Environmental stress affects niche breadth in plant-pollinator communities

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1

Abstract

what is going on here?

What determines whether or not a species is a generalist or a specialist?
Evidence that the environment can influence species interactions is rapidly
accumulating.However, a systematic link between environment and the num-
ber of partners a species interacts with—the species degree—has been elusive
so far; presumably, because environmental gradients appear to have con- *not grammatically correct*
trasting effects on species depending on the environmental variable.Here, we
test for a
~~explore whether there is~~ a relationship between the stresses imposed by the
environment, instead of environmental gradients directly, and *species* degree using
a global dataset of plant-pollinator interactions.We found that the environ-
ment can play a significant effect on species degree, even when accounting
for community composition, likely by an interaction interact with species'
traits and evolutionary history.Specifically, species are more likely to attain
intermediate levels of partners when environmental stress increases.Species *very hard to follow*
that have a large number of interactions are more likely to focus on a
smaller number of, presumably higher-quality, interactions. Contrastingly,
the specialists that can cope with increased stress are more likely to broaden *in what environmental context?*
their niche, presumably engaging in opportunistic interactions.Many of the
species we analysed are not inherently generalist or specialist, many as some
specialists can effectively behave as facultative generalists.Species' degree of
generalisation should be measured on a relative scale depending on where
they are found and the environmental conditions at that location.

terrible grammar

why is this conditional?

terrible grammar

2

Introduction

Species interactions are known to vary widely across space and time. There are multiple examples of species that interact with a large number of partners in a particular community or season, but with fewer in another. Some of this variation can be attributed to environmental drivers. However, how exactly the environment, specifically the stress it imposes on species, affects whether two species interact or not, and ultimately the number of partners a species has is still unknown. Understanding how the number of partners—the species degree—is driven by the environment is crucial because it underpins the species role in its community and shapes the structure of the network of interactions. This structure, in turn, determines ecosystem function and stability.

Species interactions are determined in part by niche processes (the matching of traits) and partly by neutral processes (more abundant species are more likely to encounter each other and, thus, interact). The environment can influence both of these processes. It is, therefore, not surprising that, despite limitations on the spatial extent or the number of environmental gradients considered, multiple studies have been able to show how changes to interactions can be related to environmental change (Tylianakis and Morris 2017). For instance, some studies suggest that the strength of some trophic interactions, like predation (McKinnon et al. 2010; Vucic-Pestic et al. 2011) and herbivory (Baskett and Schemske 2018), can increase with temperature but might decrease with precipitation (Pires et al. 2016). Some other studies, however, have shown either no effect (on average) or non-linear effects of temperature or precipitation on plant-pollinator interactions (Devoto, Medan, and Montaldo 2005; Gravel et al. 2018). Overall, while it looks clear that pairwise interactions respond to environmental drivers, there is high variability in the response (Tylianakis et al. 2008).

66 One possible explanation for the seemingly contradictory evidence is that

67 each species can have multiple partners. Each of these partners, as well as the

68 interactions with them, can be simultaneously affected by the environmental

69 conditions. Therefore environmental stress may affect the number of partners

70 in different ways depending on its role in the community (for example its

71 trophic guild) or even the species itself. Previous research suggests that there

72 might be two alternative hypotheses of how environmental stress may affect

73 species degree (Tylianakis and Morris 2017). On the one hand, it is possible

74 that when species are under environmental stress, they might be "pressured"

75 to focus on partners with which they are best adapted to interact. For

76 instance, Hoiss et al. (2012) found increased phylogenetic clustering between

77 plants and pollinators at higher altitudes; while Peralta et al. (2015) found

78 that parasitoids in plantation forest, where environmental stress was higher

79 than in native forests, were constrained to interact with hosts they were

80 best adapted to attack. Similarly, Lavandero and Tylianakis (2013) found

81 that environmental stress due to higher temperature reduced the breadth of

82 the Eltonian niche of parasitoids.

83 On the other hand, it is also possible that when species are under environ-

84 mental stress, they are forced to be more flexible in their interactions as

85 higher environmental stress is likely to be reflected in greater energetic or

86 reproductive costs. Therefore they might not be able to sustain encounter

87 rates with their preferred partners at sufficient levels. In line with this

88 hypothesis, Hoiss, Krauss, and Steffan-Dewenter (2015) found that the spe-

89 cialisation of plant-pollinator networks decreased both with elevation and

90 after extreme drought events. Likewise, Pellissier et al. (2010) found a

91 positive relationship between niche breadth and environmental stress: disk-

92 or bowl-shaped blossoms (which allow a large number of potential pollinator

93 species to access pollen and nectar rewards) dominated at high altitude

94 flower communities.

4

Here, we investigate whether, and how, environmental stress can system-
atically affect species degree. Our main aim is to test the two ~~competing~~ aforementioned
hypotheses that relate environmental stress and species degree and to inves-
tigate whether this changes across species or between trophic guilds. We
propose that specialist species can become "facultative" generalists to reduce
their vulnerability to the absence of preferred partners (for example, when
variations in climate decouple phenologies; Benadi et al. 2014). We therefore
also expect that, as environmental stress increases, species with a relatively
small number of partners are more likely to engage with more partners and
broaden their trophic niche. Species with a large number of partners, on
the other ~~hand, should~~ have a larger pool of available partners and might,
therefore, be more likely to narrow their niche under environmental stress
by focusing on the most beneficial partners. Importantly, when testing
these hypotheses, we control for the potential effects of the environment in
community composition and the size of ~~the~~ species' fundamental niche, both
from an Eltonian (interactions) and Grinellian (environment) perspective.

