

Environmental stress affects niche breadth in plant-pollinator communities

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Running title: XX

Keywords: environmental effects, generalisation & specialisation, and
species interactions

Type of article: XX

Number of words: 151 in abstract; 4,182 in main text.

Number of displays: 4 figures; 1 tables; 0 text boxes.

Number of references: 86

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Data accessibility: Data supporting the results will be accessible in an
appropriate data repository after publication. We will include the DOI here.

Author contributions: XX

16 Abstract

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

31 Introduction

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

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

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

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

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

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

110 **Methods**

111 We retrieved plant-pollinator networks from the Web of Life database (For-
112 tuna, Ortega, and Bascompte 2014). This database contains datasets origi-
113 nating from 57 studies published in the primary literature between 1923 and
114 2016. Calculating the environmental stress of species in their community

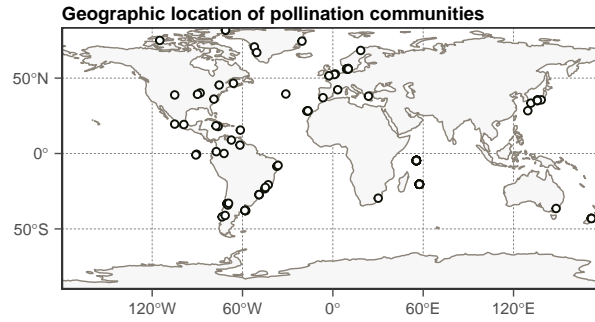


Figure 1: Worldwide distribution of pollination communities included in this study

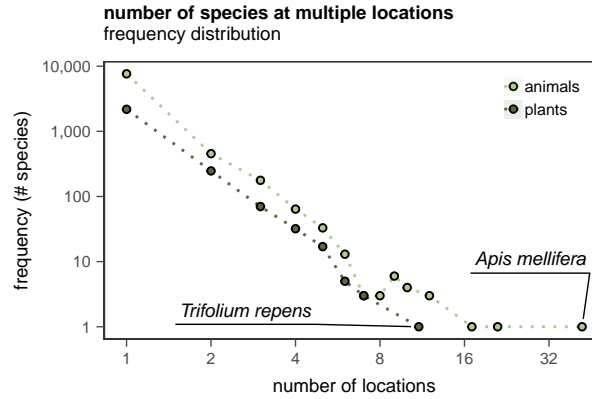


Figure 2: Frequency distribution of the number of locations in which a species is present. The most common pollinator species was *Apis mellifera*, which was sampled on 42 locations, while the most common plant species was *Trifolium repens*, which was sampled on 11 locations.

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

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

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

134 **Species suitability**

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

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

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

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

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

183 more weight to areas with a high number of occurrences, a common scenario
184 in occurrence records collected opportunistically as the ones we use here. In
185 this step we removed 85.4% of the occurrences which resulted in a total of
186 4.5 million occurrences used in our niche analysis.

187 A common issue of terrestrial bioclimatic datasets is that the boundaries of
188 the cells with information do not precisely match the landmass boundaries.
189 The result of this mismatch is that not all environmental variables was not
190 available for 3,273 of the raster cells with occurrences (0.8% of the total).
191 As expected, the vast majority of these problematic cells were close to the
192 shore. To address this issue, we calculated the average value of environmental
193 variables within an 5km buffer of the centre of the cell where the variable
194 was missing and used it to approximate the value of the variable in that
195 cell. Using this procedure, we were able to fill environmental variables for
196 89.3% of the cells where they were missing. To fill the remaining 350 cells, we
197 repeated the aforementioned procedure but instead using a 10km buffer. We
198 removed from further analysis occurrences located within the 135 cells for
199 which we were unable to fill environmental variables.

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

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

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

227 **Data analysis**

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

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

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

259 We allowed the intercept of degree and slope of the suitability-degree rela-
260 tionship to vary among species. This approach allowed us to investigate two
261 questions. First, it allows us to inspect the extent to which suitability is a
262 population or a group level effect. Second, by investigating the correlation
263 between the intercept and the slope as a model parameter, it allowed us to
264 inspect the extent by which species with a small or large number of interac-
265 tions respond to increasing levels of environmental stress. To account for
266 unmeasured differences between communities, like sampling effort, sampling
267 method, or diversity, we also calculated an intercept for each community in
268 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.

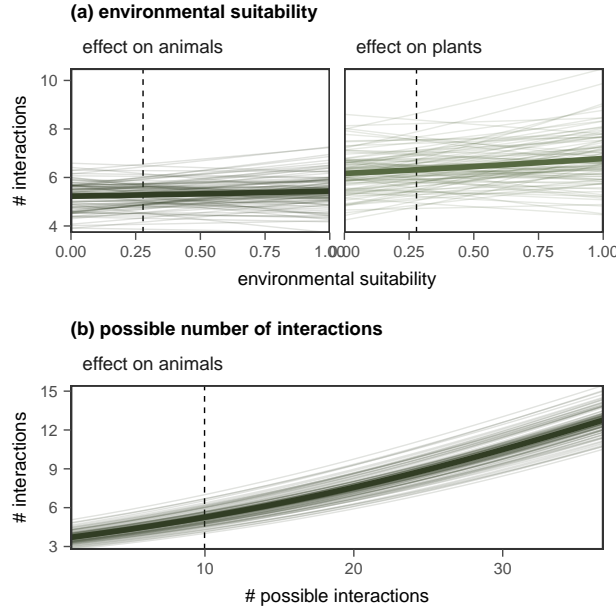


Figure 3: Conditional effects of predictors in our baseline model. The predicted values of the number of interacting species are based on a hypothetical community with 76 plants and 33 pollinators. These values correspond to the median number of species in each guild, respectively. In each panel, we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

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

302 While for some species there is a strong negative relationship between
 303 suitability and normalised degree, for some others with a strong positive
 304 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).

