

Environmental stress affects niche breadth in plant-pollinator communities

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15 Abstract

16 Evidence that the environment influences the interaction between species
17 is rapidly accumulating. However, how it happens is currently unclear as
18 environmental gradients appear to have contrasting or non-linear effects on
19 the species' trophic niche breadth depending on the environmental variable.
20 Here, we explore the relationship between the stresses imposed by the envi-
21 ronment, instead of environmental gradients directly, and niche breadth using
22 a global dataset of plant-pollinator interactions. We found that environmental
23 stress plays a significant role in determining the number of partners a species
24 interacts with, but this role is highly variable across species. In particular,
25 when faced with environmental stress, species that have a large number of
26 interactions are more likely to focus on a smaller number of, presumably
27 higher-quality, interactions. Contrastingly, the specialists that can cope
28 with increased stress are more likely to broaden their niche and engage in
29 opportunistic interactions, effectively behaving as facultative generalists.

30 Introduction

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

42 Species interactions are determined in part by niche processes (the match-
43 ing of traits) and partly by neutral processes (more abundant species are
44 more likely to encounter each other and, thus, interact). The environment
45 can influence both of these processes. It is, therefore, not surprising that,
46 despite limitations on the spatial extent or the number of environmental
47 gradients considered, multiple studies have been able to show how changes to
48 interactions can be related to environmental change (Tylianakis and Morris
49 2017). For instance, some studies suggest that the strength of some trophic
50 interactions, like predation (McKinnon et al. 2010; Vucic-Pestic et al. 2011)
51 and herbivory (Baskett and Schemske 2018), can increase with temperature
52 but might decrease with precipitation (Pires et al. 2016). Some other stud-
53 ies, however, have shown either no effect (on average) or non-linear effects
54 of temperature or precipitation on plant-pollinator interactions (Devoto,
55 Medan, and Montaldo 2005; Gravel et al. 2018). Overall, while it looks clear
56 that pairwise interactions respond to environmental drivers, there is high
57 variability in the response (Tylianakis et al. 2008).

58 One possible explanation for the seemingly contradictory evidence is that
59 each species can have multiple partners. Each of these partners, as well as the
60 interactions with them, can be simultaneously affected by the environmental
61 conditions. Therefore environmental stress may affect the number of partners
62 in different ways depending on its role in the community (for example its
63 trophic guild) or even the species itself. Previous research suggests that there
64 might be two alternative hypotheses of how environmental stress may affect
65 species degree (Tylianakis and Morris 2017). On the one hand, it is possible
66 that when species are under environmental stress, they might be “pressured”
67 to focus on partners with which they are best adapted to interact. For
68 instance, Hoiss et al. (2012) found increased phylogenetic clustering between
69 plants and pollinators at higher altitudes; while Peralta et al. (2015) found
70 that parasitoids in plantation forest, where environmental stress was higher
71 than in native forests, were constrained to interact with hosts, they were
72 best adapted to attack. Similarly, Lavandero and Tylianakis (2013) found
73 that environmental stress due to higher temperature reduced the breadth of
74 the Eltonian niche of parasitoids.

75 On the other hand, it is also possible that when species are under environ-
76 mental stress, they are forced to be more flexible in their interactions as
77 higher environmental stress is likely to be reflected in greater energetic or
78 reproductive costs. Therefore they might not be able to sustain encounter
79 rates with their preferred partners at sufficient levels. In line with this
80 hypothesis, Hoiss, Krauss, and Steffan-Dewenter (2015) found that the spe-
81 cialisation of plant-pollinator networks decreased both with elevation and
82 after extreme drought events. Likewise, Pellissier et al. (2010) found a
83 positive relationship between niche breadth and environmental stress: disk-
84 or bowl-shaped blossoms (which allow a large number of potential pollinator
85 species to access pollen and nectar rewards) dominated at high altitude
86 flower communities.