We test these hypotheses using data on plant-pollinator interactions. We use
the species' patterns of occurrence to estimate the environmental suitability
in their communities as an indirect measure of the environmental stress they
might experience. Condensing the environmental variation over multiple
factors (like temperature and precipitation) into a single metric is crucial to
generalise our findings at a global scale.

Methods

We retrieved plant-pollinator networks from the Web of Life database (For-
tuna, Ortega, and Bascompte 2014). This database contains datasets origi-
nating from 57 studies published in the primary literature between 1923 and
2016. Calculating the environmental stress of species in their community
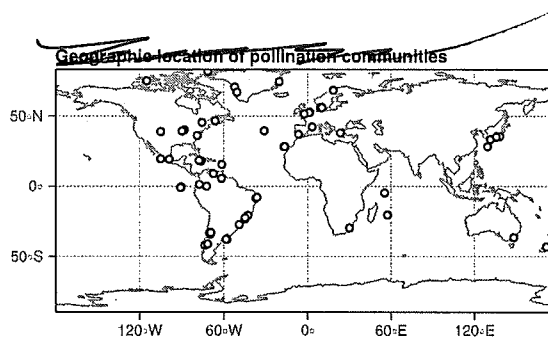
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is this needed or helpful?

Figure 1: Worldwide distribution of pollination communities included in this study
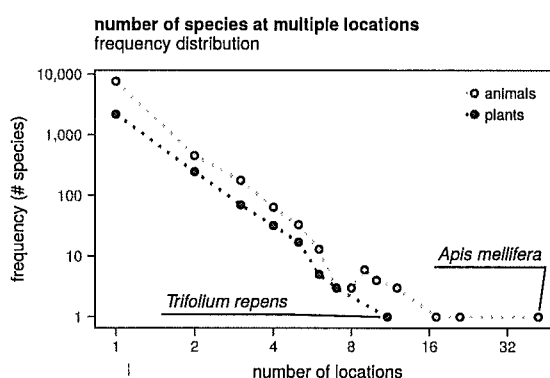

Figure 2: Frequency distribution of the number of locations in which a species is present. The most common pollinator species was *Apis mellifera*, which was sampled on 42 locations, while the most common plant species was *Trifolium repens*, which was sampled on 11 locations.

and another!

122 and their Eltonian niche breadth required us to reduce both the taxonomic

123 and distributional/locational uncertainty. A critical step towards reducing

124 this uncertainty is to ensure that the names used to identify species are valid

125 and unambiguous, which in turn allow us to obtain further information from

126 biological databases and accurately match species across studies. Therefore,

127 our first step was to ensure consistent spelling and standardisation of species

128 names synonyms (See Supplementary Methods) This step ensured that

129 the matching of species across studies was as accurate as possible. The   why repeat this?

130 cleaning process resulted on a total of 2,555 plants and 8,406 pollinator

131 species distributed across 73 locations arround the globe (Figure 1, 2).

132 Second, we calculated the suitability of the environment for a species in a

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[Handwritten note at top: Why not just use suitability? is it necessary to make it a proxy?]

133 particular community as a proxy of environmental stress. We assume that the

134 environmental stress a species experience in a particular location is inversely

135 related to the suitability of the average environmental conditions in that

136 place. Our third and final step was to relate the environmental suitability

137 to the relative number of partners a species has in a community, as a proxy

138 for Eltonian niche breadth. To explore this relationship within and across

139 species, we used a multilevel Bayesian model in which we controlled for the

140 potential effects of the environment on co-occurrence.

[Handwritten note at right: Why is this a proxy? I feel like this needs to be spelled out explicitly in the intro]

[Handwritten note at left: this feels out of order]

141 Species suitability

142 Our next step was to determine the habitat suitability of the species as

143 a proxy of the environmental stress they experience in their community.

144 As we aim to compare the trophic niche for different suitability levels, we

145 only do this for species that were present in at least two communities. To

146 calculate the suitability of a species in a particular location, we used a

147 niche-factor analysis (Hirzel et al. 2002; Broennimann et al. 2012). This

148 approach is based on the probability density function of species distribution

149 in an environmental variable space. In a nutshell, habitats (characterised

150 by a collection of environmental variables) in which the species occurs most

151 often are deemed to be *more* suitable for the species than habitats in which the

152 species has never been observed. This approach to estimating the habitat

153 suitability requires two critical pieces of information. First, we require

154 information about the occurrences of the species of interest. Second, we

155 require information about the environmental conditions for all the locations

156 in which the species occurs.

157 We retrieved 38.1 million occurrences from the Global Biodiversity Infor-

158 mation Facility (GBIF; https://www.gbif.org). Issues with data quality are

159 a central issue hampering the use of publicly available species occurrence

160 GBIF data in ecology and biogeography (Jetz et al. 2019). We, therefore

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161 *We* followed a series of filters and geographic heuristics to correct or remove

162 erroneous and imprecise referencing records (See supplementary methods;

163 Zizka et al. 2019) which allowed us to identify and remove 7.5 million *potentially* prob-

164 lematic occurrences from further analysis. We integrated the occurrences

165 from our plant-pollinator communities to the cleaned occurrences retrieved

166 from GBIF.

