

Environment affects specialisation of plants and pollinators

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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
20 number of partners a species interacts with has been elusive so far, presum-
21 ably, because environmental gradients appear to have contrasting effects
22 on species depending on the environmental variable. Here, we test for a
23 relationship between the stresses imposed by the environment, instead of
24 environmental gradients directly, and species specialisation using a global
25 dataset of plant-pollinator interactions. We found that the environment can
26 play a significant effect on specialisation, even when accounting for commu-
27 nity composition, likely by interacting with species' traits and evolutionary
28 history. Species that have a large number of interactions are more likely to
29 focus on a smaller number of, presumably higher-quality, interactions under
30 stressful environmental conditions. Contrastingly, the specialists present
31 in multiple locations are more likely to broaden their niche, presumably
32 engaging in opportunistic interactions to cope with increased environmental
33 stress. Indeed, many apparent specialist effectively behave as facultative gen-
34 eralists. Overall, many of the species we analysed are not inherently generalist
35 or specialist. Instead, species' level of specialisation should be considered on
36 a relative scale depending on where they are found and the environmental
37 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 species' specialisation.
45 Understanding how the environment drives the number of partners is crucial
46 because it underpins the species role in its community and shapes the
47 structure of the network of interactions. This structure, in turn, determines
48 ecosystem function and stability.

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

65 One possible explanation for the seemingly contradictory evidence is that

66 different bioclimatic factors (like temperature or precipitation) can have
 67 contrasting effects on species and their partners. Here we attempt to sim-
 68 plify this situation by reducing multiple factors into a single measure of
 69 environmental stress. Previous research suggests that environmental stress
 70 may affect the number of partners in different ways depending on its role
 71 in the community (for example its trophic guild) or even the species itself.
 72 Specifically, we propose two alternative hypotheses of how environmental
 73 stress may affect specialisation (Tylianakis and Morris 2017). On the one
 74 hand, it is possible that when species are under environmental stress, they
 75 might be “pressured” to focus on partners with which they are best adapted
 76 to interact. For instance, Hoiss et al. (2012) found increased phylogenetic
 77 clustering between plants and pollinators at higher altitudes; while Peralta et
 78 al. (2015) found that parasitoids in plantation forest, where environmental
 79 stress was higher than in native forests, were constrained to interact with
 80 hosts, they were best adapted to attack. Similarly, Lavandero and Tylianakis
 81 (2013) found that environmental stress due to higher temperature reduced
 82 the trophic niche breadth of parasitoids suggesting higher specialisation.

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. Higher
 85 environmental stress is likely to be reflected in greater energetic or repro-
 86 ductive costs. Therefore they might not be able to sustain encounter rates
 87 with their preferred partners at sufficient levels. In line with this hypothesis,
 88 Hoiss, Krauss, and Steffan-Dewenter (2015) found that the specialisation of
 89 plant-pollinator networks decreased both with elevation and after extreme
 90 drought events. Likewise, Pellissier et al. (2010) found a positive relationship
 91 between niche breadth and environmental stress: disk- or bowl-shaped blos-
 92 soms (which allow a large number of potential pollinator species to access
 93 pollen and nectar rewards) dominated at high altitude flower communities.

94 Here, we investigate whether and how environmental stress can systemati-

95 cally affect specialisation.

96 Our main aim is to test the two hypotheses mentioned above that relate envi-
 97 ronmental stress and species’ number of partners and investigate whether this
 98 changes across species or between trophic guilds. We propose that specialist
 99 species can become “facultative” generalists to reduce their vulnerability to
 100 the absence of preferred partners (for example, when variations in climate
 101 decouple phenologies; Benadi et al. 2014). In other words, we expect that,
 102 as environmental stress increases, specialists should be more likely to engage
 103 with more partners. Species with a large number of partners, on the other
 104 hand, should have a larger pool of available partners and might, therefore,
 105 be more likely to specialise under environmental stress and focus on the
 106 most beneficial partners. Importantly, when testing these hypotheses, we
 107 control for the potential effects of the environment in community composition
 108 (which has been previously shown to be a determinant factor; Gravel et al.
 109 2018) We test these hypotheses using data on plant-pollinator interactions.
 110 These interactions provide a particularly interesting system to test these
 111 hypotheses because, due to the multiple trade-offs involved in the pollination
 112 service, there are multiple intuitive ways in which we could imagine species
 113 respond to environmental stress given the available partners. We estimate
 114 the stress species might experience in their community by calculating the
 115 bioclimatic suitability of their communities given the species’ patterns of
 116 global occurrence.