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

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

109 **Methods**

110 We retrieved plant-pollinator networks from the Web of Life database (For-
111 tuna, Ortega, and Bascompte 2014). This database contains datasets origi-
112 nating from 57 studies published in the primary literature between 1923 and
113 2016. Calculating the environmental stress of species in their community

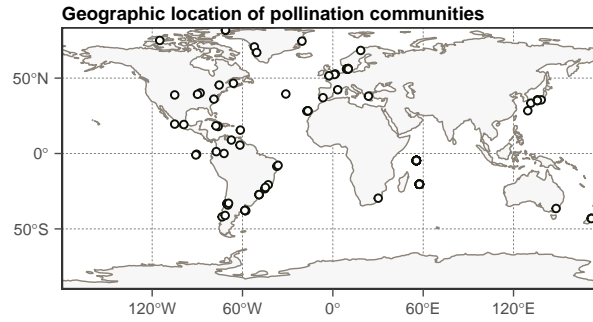


Figure 1: Worldwide distribution of pollination communities included in this study

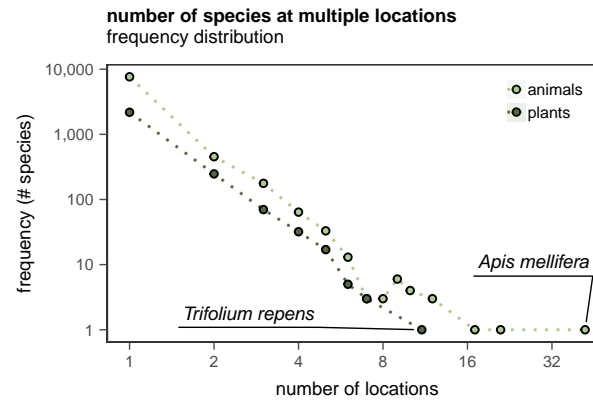


Figure 2: Frequency distribution of the number of locations in which a species is present. The most common pollinator species was *Apis mellifera*, which was sampled on 42 locations, while the most common plant species was *Trifolium repens*, which was sampled on 11 locations.

114 and their Eltonian niche breadth required us to reduce both the taxonomic
 115 and distributional/location uncertainty. A critical step towards reducing
 116 this uncertainty is to ensure that the names used to identify species are valid
 117 and unambiguous, which in turn allow us to obtain further information from
 118 biological databases and accurately match species across studies. Therefore,
 119 our first step was to ensure consistent spelling and standardisation of species
 120 names synonyms (See Supplementary Methods). This step ensured that
 121 the matching of species across studies was as accurate as possible. The
 122 cleaning process resulted on a total of 2,555 plants and 8,406 pollinator
 123 species distributed across 73 locations around the globe (Figure 1, 2).

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

125 particular community as a proxy of environmental stress. We assume that the
126 environmental stress a species experience in a particular location is inversely
127 related to the suitability of the average environmental conditions in that
128 place. Our third and final step was to relate the environmental suitability
129 to the relative number of partners a species has in a community, as a proxy
130 for Eltonian niche breadth. To explore this relationship within and across
131 species, we used a multilevel Bayesian model in which we controlled for the
132 potential effects of the environment on co-occurrence.

133 **Species suitability**

134 Our next step was to determine the habitat suitability of the species as
135 a proxy of the environmental stress they experience in their community.
136 As we aim to compare the trophic niche for different suitability levels, we
137 only do this for species that were present in at least two communities. To
138 calculate the suitability of a species in a particular location, we used a
139 niche-factor analysis (Hirzel et al. 2002; Broennimann et al. 2012). This
140 approach is based on the probability density function of species distribution
141 in an environmental variable space. In a nutshell, habitats (characterised
142 by a collection of environmental variables) in which the species occurs most
143 often are deemed to be suitable for the species than habitats in which the
144 species has never been observed. This approach to estimating the habitat
145 suitability requires two critical pieces of information. First, we require
146 information about the occurrences of the species of interest. Second, we
147 require information about the environmental conditions for all the locations
148 in which the species occurs.

149 We retrieved 38.1 million occurrences from the Global Biodiversity Infor-
150 mation Facility (GBIF; <https://www.gbif.org>). Issues with data quality are
151 a central issue hampering the use of publicly available species occurrence
152 GBIF data in ecology and biogeography (Jetz et al. 2019). We, therefore

153 we followed a series of filters and geographic heuristics to correct or remove
154 erroneous and imprecise referencing records (See supplementary methods;
155 Zizka et al. 2019) which allowed us to identify and remove 7.5 million prob-
156 lematic occurrences from further analysis. We integrated the occurrences
157 from our plant-pollinator communities to the cleaned occurrences retrieved
158 from GBIF.