167 We retrieved environmental data from WorldClim V2.0, which includes 19

168 bioclimatic variables commonly used in species distribution modelling (Fick

169 and Hijmans 2017). We then complemented data obtained from WorldClim

170 with data from Envirem (Title and Bemmels 2017), which includes 16 extra

171 bioclimatic and two topographic variables. The additional set of variables

172 from Envirem are relevant to ecological or physiological processes and *that*

173 *thus* have the potential to improve our suitability estimation (Title and

174 Bemmels 2018). We obtained all environmental data as rasters composed

175 by cells of 2.5 arc-minutes. We chose this resolution because it provides

176 a reasonable match to the locational accuracy of the species occurrences

177 found in GBIF, particularly those that come preserved specimens in museum

178 collections. *— bad grammar*

179 After obtaining information about species occurrence and the environment,

180 we then merged these two datasets such that a vector with details of our

181 37 bioclimatic and topographic variables characterised the location of each

182 occurrence. Sets of occurrence data tend to be spatially aggregated due to

183 sample bias (tendency to collect close to cities, certain countries) *Moreover,* Spatial

184 autocorrelation arises in ecological data because geographically clumped

185 records tend to be more similar in physical characteristics and/or species

186 abundances than *do* pairs of locations that are farther apart. To account

187 for such spatial dependency in occurrence data, if a species had more than

188 one *occurrence records* within *one of the* a cells of the bioclimatic raster, we

189 only included one *single* occurrence records We did this to avoid giving

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190 more weight to areas with a high number of occurrences, a common scenario

191 in occurrence records collected opportunistically as the ones we use here. In

192 this step we removed 85.4% of the occurrences which resulted in a total of

193 4.5 million occurrences used in our niche analysis.

194 A common issue of terrestrial bioclimatic datasets is that the boundaries of

195 the cells with information do not precisely match the landmass boundaries.

196 The result of this missmatch is that not all environmental variables were ~~was not~~

197 available for 3,273 of the raster cells with occurrences (0.8% of the total).

198 As expected, the vast majority of these problematic cells were close to the

199 shore. To address this issue, we calculated the average value of environmental

200 variables within an 5km buffer of the centre of the cell where the variable

201 was missing and used it to approximate the value of the variable in that

202 cell. Using this procedure, we were able to fill environmental variables for

203 89.3% of the cells where ~~wow~~ they were missing. To fill the remaining 350 cells, we

204 repeated the aforementioned procedure but instead using a 10km buffer. We

205 removed from further analysis occurrences located within the 135 cells for

206 which we were unable to fill environmental variables. $\left(\times \, °/_o \right)$

207 Next, we calculate the probability density function of the species distribution

208 in environmental space. To determine the environmental space, we use

209 the first two components from a principal component analysis of the 37

210 bioclimatic variables associated with the species occurrences. Specifically

211 we use the dudi.pca function from the R package ade4 1.7.13 (Dray and

212 Dufour 2007) and center and scale all bioclimatic variables to have a mean

213 of 0 and a unit standard deviation. We then determine the position of

214 species occurrences in the environmental space and estimate their bivariate

215 probability density function. We use a kernel method to estimate this density

216 and normalise it such that it ranges between zero and one. Specifically, to

217 calculate the probability density function we use ecospat.grid.clim.dyn

218 from the R package ecospat 3.0 (Broennimann, Di Cola, and Guisan 2018)

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219 with a grid resolution of 200. We then determine the location in the environ-

220 mental space of the plant-pollinator communities using the function suprow

221 from ade4. The normalised density at that particular location corresponds

222 to our suitability metric, which we calculate using the R package raster

223 2.8.19 (Hijmans 2019). We use the kernel density method in the niche-factor

224 analysis (Broennimann et al. 2012) rather than the distance from the mode

225 (Hirzel et al. 2002), as it has been proposed earlier, as it has been shown to

226 reduce the procedure's sensitivity to sampling effort and the resolution of

227 the environmental space. *there are so many seemingly technical steps here I think you should summarise the "output"*

228 We used a sensitivity analysis to determine the minimum number of occur-

229 rences that are necessary to have robust environmental suitability values

230 in our communities. For that we used the species with most occurrences

231 available, *Archilochus colubris*, and calculated the mean absolute error of the

232 suitability values obtained with one thousand subsamples from the 74,791

233 occurrences available from GBIF.

234 Data analysis

235 We then used a set of Bayesian multilevel models to evaluate the impact of

236 environmental suitability on the number of partners a species has. Specifically,

237 we use the normalised degree of species as our response variable; *that i)* this is, the

238 number of species it interacts with *given by* the number of species in the opposite

239 guild (Martín González, Dalsgaard, and Olesen 2010). The normalised degree

240 was modelled using a logit link function, and a binomial distribution in which

241 the number of species *a focal* interacts with is the number of successes, and the

242 number of species in the opposite guild is the number of trials. We are

243 aware that whether species interact or not is not a Bernoulli process as

244 species interactions are not strictly independent from each other. However,

the use of 245 a binomial distribution allows us to account for the differences in species

246 richness across communities indirectly. Importantly, however, results are

247 qualitatively similar when we model species degree directly using a Poisson

248 distribution and a logarithmic link function.

249 We evaluate four models to assess the relative importance of suitability. A

250 first model, our baseline model, included three population-level predictors

251 and two grouping levels, species and the community. The population-level

252 predictors in the baseline model, commonly called fixed effects, were the

253 habitat suitability, the species guild (plant or a pollinator), and its number of

254 known possible partners. We included the number of known possible partners

255 as a predictor in our models as it allows us to control for the environmental

256 effects on species co-occurrence. We calculate this metric by determining the

257 number of partners with which the species is known to interact in any other

258 community. Controlling for the number of potential partners makes our

259 model a particularly stringent test of our environmental stress hypotheses

260 because this variable could explain a large proportion of variance. Often the

261 potential and the actual number of partners is the same or very close to each

262 other, especially for rare species present only in a few communities. As we

263 were interested in understanding whether the effect of habitat suitability is

264 conditional on the species guild (plant or pollinator), we therefore included both

265 guild and its interaction with suitability in the model. Is this the only interaction?

