, A., Estrada, A., Font, X., Matias, M.G., Meireles, C., Mendoza, M., Honrado,
543     J.P., Prasad, H.D., Vicente, J.R. & Early, R. (2018) Community structure informs species
544     geographic distributions. *PLOS ONE*, **13**, e0197877.

545 Moricca, S. & Ragazzi, A. (2011) The Holomorph Apiognomonia quercina/Discula quercina as a
546     Pathogen/Endophyte in Oak. *Endophytes of Forest Trees: Biology and Applications* (ed. by
547     A.M. Pirttilä and A.C. Frank), pp. 47-66. Springer Netherlands, Dordrecht.

548 Morueta-Holme, N., Blonder, B., Sandel, B., McGill, B.J., Peet, R.K., Ott, J.E., Violle, C., Enquist, B.J.,
549     Jørgensen, P.M. & Svenning, J.-C. (2016) A network approach for inferring species
550     associations from co-occurrence data. *Ecography*, **39**, 1139-1150.

551 Nash, K.L., Graham, N.A.J., Wilson, S.K. & Bellwood, D.R. (2013) Cross-scale Habitat Structure Drives
552     Fish Body Size Distributions on Coral Reefs. *Ecosystems*, **16**, 478-490.

553 Newsome, T.M., Greenville, A.C., Ćirović, D., Dickman, C.R., Johnson, C.N., Krofel, M., Letnic, M.,
554     Ripple, W.J., Ritchie, E.G., Stoyanov, S. & Wirsing, A.J. (2017) Top predators constrain
555     mesopredator distributions. *Nature Communications*, **8**, 15469.

556 Nielsen, S.E., Johnson, C.J., Heard, D.C. & Boyce, M.S. (2005) Can Models of Presence-Absence be
557     Used to Scale Abundance? Two Case Studies Considering Extremes in Life History.
558     *Ecography*, **28**, 197-208.