159 We retrieved environmental data from WorldClim V2.0, which includes 19
160 bioclimatic variables commonly used in species distribution modelling (Fick
161 and Hijmans 2017). We then complemented data obtained from WorldClim
162 with data from Envirem (Title and Bemmels 2017), which includes 16 extra
163 bioclimatic and two topographic variables. The additional set of variables
164 from Envirem are relevant to ecological or physiological processes and as
165 such, have the potential to improve our suitability estimation (Title and
166 Bemmels 2018). We obtained all environmental data as rasters composed
167 by cells of 2.5 arc-minutes. We chose this resolution because it provides
168 a reasonable match to the locational accuracy of the species occurrences
169 found in GBIF, particularly those that come preserved specimens in museum
170 collections.

171 After obtaining information about species occurrence and the environment,
172 we then merged these two datasets such that a vector with details of our
173 37 bioclimatic and topographic variables characterised the location of each
174 occurrence. Sets of occurrence data tend to be spatially aggregated due to
175 sample bias (tendency to collect close to cities, certain countries). Spatial
176 autocorrelation arises in ecological data because geographically clumped
177 records tend to be more similar, in physical characteristics and/or species
178 abundances, than are pairs of locations that are farther apart. To account
179 for such spatial dependency in occurrence data, if a species had more than
180 one occurrence records within one of the cells of the bioclimatic raster, we
181 only included one of the occurrence records. We did this to avoid giving

more weight to areas with a high number of occurrences, a common scenario in occurrence records collected opportunistically as the ones we use here. In this step we removed 85.4% of the occurrences which resulted in a total of 4.5 million occurrences used in our niche analysis.

A common issue of terrestrial bioclimatic datasets is that the boundaries of the cells with information do not precisely match the landmass boundaries. The result of this mismatch is that not all environmental variables was not available for 3,273 of the raster cells with occurrences (0.8% of the total). As expected, the vast majority of these problematic cells were close to the shore. To address this issue, we calculated the average value of environmental variables within an 5km buffer of the centre of the cell where the variable was missing and used it to approximate the value of the variable in that cell. Using this procedure, we were able to fill environmental variables for 89.3% of the cells where they were missing. To fill the remaining 350 cells, we repeated the aforementioned procedure but instead using a 10km buffer. We removed from further analysis occurrences located within the 135 cells for which we were unable to fill environmental variables.

Next, we calculate the probability density function of the species distribution in environmental space. To determine the environmental space, we use the first two components from a principal component analysis of the 37 bioclimatic variables associated with the species occurrences. Specifically we use the `dudi.pca` function from the R package `ade4` 1.7.13 (Dray and Dufour 2007) and center and scale all bioclimatic variables to have a mean of 0 and a unit standard deviation. We then determine the position of species occurrences in the environmental space and estimate their bivariate probability density function. We use a kernel method to estimate this density and normalise it such that it ranges between zero and one. Specifically, to calculate the probability density function we use `ecospat.grid.clim.dyn` from the R package `ecospat` 3.0 (Broennimann, Di Cola, and Guisan 2018)

211 with a grid resolution of 200. We then determine the location in the environ-
212 mental space of the plant-pollinator communities using the function `suprow`
213 from `ade4`. The normalised density at that particular location corresponds
214 to our suitability metric, which we calculate using the R package `raster`
215 2.8.19 (Hijmans 2019). We use the kernel density method in the niche-factor
216 analysis (Broennimann et al. 2012) rather than the distance from the mode
217 (Hirzel et al. 2002), as it has been proposed earlier, as it has been shown to
218 reduce the procedure’s sensitivity to sampling effort and the resolution of
219 the environmental space.

220 We used a sensitivity analysis to determine the minimum number of occur-
221 rences that are necessary to have robust environmental suitability values
222 in our communities. For that we used the species with most occurrences
223 available, *Archilochus colubris*, and calculated the mean absolute error of the
224 suitability values obtained with one thousand subsamples from the 74,791
225 occurrences available from GBIF.

