

Environmental stress affects niche breadth in plant-pollinator communities

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16 Abstract

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

38 Introduction

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

50 Species interactions are determined in part by niche processes (the match-
51 ing of traits) and partly by neutral processes (more abundant species are
52 more likely to encounter each other and, thus, interact). The environment
53 can influence both of these processes. It is, therefore, not surprising that,
54 despite limitations on the spatial extent or the number of environmental
55 gradients considered, multiple studies have been able to show how changes to
56 interactions can be related to environmental change (Tylianakis and Morris
57 2017). For instance, some studies suggest that the strength of some trophic
58 interactions, like predation (McKinnon et al. 2010; Vucic-Pestic et al. 2011)
59 and herbivory (Baskett and Schemske 2018), can increase with temperature
60 but might decrease with precipitation (Pires et al. 2016). Some other stud-
61 ies, however, have shown either no effect (on average) or non-linear effects
62 of temperature or precipitation on plant-pollinator interactions (Devoto,
63 Medan, and Montaldo 2005; Gravel et al. 2018). Overall, while it looks clear
64 that pairwise interactions respond to environmental drivers, there is high
65 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.

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

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

117 **Methods**

118 We retrieved plant-pollinator networks from the Web of Life database (For-
119 tuna, Ortega, and Bascompte 2014). This database contains datasets origi-
120 nating from 57 studies published in the primary literature between 1923 and
121 2016. Calculating the environmental stress of species in their community

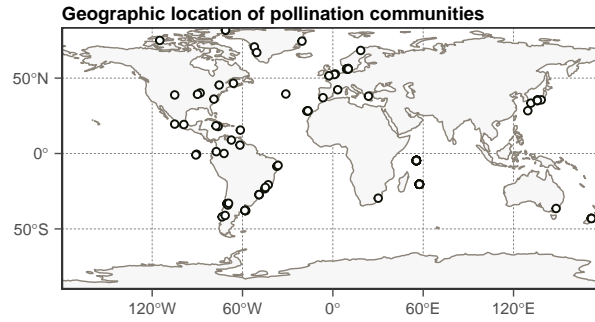


Figure 1: Worldwide distribution of pollination communities included in this study

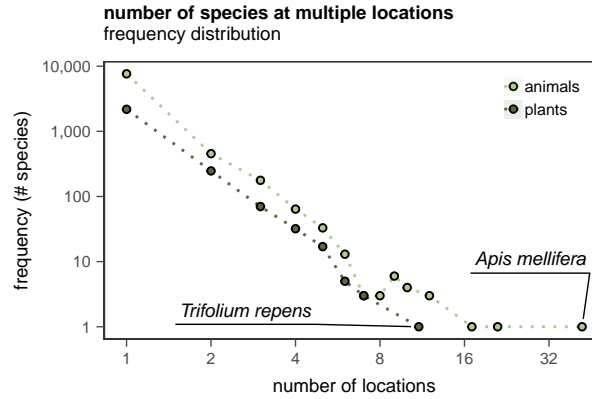


Figure 2: Frequency distribution of the number of locations in which a species is present. The most common pollinator species was *Apis mellifera*, which was sampled on 42 locations, while the most common plant species was *Trifolium repens*, which was sampled on 11 locations.

122 and their Eltonian niche breadth required us to reduce both the taxonomic
 123 and distributional/location 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
 130 cleaning process resulted on a total of 2,555 plants and 8,406 pollinator
 131 species distributed across 73 locations around the globe (Figure 1, 2).

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

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.

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 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

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 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 as
173 such, 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.

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). 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 are 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 cells of the bioclimatic raster, we
189 only included one of the occurrence records. We did this to avoid giving

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 mismatch is that not all environmental variables 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 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.

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)

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.

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; this is, the
238 number of species it interacts with given 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 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,
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
265 guild and its interaction with suitability in the model.