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
 122 and their potential partners required us to reduce both the taxonomic and

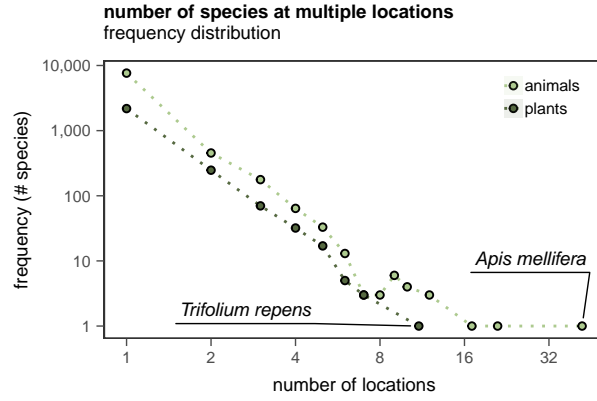


Figure 1: Frequency distribution of the number of locations in which a species is present. The most common pollinator species was *Apis mellifera*, which was sampled on 42 locations, while the most common plant species was *Trifolium repens*, which was sampled on 11 locations.

123 distributional/locational uncertainty. A critical step towards reducing this
 124 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). The cleaning process re-
 129 sulted on a total of 2,555 plants and 8,406 pollinator species distributed
 130 across 73 locations around the globe (Figure S1, 1).

131 After matching species across studies as accurate as possible, we carried on
 132 two more steps. First, we calculated the environmental stress of species in
 133 their communities. Second, we relate the species stress in their community
 134 with the number of partner species it has as a metric of their level of
 135 specialisation.

136 Environmental stress

137 Our third and final step was to relate the environmental suitability to the
 138 relative number of partners a species has in a community, as a proxy for
 139 Eltonian niche breadth. To explore this relationship within and across

140 species, we used a multilevel Bayesian model in which we controlled for the
141 potential effects of the environment on co-occurrence.

142 We assume that stress a species experience in a particular location is inversely
143 related to the suitability of the average environmental conditions in that
144 place. As we aim to compare specialisation levels for different levels of
145 environmental stress, we only calculate bioclimatic suitability for species
146 that were present in at least two communities. To calculate the bioclimatic
147 suitability of a species in a particular location, we used a niche-factor analysis
148 (Hirzel et al. 2002; Broennimann et al. 2012). This approach is based on
149 the probability density function of species distribution in an environmental
150 variable space. Habitats are characterised by a collection of environmental
151 variables. In a nutshell, those habitats in which the species occurs more
152 often are deemed to be more suitable for the species than habitats in which
153 the species has never been observed. As bioclimatic suitability is calculated
154 in a scale from zero to one following the niche-factor analysis, for simplicity,
155 we define environmental stress as one minus suitability.

156 The niche factor analysis requires two critical pieces of information. First,
157 we require information about the occurrences of the species of interest.
158 Second, we require information about the environmental conditions for
159 all the locations in which the species occurs. We retrieved 38.1 million
160 occurrences from the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org>). Issues with data quality are a central issue hampering
161 the use of publicly available species occurrence GBIF data in ecology and
162 biogeography (Jetz et al. 2019). We, therefore, followed a series of filters and
163 geographic heuristics to correct or remove erroneous and imprecise referencing
164 records (see supplementary methods; Zizka et al. 2019) which allowed us
165 to identify and remove 7.5 million potentially problematic occurrences from
166 further analysis. We integrated the occurrences from our plant-pollinator
167 communities to the cleaned occurrences retrieved from GBIF.
168

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

181 After obtaining information about species occurrence and the environment,
182 we then merged these two datasets such that a vector with details of our
183 37 bioclimatic and topographic variables characterised the location of each
184 occurrence. Sets of occurrence data tend to be spatially aggregated due to
185 sample bias (tendency to collect close to cities, certain countries). More-
186 over, spatial autocorrelation arises in ecological data because geographically
187 clumped records tend to be more similar in physical characteristics and/or
188 species abundances than do pairs of locations that are farther apart. To
189 account for such spatial dependency in occurrence data, we only included
190 one occurrence record if a species had more than one within a cell of the
191 bioclimatic raster. We did this to avoid giving more weight to areas with
192 a high number of occurrences, a common scenario in occurrence records
193 collected opportunistically as the ones we use here. In this step we removed
194 85.4% of the occurrences which resulted in a total of 4.5 million occurrences
195 used in our niche analysis.