266 We allowed the intercept of degree and slope of the suitability-degree rela-

267 tionship to vary among species. This approach allowed us to investigate two

268 questions. First, it allows us to inspect the extent to which suitability is a

269 population or a group level effect. Second, by investigating the correlation

270 between the intercept and the slope as a model parameter, it allowed us to

271 inspect the extent by which species with a small or large number of interac-

272 tions respond to increasing levels of environmental stress. To account for

273 unmeasured differences between communities, like sampling effort, sampling

274 method, or diversity, we also calculated an intercept for each community in

275 our study. To facilitate model interpretation and convergence, we scaled all

11

Why insist on different terminology? this seems purposefully obtuse

Are you sure is definition is clear?

Why not phrase these similarly?

you wrote this differently the previous time

276 continuous variables to have a mean of zero and a unit standard deviation.

277 We compared this baseline model with three alternative models in which

278 we remove one predictor at a time. To quantify the difference between

279 models, in terms of their expected out-of-sample performance, we use the

280 Wanatabe-Akaike information criterion (WAIC). All models were fitted under

281 a Bayesian framework using the R package brms 2.8.0 (Bürkner 2017, 2018)

282 as an interface for Stan (Carpenter et al. 2017). For each model, we used

283 four Markov chains of 4,000 iterations each; we used half of the iterations

284 for warmup. We used weakly informative priors for all model parameters.

285 Specifically we used normal priors of mean zero and standard deviation ten

286 for the population-level effects and the intercepts, a half-Cauchy prior with

287 a location of zero and a scale of two for the standard deviations, and, when

288 applicable, an LKJ-correlation prior with parameter $\zeta = 1$ for the correlation

289 matrix between group-level parameters.

Results

why are there two values here?

291 After performing our sensitivity analysis, we found that we need roughly 26,

292 18 independent occurrences for each community for which we calculated a

293 suitability value in order to obtain a mean absolute error below 0.1 (Fig. S1).

294 We therefore removed from further analyses species for which we did not

295 have enough occurrences to obtain robust estimates. When inspecting the

296 suitability values of the analysed species, we found that most communities

297 included species for which habitat suitability was low and species for which

298 it was high (Fig. S2).

299 Our models performed relatively well. The Bayesian R-squared for our

300 baseline model was 0.91, which indicates our models were able to capture

301 a large proportion of the variability on the data. Overall, we found that

302 environmental suitability does not show a consistent pattern across species.

(a) environmental suitability

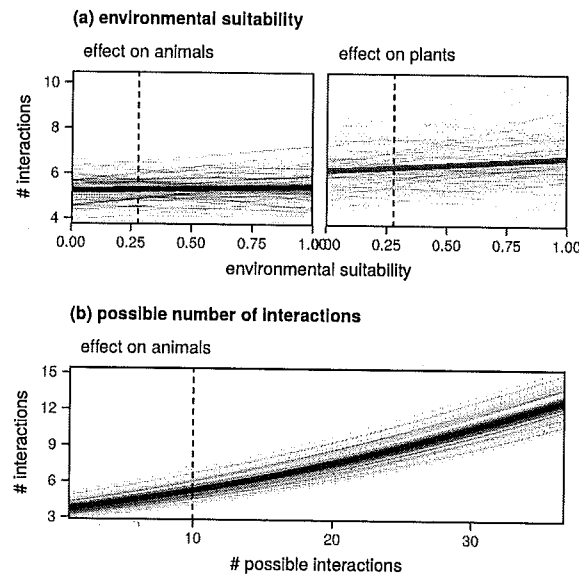**(b) possible number of interactions**

Figure 3: Conditional effects of predictors in our baseline model. The predicted values of the number of interacting species are based on a hypothetical community with 76 plants and 33 pollinators. These values correspond to the median number of species in each guild, respectively. In each panel, we condition on the mean values of all other predictors in the model. We indicate mean values for each predictor with a vertical dashed line. For model fitting, we scaled all predictors to have a mean of zero and unit variance. However, except for environmental niche size, here we show the unscaled predictors to facilitate interpretation. To illustrate the uncertainty around the fitted estimates, we plot the fits of 100 independent draws from the posterior distribution. The thick lines indicate the mean values of the response distribution. As there was no interaction between guild and generality or the number of possible interactions for these two predictors, we only show conditional the conditional effect of pollinators.

303 Indeed, when looking at the population level effects, suitability has virtually
304 no relationship with normalised degree for plants or pollinators
305 (Figure 3b). However, suitability is an important predictor as the WAIC
306 difference between our baseline model and the model that did not include suitability
307 was 581 ± 104 (Table 1). This apparent discrepancy can be explained by
308 the variability of the suitability-degree relationship across species.

309 While for some species there is a strong negative relationship between
310 suitability and normalised degree while for some others there is a strong positive
311 relationship (Figure 4a). Interestingly, the slope of this relationship correlates

13

Table 1: Comparison in out of sample predictive power of the baseline model (bold) and their alternatives. We rank models by their expected log predictive density based on their Wanatabe-Akaike information criterion (WAIC).

predictors	WAIC	SE
Suit. * Guild + Pot.	6,149	140
Suit. * Guild	7,652	273
Guild + Pot.	6,730	190
Suit. + Pot.	6,151	139

[handwritten: 1) this ordered correctly?]

312 negatively with the species' intercept in the model (Figure 4b). The mean

313 correlation coefficient was -0.43 [-0.62, -0.22]. In other words, the slope of the

314 suitability-degree relationship was more likely to be positive for species with

315 a smaller number of partners in lower-suitability *[handwritten: conditions]* and negative for species

316 with a larger number of partners in lower-suitability conditions.