559 Öhlund, G., Hedström, P., Norman, S., Hein, C.L. & Englund, G. (2015) Temperature dependence of
560      predation depends on the relative performance of predators and prey. *Proceedings of the*
561      *Royal Society B: Biological Sciences*, **282**, 20142254.
562 Pariaud, B., Ravigné, V., Halkett, F., Goyeau, H., Carlier, J. & Lannou, C. (2009) Aggressiveness and its
563      role in the adaptation of plant pathogens. *Plant Pathology*, **58**, 409-424.
564 Pasanen-Mortensen, M., Pyykönen, M. & Elmhagen, B. (2013) Where lynx prevail, foxes will fail –
565      limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, **22**, 868-877.
566 Pateman, R.M., Hill, J.K., Roy, D.B., Fox, R. & Thomas, C.D. (2012) Temperature-Dependent
567      Alterations in Host Use Drive Rapid Range Expansion in a Butterfly. *Science*, **336**, 1028-1030.
568 Pennings, S.C., Zimmer, M., Dias, N., Sprung, M., Davé, N., Ho, C.-K., Kunza, A., McFarlin, C., Mews,
569      M., Pfauder, A. & Salgado, C. (2007) Latitudinal variation in plant–herbivore interactions in
570      European salt marshes. *Oikos*, **116**, 543-549.
571 Pigot, A.L. & Tobias, J.A. (2013) Species interactions constrain geographic range expansion over
572      evolutionary time. *Ecology Letters*, **16**, 330-338.
573 Poisot, T., Stouffer, D.B. & Gravel, D. (2015) Beyond species: why ecological interaction networks
574      vary through space and time. *Oikos*, **124**, 243-251.
575 Poisot, T.E., Baiser, B., Dunne, J.A., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T.N., Stouffer, D.B.,
576      Wood, S.A. & Gravel, D. (2014) mangal - making complex ecological network analysis
577      simpler. *bioRxiv*,
578 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A. & McCarthy,
579      M.A. (2014) Understanding co-occurrence by modelling species simultaneously with a Joint
580      Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, **5**, 397-406.
581 Rogers, T.L., Gouhier, T.C. & Kimbro, D.L. (2018) Temperature dependency of intraguild predation
582      between native and invasive crabs. *Ecology*, **99**, 885-895.
583 Samia, D.S.M., Møller, A.P., Blumstein, D.T., Stankowich, T. & Cooper, W.E., Jr. (2015) Sex differences
584      in lizard escape decisions vary with latitude, but not sexual dimorphism. *Proceedings of the*
585      *Royal Society B: Biological Sciences*, **282**
586 Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. (2002) Ecological and evolutionary traps. *Trends in*
587      *Ecology & Evolution*, **17**, 474-480.
588 Soberón, J. (2007) Grinnellian and Eltonian niches and geographic distributions of species. *Ecology*
589      *Letters*, **10**, 1115-1123.
590 Soliveres, S., Smit, C. & Maestre, F.T. (2014) Moving forward on facilitation research: response to
591      changing environments and effects on the diversity, functioning and evolution of plant
592      communities. *Biological Reviews*, n/a-n/a.
593 St-Louis, V., Pidgeon, A.M., Clayton, M.K., Locke, B.A., Bash, D. & Radeloff, V.C. (2009) Satellite image
594      texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New
595      Mexico. *Ecography*, **32**, 468-480.
596 Staniczenko, P.P.A., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017) Linking macroecology
597      and community ecology: refining predictions of species distributions using biotic interaction
598      networks. *Ecol Lett*, **20**, 693-707.
599 Stotz, G.C., Pec, G.J. & Cahill, J.F. (2016) Is biotic resistance to invaders dependent upon local
600      environmental conditions or primary productivity? A meta-analysis. *Basic and Applied*
601      *Ecology*, **17**, 377-387.
602 Thomas, M.B. & Blanford, S. (2003) Thermal biology in insect-parasite interactions. *Trends in Ecology*
603      *& Evolution*, **18**, 344-350.
604 Tikhonov, G., Abrego, N., Dunson, D. & Ovaskainen, O. (2017) Using joint species distribution models
605      for evaluating how species-to-species associations depend on the environmental context.
606      *Methods in Ecology and Evolution*, **8**, 443-452.
607 Tylianakis, J.M. & Binzer, A. (2014) Effects of global environmental changes on parasitoid–host food
608      webs and biological control. *Biological Control*, **75**, 77-86.

609   Vahl, W.K., Lok, T., van der Meer, J., Piersma, T. & Weissing, F.J. (2005) Spatial clumping of food and
610        social dominance affect interference competition among ruddy turnstones. *Behavioral*
611        *Ecology*, **16**, 834-844.
612   Vale, P.F., Stjernman, M. & Little, T.J. (2008) Temperature-dependent costs of parasitism and
613        maintenance of polymorphism under genotype-by-environment interactions. *Journal of*
614        *Evolutionary Biology*, **21**, 1418-1427.
615   Valiente-Banuet, A. & Verdu, M. (2013) Plant Facilitation and Phylogenetics. *Annual Review of*
616        *Ecology, Evolution, and Systematics, Vol 44*, **44**, 347-366.
617   VanDerWal, J., Shoo, Luke P., Johnson, Christopher N. & Williams, Stephen E. (2009) Abundance and
618        the Environmental Niche: Environmental Suitability Estimated from Niche Models Predicts
619        the Upper Limit of Local Abundance. *The American Naturalist*, **174**, 282-291.
620   Wallingford, P.D. & Sorte, C.J.B. (in review) Predicting predator-prey responses to climate change
621        using community regulation models.
622   Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general,
623        hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453-470.
624   Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F.,
625        Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto,
626        M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M.,
627        Timmermann, A., Wardle, D.A., Aastrup, P. & Svenning, J.-C. (2012) The role of biotic
628        interactions in shaping distributions and realised assemblages of species: implications for
629        species distribution modelling. *Biological Reviews*, **88**, 15-30.
630   Woodroffe, R., Groom, R. & McNutt, J.W. (2017) Hot dogs: High ambient temperatures impact
631        reproductive success in a tropical carnivore. *J Anim Ecol*, **86**, 1329-1338.
632   Wootton, T.J. & Emmerson, M. (2005) Measurement of Interaction Strength in Nature. *Annual*
633        *Review of Ecology, Evolution, and Systematics*, **36**, 419-444.
634   Zhang, S., Zhang, Y. & Ma, K. (2016) Latitudinal variation in herbivory: hemispheric asymmetries and
635        the role of climatic drivers. *Journal of Ecology*, **104**, 1089-1095.