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

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

We compared this baseline model with three alternative models in which we remove one predictor at a time. To quantify the difference between models, in terms of their expected out-of-sample performance, we use the Wanatabe-Akaike information criterion (WAIC). All models were fitted under a bayesian framework using the R package `brms` 2.8.0 (Bürkner 2017, 2018) as an interface for Stan (Carpenter et al. 2017). For each model, we used four Markov chains of 4,000 iterations each; we used half of the iterations for warmup. We used weakly informative priors for all model parameters. Specifically we used normal priors of mean zero and standard deviation ten for the population-level effects and the intercepts, a half-Cauchy prior with a location of zero and a scale of two for the standard deviations, and, when applicable, an LKJ-correlation prior with parameter $\zeta = 1$ for the correlation matrix between group-level parameters.

Results

After performing our sensitivity analysis, we found that we need roughly 26, 18 independent occurrences for each community for which we calculated a suitability value in order to obtain a mean absolute error below 0.1 (Fig. S1). We, therefore, removed from further analyses species for which we did not have enough occurrences to obtain robust estimates. When inspecting the suitability values of the analysed species, we found that most communities included species for which habitat suitability was low and species for which it was high (Fig. S2).

Our models performed relatively well. The bayesian R-squared for our baseline model was 0.91, which indicates our models were able to capture a large proportion of the variability on the data. Overall we found that environmental suitability does not show a consistent pattern across species.

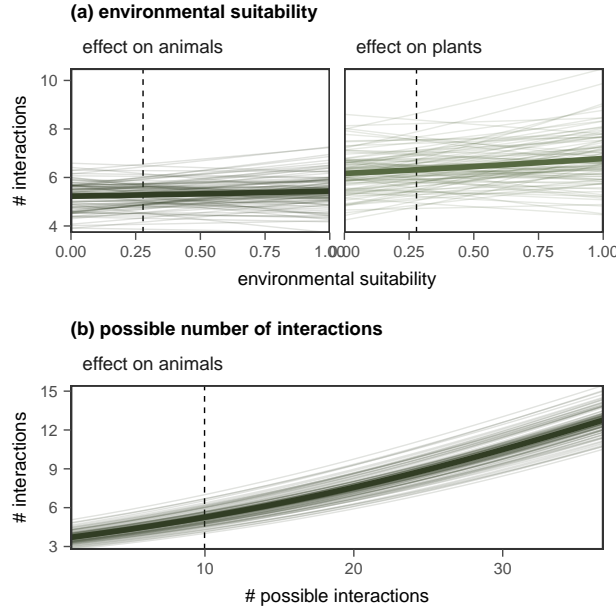


Figure 3: Conditional effects of predictors in our baseline model. The predicted values of the number of interacting species are based on a hypothetical community with 76 plants and 33 pollinators. These values correspond to the median number of species in each guild, respectively. In each panel, we 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 the normalised degree, neither for plants or pollinators
 305 (Figure 3b). However, suitability is an important predictor as the WAIC
 306 difference between our baseline model and that 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, for some others with a strong positive
 311 relationship (Figure 4a). Interestingly, the slope of this relationship correlates

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

negatively with the species' intercept in the model (Figure 4b). The mean correlation coefficient was -0.43 [-0.62, -0.22]. In other words, the slope of the suitability-degree relationship was more likely to be positive for species with a smaller number of partners in lower-suitability and negative for species with a larger number of partners in lower-suitability conditions.

As expected, we found a strong and positive relationship between the number of possible interactions and the number of realised interactions in the community. There was a large difference on WAIC between the model that included this predictor and that that excluded it. This result indicates that the availability of potential partners accounts for a large proportion of the variability on species degree.

Importantly, our findings of the suitability-degree relationship were qualitatively unchanged whether we included this variable or not.

The group-level variation among communities was larger than that among species which further indicates the importance of the local context when determining species degree. Specifically, the standard deviation (in the parameters scale) of the community intercepts was 1.03 [0.86, 1.23] while the standard deviation of the species intercept was 0.54 [0.48, 0.61], and that of the species' suitability slope was 0.35 [0.29, 0.41] (95% credible intervals shown within square brackets).