317 As expected, we found a strong and positive relationship between the num-

318 ber of possible interactions and the number of realised interactions in the

319 community. There was *[handwritten: also]* a large difference on WAIC between the model that

320 included this predictor and that that excluded it. This result indicates that

321 the availability of potential partners accounts for a large proportion of the

322 variability in species degree.

323 Importantly, our findings of the suitability-degree relationship were qualita-

324 tively unchanged whether we included this variable or not.

[handwritten: Which findings? Can you be more specific?]

325 The group-level variation among communities was larger than that among

326 species which further indicates the importance of the local context when

327 determining species degree. Specifically, the standard deviation (in the

328 parameters scale) of the community intercepts was 1.03 [0.86, 1.23] while the

329 standard deviation of the species intercept was 0.54 [0.48, 0.61], and that

330 of the species' suitability slope was 0.35 [0.29, 0.41] (95% credible intervals

331 shown within square brakets).

[handwritten: I think this needs more elaboration. You're putting a ton of faith in the reader]

14

[handwritten: Besides, these values are not really directly comparable]

(a) effect of suitability on individual species

animals

Bombus diversus

Syrphus vitripennis

interactions

plants

Ixeris dentata

Leucanthemum vulgare

environmental suitability

(b) species' specific intercept and suitability slope
all values in parameter space

species' suitability slope

species' intercept

(c) correlation coefficient

correlation
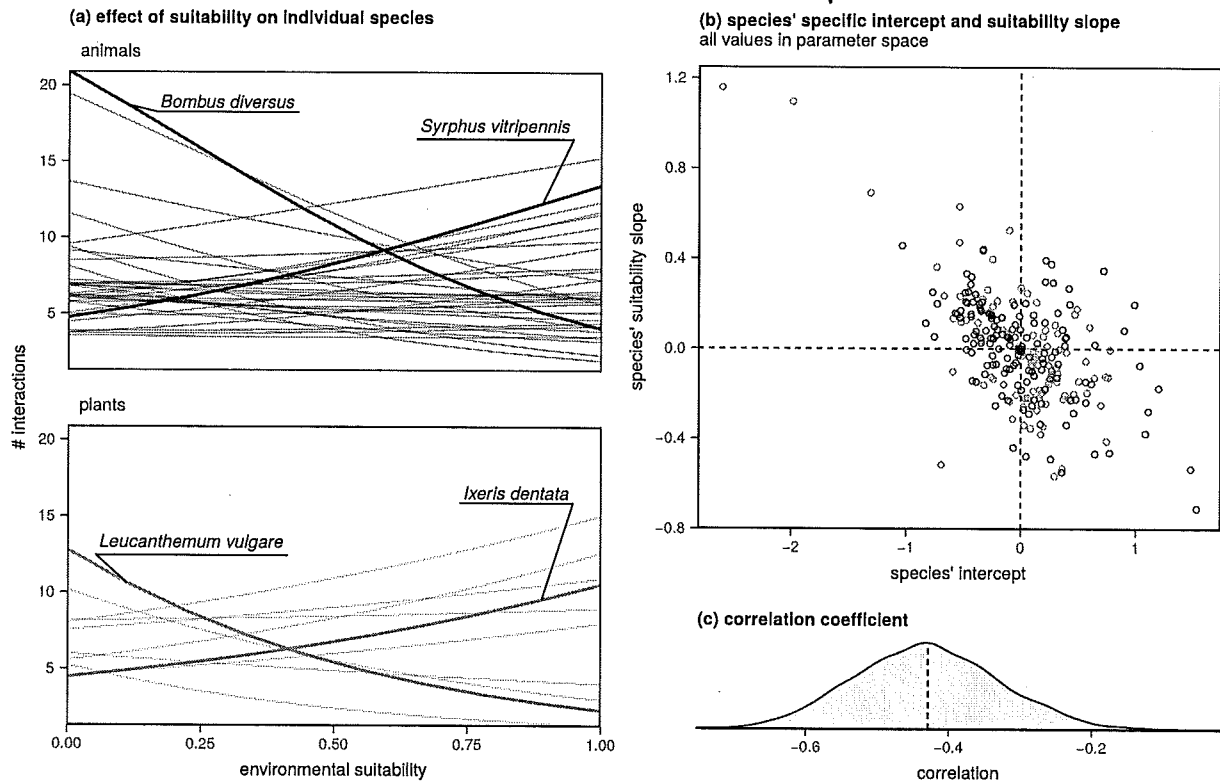
Figure 4: Species-level effects of suitability. (a) Conditional effect of suitability for individual species. To facilitate visualization, we show only species for which there is suitability information in at least six communities (10 plants and 33 pollinators). As in the previous figure, fitted values assume a hypothetical community of median size. In each panel, we highlight two species for which the relationship between environmental suitability and the normalised degree was particularly strong. (b) The correlation between the species' intercept and the species' slope of suitability was negative

15

332 Discussion

333 We set out to explore whether and how environmental stress can system-

334 atically affect species degree. After accounting for the pool of potential

335 partners, we found that ~~wwwww~~ environmental conditions contribute to deter-

336 mining whether a species is a generalist or a specialist in their community.

337 However, we also found that the particular effect of the environment is

338 strongly dependent on the species. We proposed two alternative hypotheses

339 of how environmental stress may affect the degree, and we found evidence

340 for both of them. Species with a large number of partners in low-stress

341 communities were more likely to have a negative relationship and hence

342 reduce the number of partners as stress increases. Contrastingly, species in

343 our datasets with a small number of partners in low-stress communities were

344 more likely to have a larger number of partners in more stressful communities.