636

## Data Accessibility Statement

No empirical data were used in this paper.

## Biosketch

RE aims to disentangle the effects of abiotic and biotic drivers of species' distributions, asking how

this information can be used to improve biodiversity models, and forecasts of climate change and

biological invasions. She works with a multitude of ecosystems, taxa, and geographic regions, using

field and computational studies. RE also seeks to apply fundamental biogeographic knowledge to

conservation and crop pest management. SK seeks to understand how fundamental ecological

patterns are generated and maintained by linking processes across spatial and temporal scales, from

individual behaviour to global diversity dynamics. SK focuses on coral reefs as a model system yet

will delve into whatever system is appropriate for a given question. SK's research uses a combination

of empirical and theoretical approaches, combining fieldwork, advanced statistical analysis and

simulation modelling.
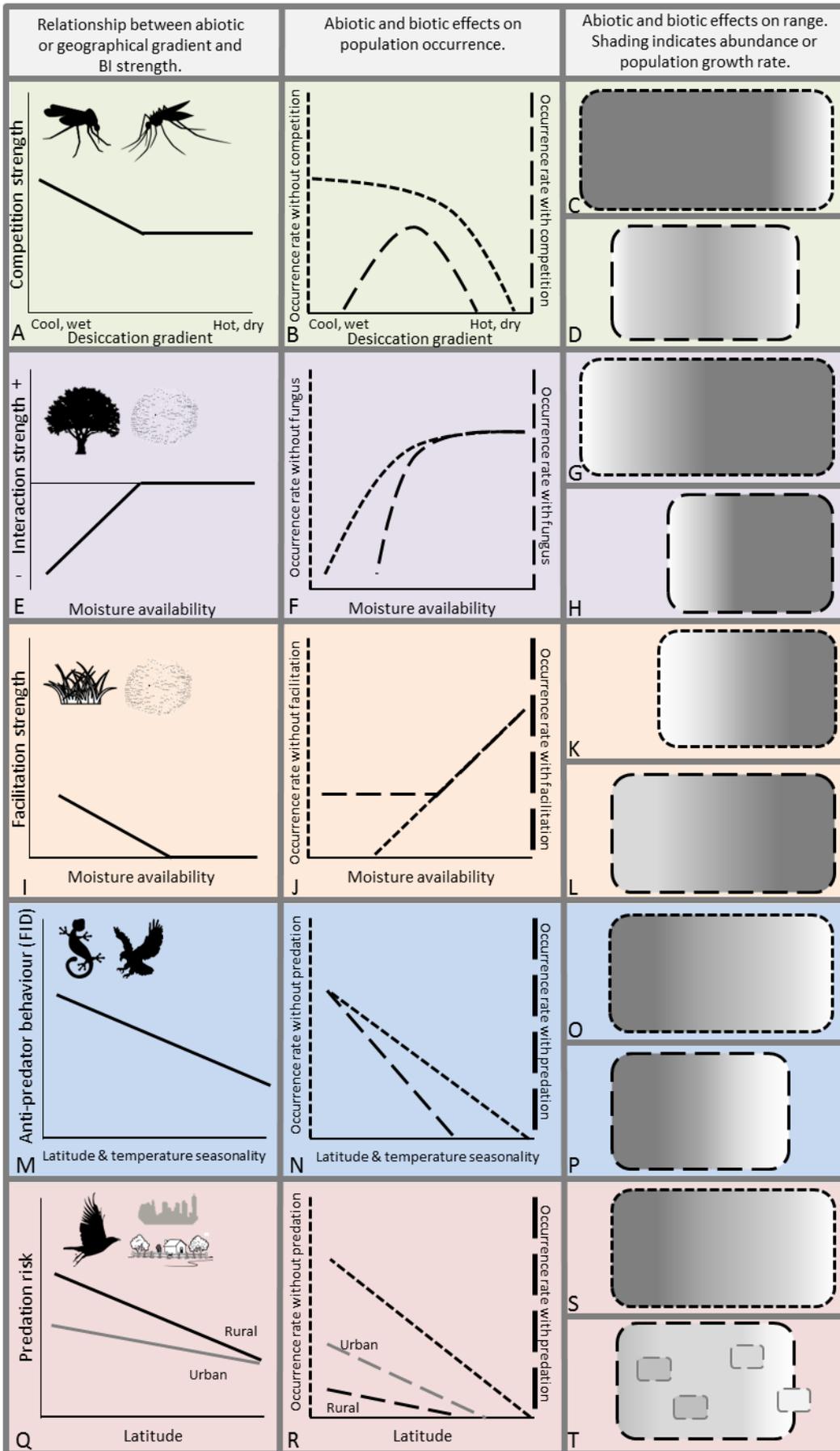
652 **Figure 1.** Proposed relationships between abiotic or geographic gradients and the strength of