196 A common issue of terrestrial bioclimatic datasets is that the boundaries of
197 the cells with information do not precisely match the landmass boundaries.

198 The result of this mismatch is that not all environmental variables were
 199 available for 3,273 of the raster cells with occurrences (0.8% of the total).
 200 As expected, the vast majority of these problematic cells were close to the
 201 shore. To address this issue, we calculated the average value of environmental
 202 variables within an 5km buffer of the centre of the cell where the variable
 203 was missing and used it to approximate the value of the variable in that cell.
 204 Using this procedure, we were able to fill environmental variables for 89.3%
 205 of the cells where they were missing. To fill the remaining 350 cells, we
 206 repeated the aforementioned procedure but instead using a 10km buffer. We
 207 removed from further analysis occurrences located within the 135 cells for
 208 which we were unable to fill environmental variables (0.0313% of the total).
 209 Next, we calculate the probability density function of the species distribution
 210 in environmental space. To determine the environmental space, we use
 211 the first two components from a principal component analysis of the 37
 212 bioclimatic variables associated with the species occurrences. Specifically we
 213 use the `dudi.pca` function from the R package `ade4` 1.7.13 (Dray and Dufour
 214 2007) and center and scale all bioclimatic variables to have a mean of zero
 215 and a unit variance. We then determine the position of species occurrences
 216 in the environmental space and estimate their bivariate probability density
 217 function. We use a kernel method to estimate this density and normalise
 218 it such that it ranges between zero and one. Specifically, to calculate the
 219 probability density function we use `ecospat.grid.clim.dyn` from the R
 220 package `ecospat` 3.0 (Broennimann, Di Cola, and Guisan 2018) with a grid
 221 resolution of 200. We then determine the location in the environmental space
 222 of the plant-pollinator communities using the function `suprow` from `ade4`.
 223 The normalised density at that particular location (which we calculate using
 224 the R package `raster` 2.8.19; Hijmans 2019) corresponds the bioclimatic
 225 suitability. We use the kernel density method in the niche-factor analysis
 226 (Broennimann et al. 2012) rather than the distance from the mode (Hirzel

et al. 2002), as it has been proposed earlier because it has been shown to reduce the procedure’s sensitivity to sampling effort and the resolution of the environmental space. The result of all these steps is the environmental stress which corresponds to one minus the bioclimatic suitability for a species of a particular location.

We used a sensitivity analysis to determine the minimum number of occurrences that are necessary to have robust environmental stress estimations. For that we used the species with most occurrences available, *Archilochus colubris*, and calculated the mean absolute error of the bioclimatic suitability values obtained with one thousand subsamples from the 74,791 occurrences available from GBIF.

Data analysis

We then used a set of Bayesian multilevel models to evaluate the impact of environmental stress on species specialisation. Specifically, we use the normalised degree of species as our response variable; that is, the number of species it interacts with given the number of species in the opposite guild (Martín González, Dalsgaard, and Olesen 2010). The normalised degree was modelled using a logit link function, and a binomial distribution in which the number of partner species a focal interacts with is the number of successes, and the number of species in the opposite guild is the number of trials. We are aware that whether species interact or not is not a Bernoulli process as species interactions are not strictly independent from each other. However, the use of a binomial distribution allows us to account for the differences in species richness across communities indirectly. Importantly, results are qualitatively similar when we model species degree directly using a Poisson distribution and a logarithmic link function.

We evaluated four models to assess the relative importance of suitability.

254 A first model, our baseline model, included five variables. The predictors
255 in the baseline model were the environmental stress, its number of known
256 possible partners in the community, and both the species guild (plant or a
257 pollinator) and its interaction with environmental stress. We included the
258 number of known possible partners as a predictor in our models as it allows
259 us to control for the effects of the environment on community composition,
260 effectively accounting for species co-occurrence. We calculate this metric
261 by determining the number of partners with which the species is known to
262 interact in any other community. Controlling for the number of potential
263 partners makes our model a particularly stringent test of our environmental-
264 stress hypotheses because this variable could explain a large proportion of
265 variance. Often, the potential and the actual number of partners is the same
266 or very close to each other, especially for rare species present only in a few
267 communities.