345 In summary, environmental stress pushes species that are flexible enough

346 to change their interaction partners towards intermediate levels of degree, a

347 so-called "regression towards the mean".

348 Our results suggest that changes in community composition are indeed

349 the primary channel through which the environment determines changes

350 interaction probability. However, they also show that, for a large number

351 of species, the environment may also play a substantial role in determining

352 their realised (Eltonian) niche. While previous research has recognised that

353 environmental factors may help explain the changes in network structure

354 along environmental gradients that cannot be explained by community

355 composition (Tylianakis, Tscharntke, and Lewis 2007), how these two factors

356 were linked had been elusive so far (Gravel et al. 2018). We believe that part

357 of this difficulty could have arisen because species, and ultimately network

358 structure, can respond in multiple and contrasting, ways depending on the

359 particular bioclimatic variable examined (e.g. temperature or precipitation).

360 Using stress to summarise the effect on species of multiple environmental

16

361 gradients allowed us to detect a clear signal of the environment in species'

362 interaction patterns.

363 Although both niche and neutral processes are relevant *in* determining

364 species interactions, our model suggests that niche processes may be the

365 predominant mechanism through which the environment *systematically* affect**S**

366 species degree. First, it is unlikely that environmental suitability correlates

367 to local species abundances (Pearce and Ferrier 2001; Sagarin, Gaines, and

368 Gaylord 2006). Second, even if there is a relationship between suitability and

369 abundances, a particular environmental gradient could have a positive effect

370 on the abundance of some species and a negative effect on others. Indeed,

371 we ~~show~~ *find* that within a community there is a wide range of suitability values,

372 even for the relatively limited number of species we were able to include in

373 our analysis.

we never really "show" this

374 Recent research suggests that species are continuously changing their inter-

375 action partners wherever environmental conditions change in space or time

376 (Raimundo, Guimarães, and Evans 2018). So far it appears that this rewiring

377 is primarily driven by generalist species (Ponisio, Gaiarsa, and Kremen 2017;

378 Burkle, Marlin, and Knight 2013), presumably because generalist species

379 are less sensitive to trait matching of their interaction partners (CaraDonna

380 et al. 2017). Our results add two important nuances to these findings.

381 First, because generalists seem to focus on a smaller number of partners as

382 environmental conditions deteriorate, we show that trait matching might still

383 play a role in determining the interactions of generalist species. Second, we

384 demonstrate that rewiring is not exclusive to generalists. At least a fraction

385 of the species that appear to be specialist in their communities might be as

386 flexible, if not more, than generalist species, effectively behaving as faculta-

387 tive generalists in the face of environmental change. These flexible specialists

388 might, therefore, have a more significant role in network persistence than

389 previously expected.

I feel like this is strange as you seem to imply that spec or gen is defined at one end of the suitability axis whereas it isn't.

17

aren't there four types?
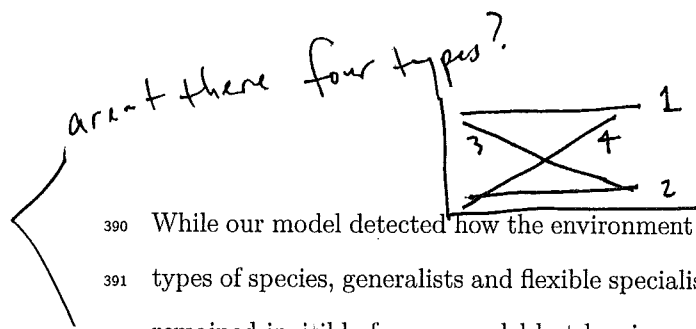
390 While our model detected how the environment affects the interactions of two
391 types of species, generalists and flexible specialists, there is a third group that
392 remained invisible for our model but has important implications for network
393 persistence and stability. Species that are able to vary their interaction
394 partners flexibly and their role in the network are more likely to persist in
395 their community as environmental conditions vary (Gaiarsa, Kremen, and
396 Ponisio 2019). We propose this third group of is composed of specialists
397 that are constrained to interact with partners of high trait-matching and
398 therefore were not likely to be found in more than one community. If
399 species that are not flexible are unlikely to persist over temporal or spatial
400 environmental gradients, we can expect specialised communities that are
401 highly constrained by trait-matching (like some plant-hummingbird networks;
402 Vizentin-Bugoni, Maruyama, and Sazima 2014; Maruyama et al. 2014) to
403 be far more vulnerable to increased climate change-induced environmental
404 stress and habitat degradation than communities where role and interaction
405 flexibility are more prevalent.

406 Similarly, if the patterns we see in our models have also played a role during
407 the evolutionary history of pollination communities, our results also help
408 explain why only a small fraction of plant-pollinator interactions show a
409 strong signature of deep co-evolutionary history (Hutchinson, Cagua, and
410 Stouffer 2017). The increases on the stress that species are predicted to
411 experience due to rapid environmental change might further erode the co-
412 evolutionary history of specialist species. Communities as a whole might be
413 in a trajectory of even more diffuse co-evolution. For specialist species, at
414 least, the longer-term benefits of being able to interact with multiple partners
415 might be more important than the shorter-term benefits of interacting with
416 partners of high trait matching.

417 The structural implications of the "regression towards the mean" that envi-
418 ronmental stress promotes are less clear. However, it is plausible to expect

18

419 that nestedness, and therefore network stability, might be reduced in the
420 face of rapid environmental change. Determining exactly how the changes
421 in degree caused by environmental stress reflect on systematic changes in
422 network structure would be an interesting avenue of research. Answering
423 this question would require expanding our suitability analysis to all species
424 in the community and compare the degree distribution of networks along a
425 gradient of stress for the community as a whole.