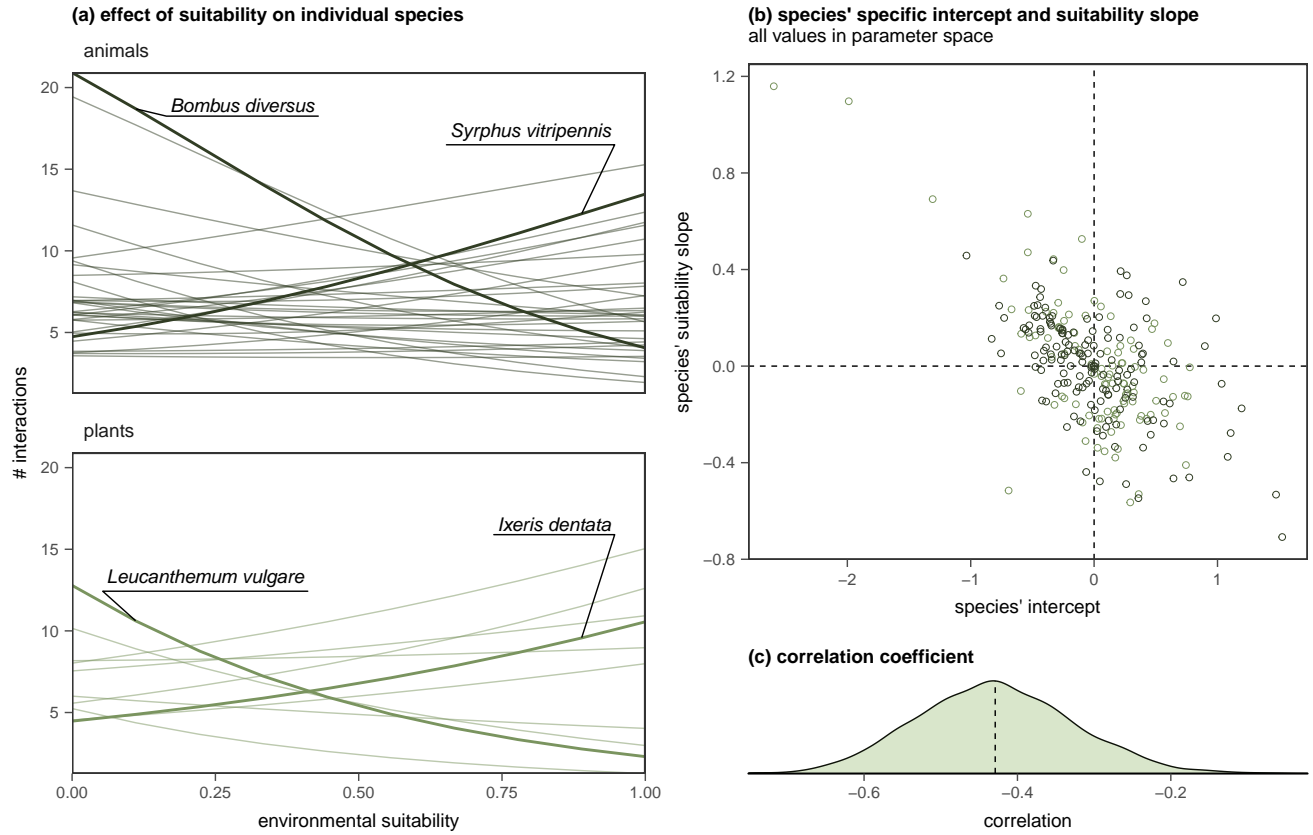


Figure 4: Species-level effects of suitability. (a) Conditional effect of suitability for individual species. To facilitate visualization we show only species for which there is suitability information in at least six communities (10 plants and 33 pollinators). As in the previous figure, fitted values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

325 Discussion

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

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

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

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

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

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

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

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

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

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

427 **Acknowledgements**

428 We thank Warwick Allen, Marilia Gaiarsa, and Guadalupe Peralta for
429 feedback and valuable discussions. EFC acknowledges the support from
430 the University of Canterbury Doctoral Scholarship and a New Zealand
431 International Doctoral Research Scholarship administered by New Zealand
432 Education. DBS and JMT acknowledge the support of Rutherford Discovery
433 Fellowships (RDF-13-UOC-003 and RDF-UOC-1002) and the Marsden Fund
434 Council (UOC-1705), administered by the Royal Society of New Zealand Te
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