226 Data analysis

227 We then used a set of bayesian multilevel models to evaluate the impact of
228 environmental suitability on the number of partners a species has. Specifically,
229 we use the normalised degree of species as our response variable; this is, the
230 number of species it interacts with given the number of species in the opposite
231 guild (Martín González, Dalsgaard, and Olesen 2010). The normalised degree
232 was modelled using a logit link function, and a binomial distribution in which
233 the number of species interacts with is the number of successes, and the
234 number of species in the opposite guild is the number of trials. We are
235 aware that whether species interact or not is not a Bernoulli process as
236 species interactions are not strictly independent from each other. However,
237 a binomial distribution allows us to account for the differences in species
238 richness across communities indirectly. Importantly, however, results are

239 qualitatively similar when we model species degree directly using a Poisson
240 distribution and a logarithmic link function.

241 We evaluate four models to assess the relative importance of suitability. A
242 first model, our baseline model, included three population-level predictors
243 and two grouping levels, species and the community. The population-level
244 predictors in the baseline model, commonly called fixed effects, were the
245 habitat suitability, the species guild (plant or a pollinator), and its number of
246 known possible partners. We included the number of known possible partners
247 as a predictor in our models as it allows us to control for the environmental
248 effects on species co-occurrence. We calculate this metric by determining the
249 number of partners with which the species is known to interact in any other
250 community. Controlling for the number of potential partners makes our
251 model a particularly stringent test of our environmental stress hypotheses
252 because this variable could explain a large proportion of variance. Often the
253 potential and the actual number of partners is the same or very close to each
254 other, especially for rare species present only in a few communities. As we
255 were interested in understanding whether the effect of habitat suitability is
256 conditional on the species guild (plant or pollinator), we, therefore, included
257 guild and its interaction with suitability in the model.

258 We allowed the intercept of degree and slope of the suitability-degree rela-
259 tionship to vary among species. This approach allowed us to investigate two
260 questions. First, it allows us to inspect the extent to which suitability is a
261 population or a group level effect. Second, by investigating the correlation
262 between the intercept and the slope as a model parameter, it allowed us to
263 inspect the extent by which species with a small or large number of interac-
264 tions respond to increasing levels of environmental stress. To account for
265 unmeasured differences between communities, like sampling effort, sampling
266 method, or diversity, we also calculated an intercept for each community in
267 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. ??). 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. ??).

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.

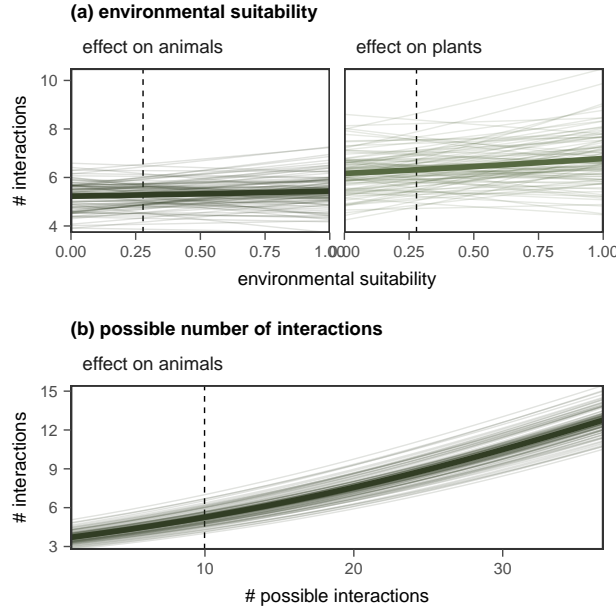


Figure 3: Conditional effects of predictors in our baseline model. The predicted values of the number of interacting species are based on a hypothetical community with 76 plants and 33 pollinators. These values correspond to the median number of species in each guild, respectively. In each panel, we 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.

295 Indeed, when looking at the population level effects, suitability has virtually
 296 no relationship with the normalised degree, neither for plants or pollinators
 297 (Figure 3b). However, suitability is an important predictor as the WAIC
 298 difference between our baseline model and that that did not include suitability
 299 was 581 ± 104 (Table 1). This apparent discrepancy can be explained by
 300 the variability of the suitability-degree relationship across species.