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

667
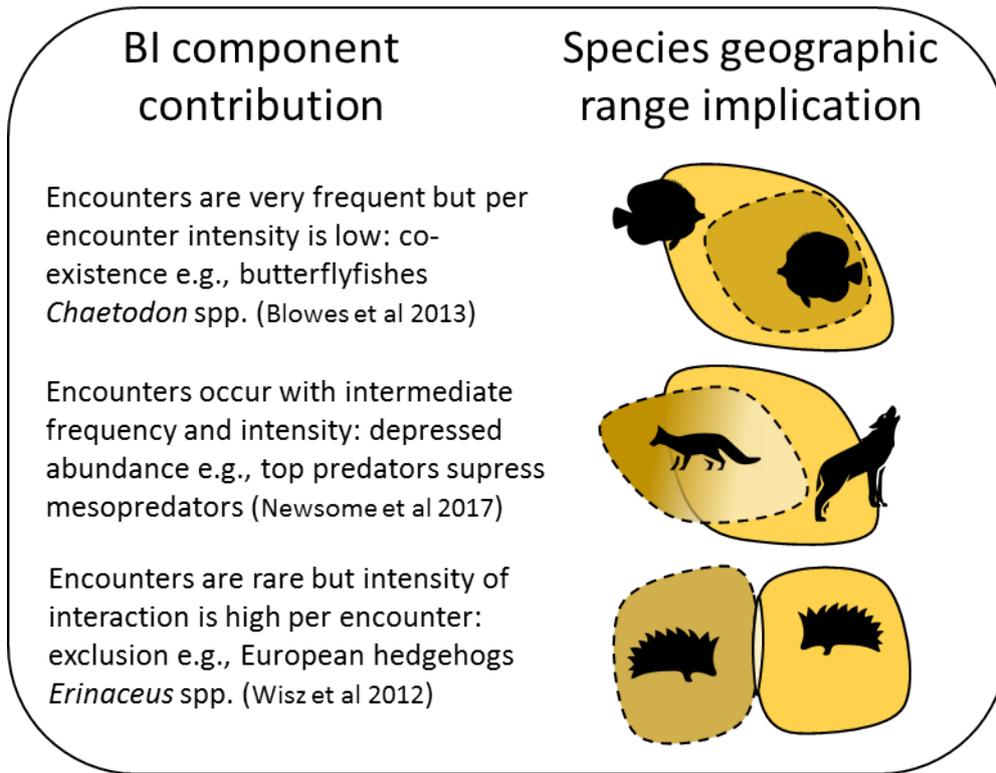


669 **Figure 2.** Effect of the relative contributions of frequency and intensity components of BI strength on