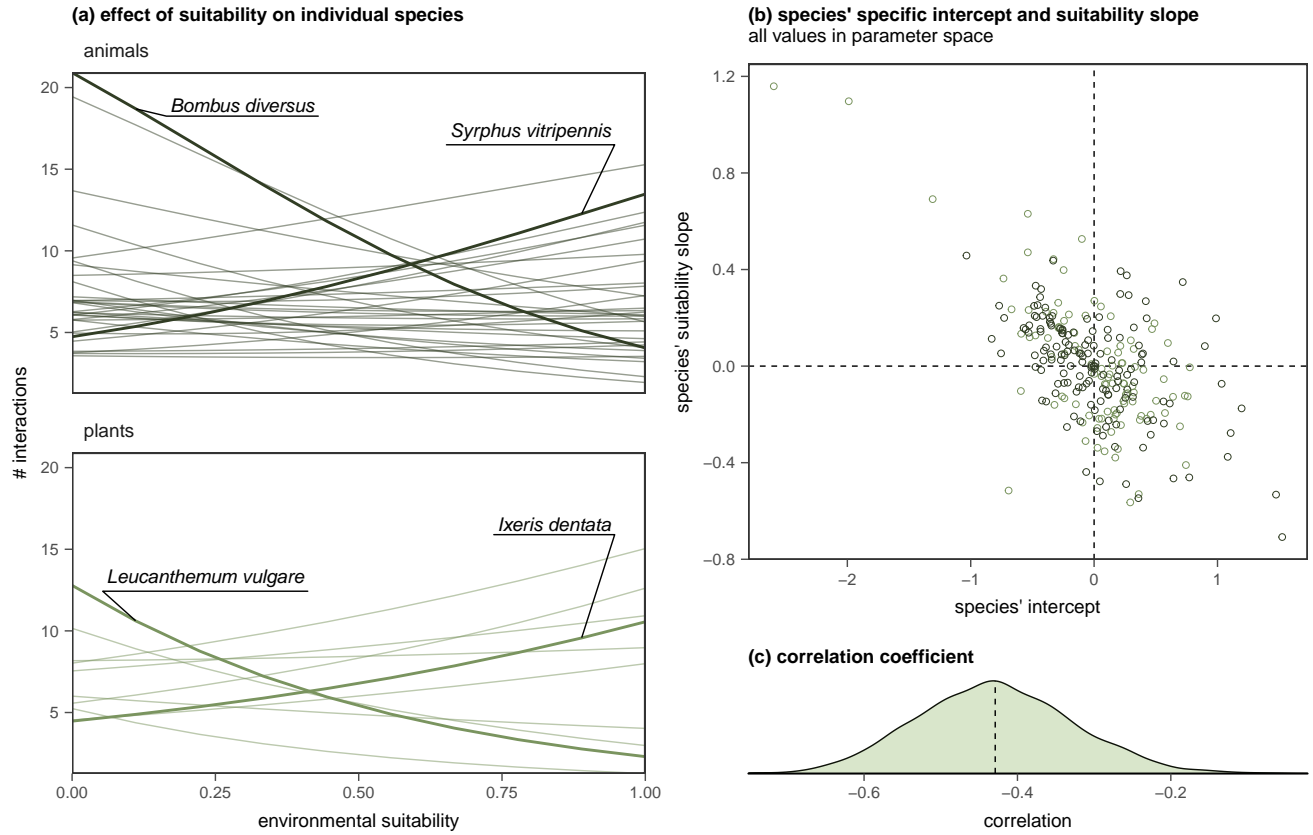


Figure 4: Species-level effects of suitability. (a) Conditional effect of suitability for individual species. To facilitate visualization we show only species for which there is suitability information in at least six communities (10 plants and 33 pollinators). As in the previous figure, fitted values 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 negatively correlated.

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 indeed 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, Tschardtke, 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

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 at determining
364 species interactions, our model suggests that niche processes may be the
365 predominant mechanism through which the environment *systematically* affect
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 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.

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.

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

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.

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.

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