301 While for some species there is a strong negative relationship between
 302 suitability and normalised degree, for some others with a strong positive
 303 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 leave-one-out cross-validation information criterion (LOO). The standard error of the LOO difference provides rough guidance to the uncertainty of the model ranking. We also show the Wanatabe-Akaike information criterion (WAIC) of each model for comparison.

predictors	WAIC	SE
Suit. + Gen. + Pot. + Env.	6,149	140
unknown	6,156	137
Suit. + Gen. + Env.	7,652	273
Gen. + Pot. + Env.	6,730	190
unknown	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).

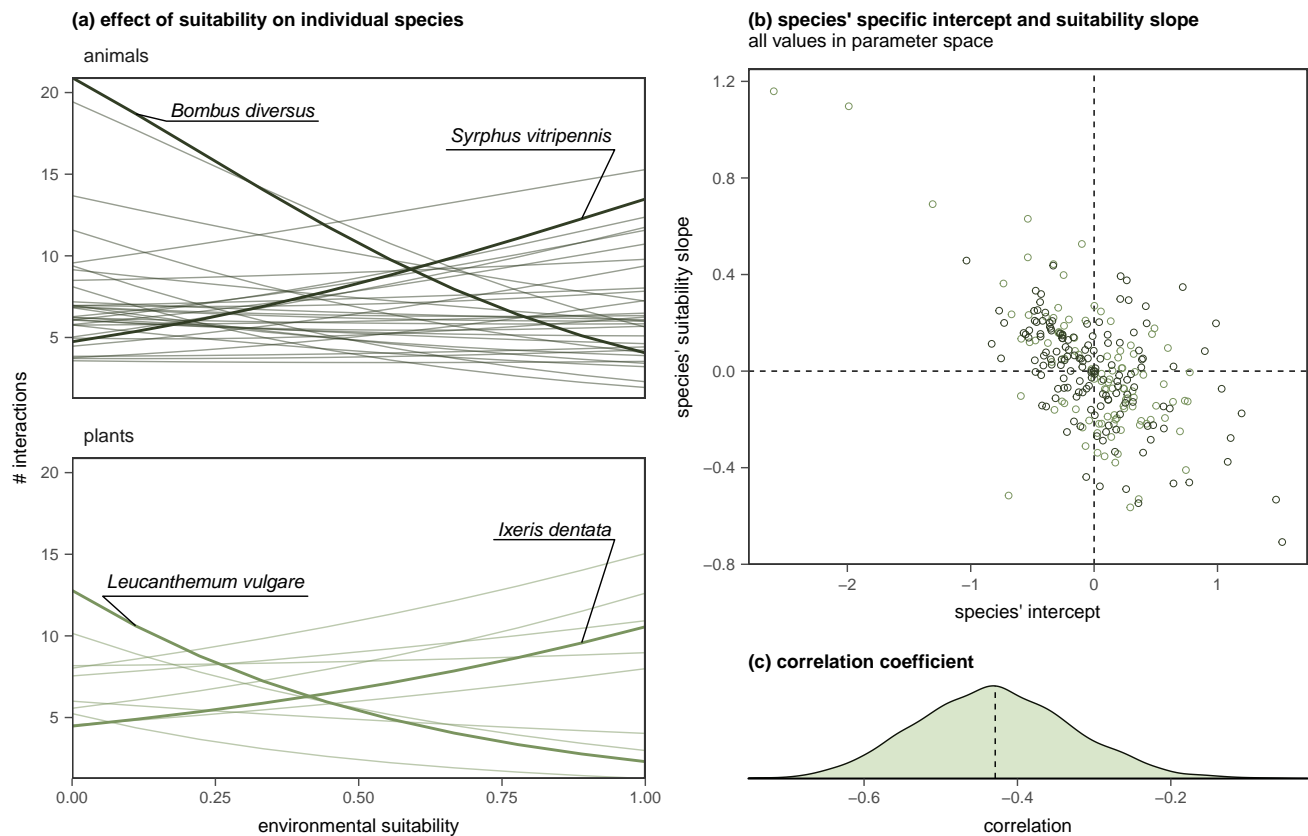


Figure 4: Species-level effects of suitability. (a) Conditional effect of suitability for individual species. To facilitate visualization we show only species for which there is suitability information in at least six communities (10 plants and 33 pollinators). As in the previous figure, fitted values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