268 We allowed the intercept and slope of the stress-specialisation relationship to
269 vary among species. This approach allowed us to investigate two questions.
270 First, it allows us to inspect the extent to which environmental stress affects
271 species similarly. Second, by investigating the correlation between the inter-
272 cept and the slope as a model parameter, it allowed us to inspect the extent
273 by which species with a small or large number of partner species respond
274 to increasing levels of environmental stress. To account for unmeasured
275 differences between communities, like sampling effort, sampling method,
276 or diversity, we also allowed the model intercept to be different for each
277 community in our study. To facilitate model interpretation and convergence,
278 we scaled all continuous variables to have a mean of zero and a unit variance.

279 We compared this baseline model with three alternative models in which
280 we removed one predictor at a time. To quantify the difference between
281 models, in terms of their expected out-of-sample performance, we use the
282 Wanatabe-Akaike information criterion (WAIC). All models were fitted under

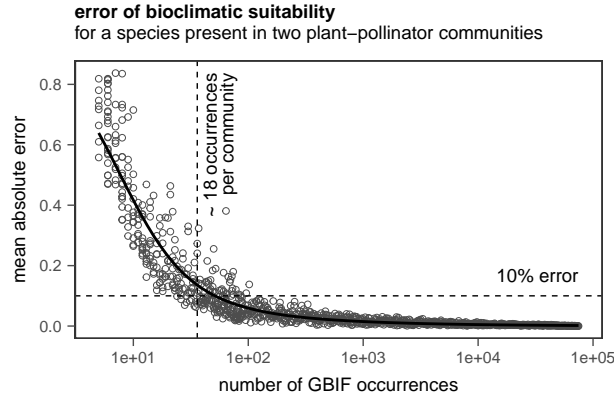


Figure 2: Sensitivity analysis of environmental stress error. The number of independent occurrences retrieved from GBIF is inversely related to the error of bioclimatic suitability for our plant-pollinator networks. The sensitivity analysis was performed by subsampling occurrences of *Archilochus colubris* the species in our dataset with the largest number of occurrences in GBIF, which was recorded in two of our communities.

283 a Bayesian framework using the R package `brms` 2.8.0 (Bürkner 2017, 2018)
 284 as an interface for Stan (Carpenter et al. 2017). For each model, we used
 285 four Markov chains of 4,000 iterations each; we used half of the iterations
 286 for warmup. We used weakly informative priors for all model parameters.
 287 Specifically we used normal priors of mean zero and standard deviation ten
 288 for the population-level effects and the intercepts, a half-Cauchy prior with
 289 a location of zero and a scale of two for the standard deviations, and, when
 290 applicable, an LKJ-correlation prior with parameter $\zeta = 1$ for the correlation
 291 matrix between group-level parameters.

292 Results

293 After performing our sensitivity analysis, we found that, for a species, we
 294 need roughly 18 independent occurrences for each community for which we
 295 aim to estimate the environmental stress. This is the number of occurrences
 296 necessary to maintain the mean absolute error of bioclimatic suitability below
 297 0.1 (Fig. 2). We therefore removed from further analyses species for which
 298 we did not have enough occurrences to obtain robust estimates.