I felt like this paragraph and the one prior were unnecessary.

426 In conclusion, we show that the environment can affect the realised niche of
427 plants and pollinators in systematic ways beyond community composition.
428 On the one hand, species that are inflexible with their interaction partners
429 are unlikely to persist under more stressful environmental conditions. On the
430 other, species that are flexible with their interactions partners experience a
431 regression towards intermediate levels of degree, where generalist species tend
432 to interact with fewer, presumably more effective, partners and specialist
433 tend to interact with more partners.

this is an incredibly confusing last sentence; it needs more revision and focus

434 Acknowledgements

isn't this Education New Zealand?

443 References

[handwritten: remove all of these]

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Environmental stress affects niche breadth in plant-pollinator communities

Supplementary information

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Supplementary methods

Reducing taxonomic uncertainty

Data were obtained from the Web of Life database (Fortuna, Ortega, and Bascompte 2014) which includes data from 57 published studies (Abreu and Vieira 2004; Arroyo, Primack, and Armesto 1982; Barrett and Helenurm 1987; Bartomeus, Vilà, and Santamaría 2008; Bek 2006; Bezerra, Machado, and Mello 2009; Bundgaard 2003; Canela 2006; Clements and Long 1923; del Coro Arizmendi and Ornelas 1990; Dicks, Corbet, and Pywell 2002; Dupont and Olesen 2009; Dupont, Hansen, and Olesen 2003; Elberling and Olesen 1999; Gutierrez, Rojas-Nossa, and Stiles 2004; Hattersley-Smith 1985; Herrera 1988; Hocking 1968; Ingversen 2006; INouE et al. 1990; Inouye and Pyke 1988; Kaiser-Bunbury et al. 2014, 2010; Kakutani et al. 1990; Kato 2000; Kato, Matsumoto, and Kato 1993; Kato and Miura 1996; Kato et al. 1990; Kevan 1970; Kohler 2011; Lara 2006; Las-Casas, Azevedo Júnior, and Dias Filho 2012; Lundgren and Olesen 2005; McMullen 1993; Medan et al. 2002; Memmott 1999; Montero 2005; Mosquin 1967; Motten 1986; Olesen, Eskildsen, and Venkatasamy 2002; Ollerton 2003; Percival 1974; Petanidou and Vokou 1993; Philipp et al. 2006; Primack 1983; Ramirez 1989; Ramirez and Brito 1992; Robertson 1929; Rosero and others 2003; Sabatino 2010; Schemske et al. 1978; Small 1976; Smith-Ramírez et al. 2005; Stald, Valido, and Olesen 2003; Vázquez 2002; Vizentin-Bugoni et al. 2016; Yamazaki and Kato 2003).

Interaction data from the included studies included 11,231 unique organism names. From these 1,166 were present in more than one study. From the total number of organisms, 159 were identified to the subspecies or variety level, 6,759 to the species level, 1,755 to the genus level, whereas the remaining 2,558 were unidentified. As the species level was the most common taxonomic rank available in our interaction datasets, in all further analysis, we grouped together subspecies or varieties within the same species.

1

We were able to confirm the validity of 5,263 of the scientific names used to identify organisms (roughly 76%). We assessed the validity of a name by querying the Global Names Resolver database (https://resolver.globalnames. org) which includes data from 98 taxonomic sources. We accessed this database using the function `gnr_resolve` from the R package `taxize` 0.9.6 (Chamberlain and Szocs 2013; S. Chamberlain, Szoecs, et al. 2019).

From the remaining 1,655 names we were unable to validate, we were able to identify and correct 726 that contained spelling mistakes. These spelling mistakes were corrected automatically by fuzzy matching the canonical names in our data sources with those in the Global Names Resolver database. However, on rare occasions, the fuzzy matching algorithm can suggest a scientific name that has a similar spelling, but that corresponds to an organism in a different taxonomic group, often a separate kingdom. To address this potential problem, we checked the taxonomic hierarchy of suggested names and confirmed that it matched our expected taxon. We retrieved all taxonomic hierarchies from the National Center for Biotechnology Information taxonomic database (https://www.ncbi.nlm.nih.gov/taxonomy).

As species names are constantly changing, we subsequently checked for possible synonyms of the canonical names in our data sources. Using data from the Integrated Taxonomic Information System database (http://www. itis.gov), we found synonyms and alternative names for 611 species.
Finding these alternative names was required for two main reasons. First, because we wanted to be able to identify the cases in which the same species might have been recorded with different names in various data sources. This can occur not only when the canonical name has been changed but also when there are widely used orthographic variants. Second, because retrieving occurrence data is often only possible using the latest accepted/valid name for a particular species.

All together, from the 1,655 names we were unable to validate, it was not possible to automatically correct or find synonyms 332 of them. We then manually consulted multiple online databases, chiefly Wikispecies (https://species.wikimedia.org/), and looked for canonical names that both, resembled the unvalidated names and matched the geographic and taxonomic expectations. In this fashion, we were able to further correct 25 names. Most manual corrections were made on names that have been abbreviated or had more than two spelling mistakes. A complete list of manual name corrections can bee seen in Table S1.