324 Discussion

325 We set out to explore whether and how environmental stress can system-
326 atically affect species degree. After accounting for the pool of potential
327 partners, we found that indeed environmental conditions contribute to deter-
328 mining whether a species is a generalist or a specialist in their community.
329 However, we also found that the particular effect of the environment is
330 strongly dependent on the species. We proposed two alternative hypotheses
331 of how environmental stress may affect the degree, and we found evidence
332 for both of them. Species with a large number of partners in low-stress
333 communities were more likely to have a negative relationship and hence
334 reduce the number of partners as stress increases. Contrastingly, species in
335 our datasets with a small number of partners in low-stress communities were
336 more likely to have a larger number of partners in more stressful communities.
337 In summary, environmental stress pushes species that are flexible enough
338 to change their interaction partners towards intermediate levels of degree, a
339 so-called “regression towards the mean”.

340 Our results suggest that changes in community composition are indeed
341 the primary channel through which the environment determines changes
342 interaction probability. However, they also show that, for a large number
343 of species, the environment may also play a substantial role in determining
344 their realised (Eltonian) niche. While previous research has recognised that
345 environmental factors may help explain the changes in network structure
346 along environmental gradients that cannot be explained by community
347 composition (Tylianakis, Tschardtke, and Lewis 2007), how these two factors
348 were linked had been elusive so far (Gravel et al. 2018). We believe that part
349 of this difficulty could have arisen because species, and ultimately network
350 structure, can respond in multiple and contrasting, ways depending on the
351 particular bioclimatic variable examined (e.g. temperature or precipitation).
352 Using stress to summarise the effect on species of multiple environmental

353 gradients allowed us to detect a clear signal of the environment in species'
354 interaction patterns.

355 Although both niche and neutral processes are relevant at determining
356 species interactions, our model suggests that niche processes may be the
357 predominant mechanism through which the environment *systematically* affect
358 species degree. First, it is unlikely that environmental suitability correlates
359 to local species abundances (Pearce and Ferrier 2001; Sagarin, Gaines, and
360 Gaylord 2006). Second, even if there is a relationship between suitability and
361 abundances, a particular environmental gradient could have a positive effect
362 on the abundance of some species and a negative effect on others. Indeed,
363 we show that within a community there is a wide range of suitability values,
364 even for the relatively limited number of species we were able to include in
365 our analysis.

366 Recent research suggests that species are continuously changing their inter-
367 action partners wherever environmental conditions change in space or time
368 (Raimundo, Guimarães, and Evans 2018). So far it appears that this rewiring
369 is primarily driven by generalist species (Ponisio, Gaiarsa, and Kremen 2017;
370 Burkle, Marlin, and Knight 2013), presumably because generalist species
371 are less sensitive to trait matching of their interaction partners (CaraDonna
372 et al. 2017). Our results add two important nuances to these findings.
373 First, because generalists seem to focus on a smaller number of partners as
374 environmental conditions deteriorate, we show that trait matching might still
375 play a role in determining the interactions of generalist species. Second, we
376 demonstrate that rewiring is not exclusive to generalists. At least a fraction
377 of the species that appear to be specialist in their communities might be as
378 flexible, if not more, than generalist species, effectively behaving as faculta-
379 tive generalists in the face of environmental change. These flexible specialists
380 might, therefore, have a more significant role in network persistence than
381 previously expected.

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

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

409 The structural implications of the “regression towards the mean” that envi-
410 ronmental stress promotes are less clear. However, it is plausible to expect

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

418 In conclusion, we show that the environment can affect the realised niche of
419 plants and pollinators in systematic ways beyond community composition.
420 On the one hand, species that are inflexible with their interaction partners
421 are unlikely to persist under more stressful environmental conditions. On the
422 other, species that are flexible with their interactions partners experience a
423 regression towards intermediate levels of degree, where generalist species tend
424 to interact with fewer, presumably more effective, partners and specialist
425 tend to interact with more partners.

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