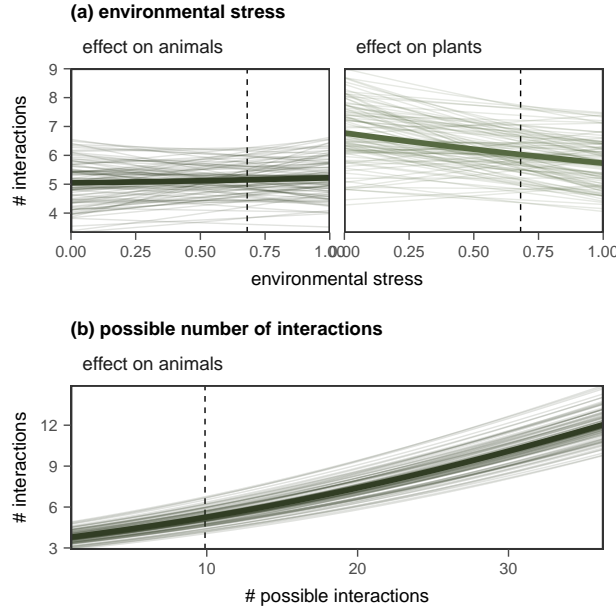


Figure 3: Conditional effects of predictors in our baseline model. The shown values are based on predictions for a hypothetical community with 76 plants and 33 pollinators. These values correspond to the median number of species in each guild across communities. In each panel, we condition on the mean value of the other predictor 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, 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 the guild and the number of possible interactions, we only show the conditional effect of pollinators.

299 Our models performed relatively well. The Bayesian R^2 for our baseline model
300 was 0.89, which indicates our models were able to capture a large proportion
301 of the variability on the data. Overall, we found that environmental stress
302 does not have a consistent effect across species. Indeed, when looking at the
303 fixed effects, stress has virtually no relationship with the normalised degree—
304 our metric of specialisation (Figure 3a). However, environmental stress was
305 still an important predictor in our model. The difference in WAIC between
306 our baseline model and the model that did not include environmental stress
307 was 489 ± 94 (Table 1). This apparent discrepancy can be explained by the
308 variability of the specialisation-stress relationship across species.

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.	6,592	170
Suit. + Pot.	6,595	166
Guild + Pot.	7,081	202
Suit. * Guild	8,041	290

For some species, there is a strong negative relationship between stress and specialisation, while for others, there is a strong positive relationship (Figure 4a). Interestingly, the slope of this relationship correlates with the species' intercept in the model (Figure 4b and c). Recall that the model estimates the intercept at the mean value for stress across communities (0.68). The mean correlation coefficient was 0.52 [0.33, 0.67]. Therefore, the slope of the stress-specialisation relationship was more likely to be positive for species with a large number of partners under average stress conditions (and negative for species with a smaller number of partners). Extrapolating to no-stress conditions: species that would interact with a small number of partners under no stress are more likely to interact with more partners as stress increases, whereas those that would interact with a large number of partners are more likely to interact with less.

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 also 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—this is, community composition—accounts for a large proportion of the variability in species degree. Importantly, our findings relating to the variability of the stress-specialisation relationship were qualitatively unchanged, whether we included this variable or not.

The standard deviation (in the parameters scale) of the community intercepts was 1.02 [0.85, 1.23] which indicates the importance of the local context when