This cleaning process allowed us to match further 270 names across data

Table S1: Manually corrected canonnical names. More than one correct name have been included when an accepted/valid synonym the cannonical name exists.

incorrect name	corrected name	guild
Acaena pinn	*Acaena pinnatifida*	plant
Adesmia brachy	*Adesmia brachysemeon*	plant
Aesculus camea	*Aesculus X carnea*	plant
Brachyome sinclairii	*Brachyscome sinclairii*	plant
Calceolaria arac	*Calceolaria arachnoidea*	plant
Equium sabulicola	*Echium sabulicola*	plant
Euonymus fo rtunei	*Euonymus fortunei*	plant
Galvezia leucantha pubescen	*Galvezia leucantha*	plant
Heliconia simulans	*Heliconia angusta*	plant
Pitcaimia flammea	*Pitcairnia flammea*	plant
Psittacanthus flavo viridis	*Psittacanthus flavo-viridis*	plant
Rodophiala bifidum	*Rhodophiala bifida*	plant
Stachys albi	*Stachys albicaulis*	plant
Stenactis annuus	*Erigeron annuus*	plant
Thaspium aureum atropurpurem	*Thaspium trifoliatum*	plant
Tristhema mauritiana	*Tristemma mauritianum*	plant
Tropaeolum polyph	*Tropaeolum polyphyllum*	plant
Tyttnera scabra	*Turnera scabra*	plant
	Turnera ulmifolia	plant
VVedelia biflora	*Melanthera biflora*	plant
	Wedelia biflora	plant
Cateres pennatus	*Kateretes pennatus*	pollinator
Eclimus harrisi	*Condylostylus crinicauda*	pollinator
Ptilandrena g. maculati	*Andrena distans*	pollinator
Tapinotaspis caerulea	*Chalepogenus caeruleus*	pollinator
Tapinotaspis herbsti	*Chalepogenus herbsti*	pollinator

sources and, by doing so, identify another 72 species that were present in more than one study. The process also allowed us to identify problematic data sources in which some names were included as both plants and pollinators. These data sources were removed from further analysis. In seven of our data sources interaction data was recorded at multiple points in time. When this was the case, we combined interaction data into one single interaction network.

Reducing location uncertainty

We retrieved occurrences from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org) using the R package rgbif 0.9.6 (Chamberlain and Boettiger 2017; S. Chamberlain, Barve, et al. 2019). Specifically, for each species, we only requested occurrences for which the coordinates of the observation were available and that had no known geospatial issue in the GBIF database. Roughly, we downloaded 38.1 million occurrences for the 986 species we were interested on. This occurrences, however, contain observations of mixed quality. Therefore, we followed Zizka et al. (2019) and

error of environmental suitability of communities
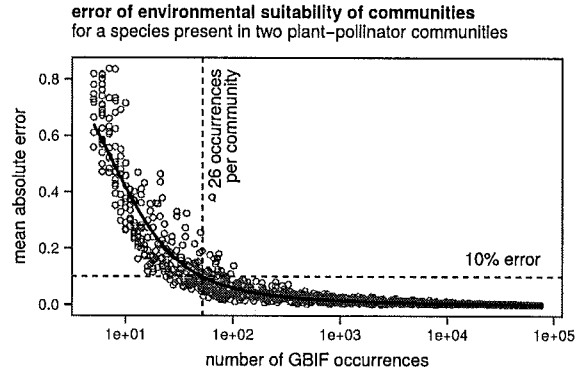**for a species present in two plant–pollinator communities**

Figure S1: Sensitivity analysis of environmental suitability error. The number of independent occurrences retrieved from GBIF is inversely related to the error of environmental suitability for our plant-pollinator networks.The sensitivity analysis was performed by subsampling occurrences of *Archilochus colubris* the species in our dataset with the largest number of occurrences in GBIF, which was recorded in two of our communities.

applied a series of simple filters and geographic heuristics to remove those of lower quality. Specifically, we removed all occurrences with (*i*) a coordinate uncertainty larger than 100km; (*ii*) those recorded prior to 1945 (as records prior to this date have been shown to be often imprecise); (*iii*) those in which the number of counts in the occurrence was registered was either zero (as that indicates that the species has not been recorded); and (*iv*) those occurrences in which the "basis of record" was not a human observation or a preserved specimen (as occurrences from unknown and fossil records are known to be highly unreliable). We then used the R package CoordinateCleaner 0.9.6 (Zizka et al. 2019) and land mass and country data from Natural Earth (https://www.naturalearthdata.com) with a 1:10,000,000 scale to further identify and remove problematic occurrences. We removed occurrences for which their coordinates (*v*) fell outside the borders of the country where they were recorded; (*vi*) those around a country capital or the centroid of the country and province centroids; (*vii*) those around a biodiversity institution; and (*viii*) those located within oceans. Thorugh this cleaning process, we removed with 7.5 million occurrences distributed accross 916 species.
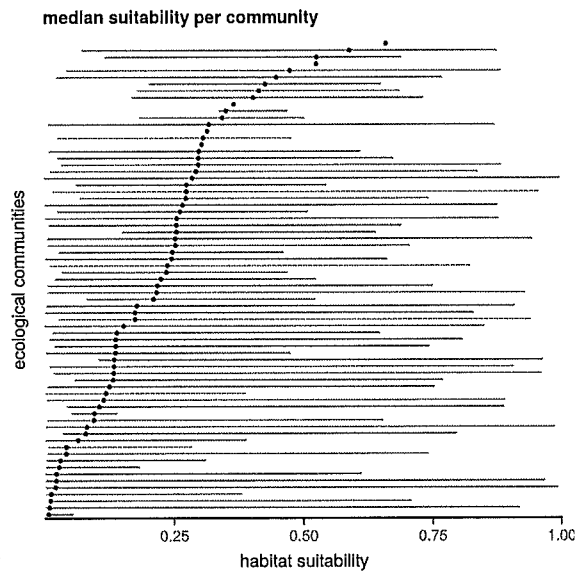
Figure S2: Median habitat suitability of communities in our dataset. Each row represents a different community and horizontal lines represent span the 2.5 and 97.5 quantiles.

Supplementary results

Supplementary references

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