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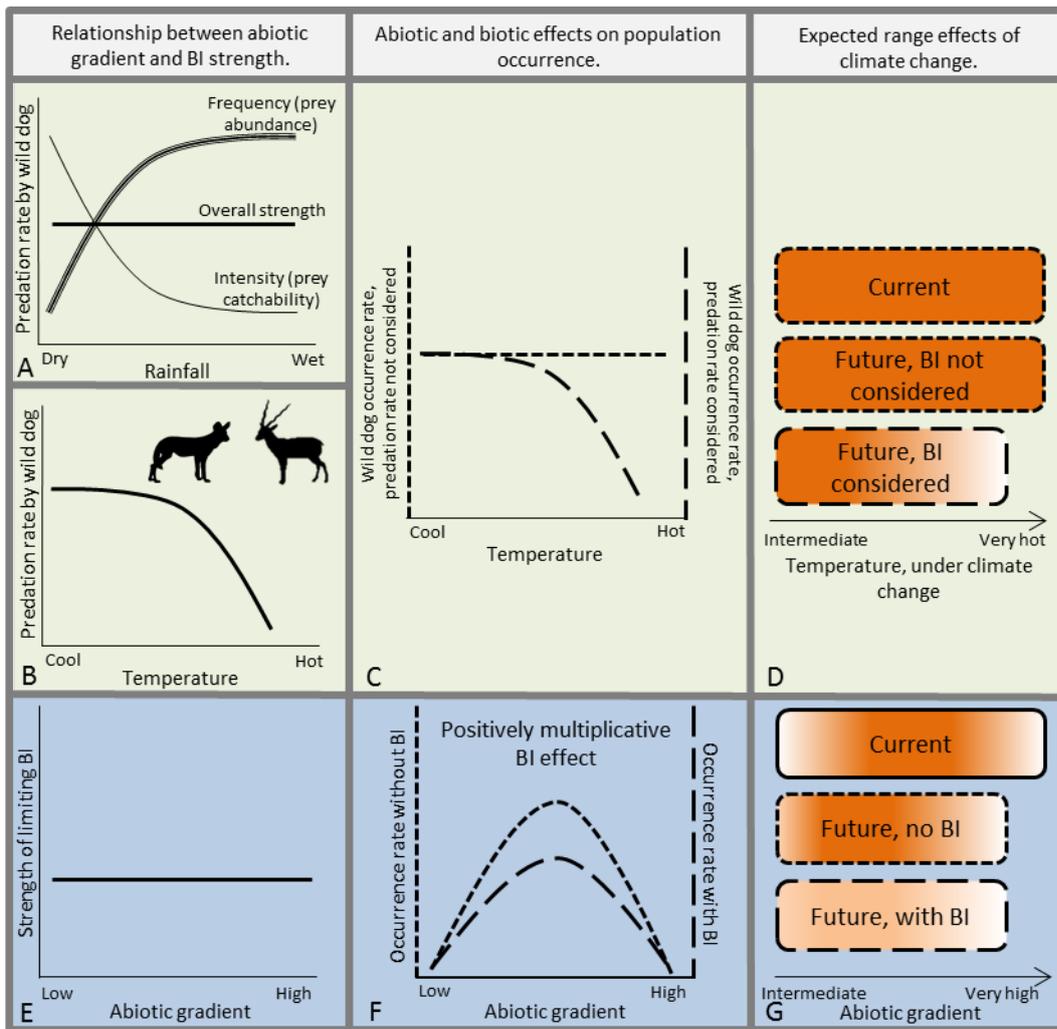
**Figure 3.** Biotic interactions (BIs) mediated by the abiotic niche of the interacting species. The left-hand and centre columns follow Fig. 1, with the exception that in panel A, two components of BI strength are shown, as well as overall BI strength. The right-hand column shows the impacts of change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