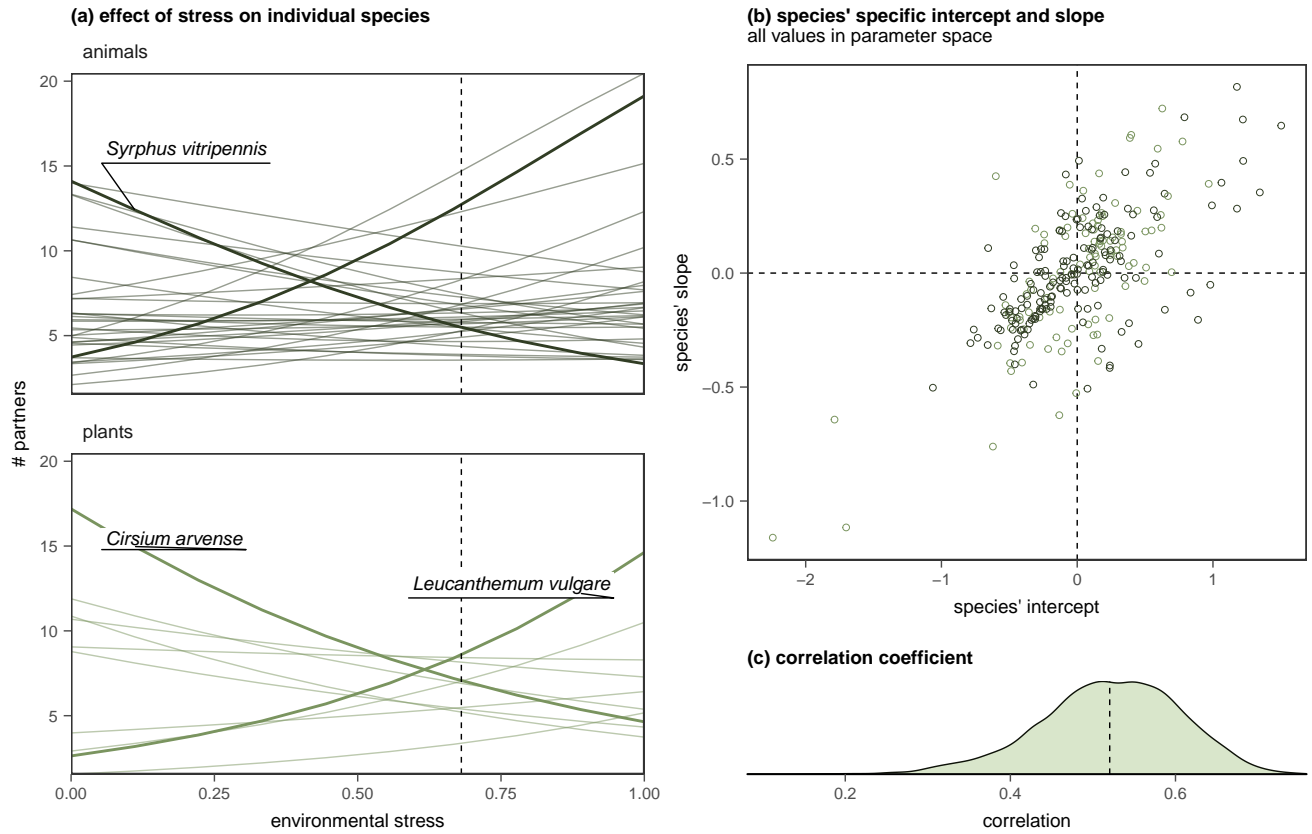


Figure 4: Species-level effects of environmental stress (a) Conditional effect of stress for individual species. Each line corresponds to the median relationship for each species. Although we included in the analysis of all species that are present in two or core communities, to facilitate visualisation here, 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 and c) The correlation between the species' intercept and the species' slope of suitability was negative. The species' intercept can be interpreted as the relative difference between the number of partners a species has under mean levels of environmental stress and the mean number of partners across all species. Positive values of species' slope indicate a positive relationship between stress and the number of partners and vice-versa.

determining specialisation. The standard deviation of the species intercept was 0.54 [0.48, 0.61], and that of the species' suitability slope was 0.38 [0.32, 0.44] (95% credible intervals shown within square brackets).

Discussion

We set out to explore whether and how environmental stress can systematically affect specialisation. After accounting for the pool of potential partners, we found that environmental conditions contribute to determining whether a species is a generalist or a specialist *in their community*. We also found that the particular effect of the environment is strongly dependent on the species. Based on existing literature, we proposed two alternative hypotheses of how environmental stress may affect species' specialisation, and we found evidence for both of them. Species with a large number of partners in low-stress communities were more likely to have a negative relationship and hence reduce the number of partners as stress increases. Contrastingly, species in our datasets with a small number of partners in low-stress communities were more likely to have a larger number of partners in more stressful communities. In summary, environmental stress pushes species that are flexible enough to change their interaction partners towards intermediate levels of specialisation, a so-called "regression towards the mean".

Our results suggest that changes in community composition are indeed the primary channel through which the environment determines changes interaction probability. However, they also show that, for a large number of species, the environment may also play a substantial role in determining their level of specialisation. Previous research has recognised that environmental factors may help explain the changes in network structure along environmental gradients that cannot be explained by community composition (Tylianakis, Tschardtke, and Lewis 2007). However, how these two factors were linked

359 had been elusive so far (Gravel et al. 2018). We believe that part of this
360 difficulty could have arisen because species, and ultimately network structure,
361 can respond in multiple, and contrasting, ways depending on the particular
362 bioclimatic variable examined (e.g. temperature or precipitation). Using
363 stress to summarise the effect on species of multiple environmental gradients
364 allowed us to detect a clear signal of the environment in species' interaction
365 patterns.

366 Although both niche and neutral processes are relevant in determining species
367 interactions, our model suggests that niche processes may be the predominant
368 mechanism through which the environment *systematically* affects specialisa-
369 tion. First, it is unlikely that environmental stress correlates to local species
370 abundances (Pearce and Ferrier 2001; Sagarin, Gaines, and Gaylord 2006).
371 Second, even if there is a relationship between stress and abundances, a par-
372 ticular environmental gradient could have a positive effect on the abundance
373 of some species and a negative effect on others. Indeed, we find that within
374 a community there is a wide range of stress values, even for the relatively
375 limited number of species we were able to include in our analysis.

376 Recent research suggests that species are continuously changing their inter-
377 action partners wherever environmental conditions change in space or time
378 (Raimundo, Guimarães, and Evans 2018). So far it appears that this rewiring
379 is primarily driven by generalist species (Ponisio, Gaiarsa, and Kremen 2017;
380 Burkle, Marlin, and Knight 2013), presumably because generalist species are
381 less sensitive to trait matching of their interaction partners (CaraDonna et
382 al. 2017). Our results add two important nuances to these findings. First,
383 because “generalists” seem to focus on a smaller number of partners as
384 environmental conditions deteriorate, we show that trait matching might still
385 play a role in determining the interactions of generalist species. Second, and
386 most importantly, our results suggest that only a small proportion of species
387 are “true generalists” or “true specialists” this is, species that interact with

388 a large or small number of partners regardless of the environmental stress,
389 respectively. This pattern implies that rewiring is not exclusive of species
390 with a large number of partners. Instead, at least a fraction of the species
391 that appear to be specialist *in their communities* might be as flexible, if
392 not more, than those with a large number of partners, effectively behaving
393 as facultative generalists in the face of environmental change. These flex-
394 ible “specialists” might therefore have a more significant role in network
395 persistence than previously expected.

396 In our model, we can roughly divide species between true specialists, true
397 generalists, and flexible species. However, there is a fourth group that
398 remained invisible to our model but has important implications for network
399 persistence and stability. Species that can vary their interaction partners
400 flexibly and their role in the network are more likely to persist in their
401 community as environmental conditions vary (Gaiarsa, Kremen, and Ponisio
402 2019). We propose this fourth group is composed of true specialists that are
403 constrained to interact with partners of high trait-matching and therefore
404 were not likely to be found in more than one community. If species that are
405 not flexible are unlikely to persist over temporal or spatial environmental
406 gradients, we can expect specialised communities that are highly constrained
407 by trait-matching (like some plant-hummingbird networks; Vizentin-Bugoni,
408 Maruyama, and Sazima 2014; Maruyama et al. 2014) to be far more
409 vulnerable to increased climate change-induced environmental stress and
410 habitat degradation than communities where role and interaction flexibility
411 are more prevalent.

412 Similarly, if the patterns we see in our models have also played a role during
413 the evolutionary history of pollination communities, our results also help
414 explain why only a small fraction of plant-pollinator interactions show a
415 strong signature of deep co-evolutionary history (Hutchinson, Cagua, and
416 Stouffer 2017). The increases on the stress that species are predicted to

417 experience due to rapid environmental change might further erode the co-
418 evolutionary history of specialist species. Communities as a whole might be
419 in a trajectory of even more diffuse co-evolution. For specialist, at least, the
420 longer-term benefits of being able to interact with multiple partners might be
421 more important than the shorter-term benefits of interacting with partners
422 of high trait matching.

423 The structural implications of the “regression towards the mean” that envi-
424 ronmental stress promotes are less clear. However, it is plausible to expect
425 that nestedness, and therefore network stability, might be reduced in the
426 face of rapid environmental change. Determining exactly how the changes
427 in degree caused by environmental stress reflect on systematic changes in
428 network structure would be an interesting avenue of research. Answering
429 this question would require expanding our suitability analysis to all species
430 in the community and compare the degree distribution of networks along a
431 gradient of stress for the community as a whole.

432 In conclusion, we show that the environment can affect the specialisation level
433 of plants and pollinators in systematic ways beyond community composition.
434 Species that are inflexible with their interaction partners are unlikely to
435 persist under more stressful environmental conditions. However, we show
436 that many species are flexible in regards to their specialisation levels and
437 therefore are not inherently generalists or specialists. Instead, the species’
438 level of specialisation/generalisation should be considered on a relative scale
439 depending on where they are found and the environmental conditions at that
440 location.

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