

Exploring How Functional Traits Modulate Species Response to Topography in Baxian Mountain, North China

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1 **Exploring how functional traits modulate species response to**
2 **topography in Baxian Mountain, North China**

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16 **Abstract:**

17 The associations between functional traits and species response to environments
18 have aroused more and more ecologists' interest and can provide insights into
19 understanding and explaining how plants respond to the environment. Here, we
20 applied a hierarchical generalized linear model to quantifying the role of

21 functional traits in plants response to topography. Functional traits data, including
22 specific leaf area, maximum height, seed mass and stem wood density, together
23 with elevation, aspect and slope were used in the model. In our results, species
24 response to elevation and aspect were modulated by maximum height and seed
25 mass. Shorter-statured tree species had a more positive response than taller ones
26 to an increase in elevation. Compared to light-seeded trees, heavy-seeded trees
27 responded more positively to more southerly aspects where the soil was drier. In
28 this study, the roles of maximum height and seed mass in determining species
29 distribution along elevation and aspect gradients were highlighted respectively
30 where plants are confronted with low-temperature and soil moisture deficit
31 conditions. This work contributes to the understanding of how traits may be
32 associated with species responses along mesoscale environmental gradients.

33 **Keywords**

34 Functional traits, species distribution, trait-environment associations, hierarchical
35 generalized linear model, topography.

36 **Introduction**

37 Functional traits are associated with environmental conditions and can provide
38 insights into understanding and explaining how plants respond to environments.
39 A trait-environment association is a consistent and general pattern linking a
40 biological attribute and an environmental gradient without considering taxonomic
41 identity (Díaz, Cabido, & Casanoves, 1999). Trait-environment associations may

42 mean that only species with particular traits have the opportunity to become
43 abundant under certain environmental conditions. For instance, high-SLA
44 (specific leaf area) species that have fast growth rates and take up nutrients
45 quickly have an advantage in resource-rich environments (Ordoñez et al., 2009;
46 Westoby, Falster, Moles, Vesk, & Wright, 2002). In contrast, low-SLA species,
47 which have long-lived leaves and a low resource turnover rate, are more tolerant
48 of resource-poor conditions (Ordoñez et al., 2009; Westoby et al., 2002).

49 Species distribution models (SDMs) incorporating functional traits have been
50 used to identify and measure trait-environment associations (Brown et al., 2014;
51 Jamil, Ozinga, Kleyer, & ter Braak, 2013; Pollock, Morris, & Vesk, 2012). In
52 these “model-based” methods, traits are treated as covariates rather than the
53 response as in “community-weighted mean” methods (Funk et al., 2017; Lavorel
54 et al., 2008; Ricotta & Moretti, 2011). Additionally, the coherent hierarchical
55 framework of statistical models can facilitate simpler interpretation than complex,
56 multistep analysis in “weighted-correlation” methods such as fourth-corner
57 analyses (Peres-Neto, Dray, & ter Braak, 2017) and RLQ ordination (Choler,
58 2005). Moreover, comparison studies have also shown that “model-based”
59 methods were more reliable than “community-weighted mean” and “weighted-
60 correlation” methods (Jamil et al., 2013; Miller, Damschen, & Ives, 2019).

61 Plant species distributions are associated with topography at various scales,
62 although the effect is indirect (Elith & Leathwick, 2009; Moeslund, Arge, Bøcher,
63 Dalgaard, & Svenning, 2013). Topography, including elevation, aspect and slope,

64 controls microclimate patterns, such as soil moisture and micro-temperature,
65 which then influence species distributions (Elith & Leathwick, 2009; Moeslund
66 et al., 2013). For example, soil moisture and micro-temperature vary from south-
67 facing slopes to north-facing slopes (Burnett, Meyer, & McFadden, 2008; Hais,
68 Chytrý, & Horsák, 2016; Holden & Jolly, 2011), from high altitudes to low
69 altitudes, as well as from steep slopes to flat slopes (Dyer, 2009). Many studies
70 have presented the patterns of species response to topography (Lan, Hu, Cao, &
71 Zhu, 2011; PUNCHI-MANAGE et al., 2013; Rubino & McCarthy, 2003; Sefidi,
72 Esfandiary Darabad, & Azaryan, 2016). However, details of how plant traits
73 modulate plant responses to topography are unknown, and the mechanisms
74 behind them could provide a way to understand how topography influences plant
75 distribution.

76 Here, we applied a model-based method to data on species traits and occurrences,
77 and topography from a broadleaved deciduous forest in North China, to explore
78 the role of functional traits in plant distribution along topographic gradients. We
79 addressed this issue by asking how the response of species to topography is
80 modulated by traits? To do so, we selected three basic topographic variables
81 (elevation, aspect and slope), and five traits across 31 woody species, including
82 their specific leaf area (SLA), seed mass (SM), stem wood density (SD) and
83 maximum height (MH). These traits represent the leading dimensions of plant
84 ecological strategic variation (Díaz et al., 2016; Westoby, 1998; Westoby et al.,
85 2002), and influence species performance under different environmental

86 conditions (Díaz et al., 1999; Ordoñez et al., 2009; Pollock et al., 2012; Westoby
87 et al., 2002). In addition, to help us understand the associations between
88 topographic features and functional traits further, we also fitted a model with
89 microclimatic data that estimated by microclimate modelling, while the
90 microclimatic variable we picked here are much relevant to topology since those
91 topographic variables were our main focus.

92 **Results**

93 As explained above, we generated 10 species occurrence datasets to fit the
94 topographic model, according to the Moran's I results, there are no spatial
95 autocorrelations in the residuals of these 10 models ($p > 0.05$). Here we picked the
96 first one to present and discuss the results, and the averaged coefficient results
97 among these ten can be found Supplementary Fig. S1 online. The conditional R-
98 squared value of our picked model was 0.55, and the AUROC value across all
99 species was 0.87. According to AUPRC/prevalence, the performance of the
100 topographic model was 4.16 (ranging from 1.17 to 18.90 individually) times
101 better than a random classifier. The mean prevalence of 31 species on logit scale
102 was -2.23 ± 0.22 (Table 1), indicating that species with mean trait values have 7%
103 to 11% occurrence under the average environmental conditions. *Fraxinus*
104 *chinensis*, *Carpinus turczaninowii*, *Acer truncatum*, *Quercus aliena* and *Q.*
105 *mongolica* were the most prevalent species (Fig 2). Aspect had greater influence
106 on species occurrence than the other two topographic factors, and its effect was

107 also more consistent across species (Table 1). The results from 10 sample datasets
108 also indicated that (Supplementary Fig. S1 online). In contrast, the effect of
109 elevation on occurrences differed more widely from one species to another (Table
110 1).

111 Species responses to elevation had the highest observed level of trait modulation,
112 following by aspect and slope (Fig 3). Maximum height interacting with elevation
113 and seed mass interacting with aspect stood out from our topographic model
114 (Table 1). The results from 10 grid sample datasets also showed this trend
115 (Supplementary Fig. S1 online), although some coefficients varied across the
116 subsets. SLA and stem wood density were not significantly associated with the
117 response to aspect (Table 1, Supplementary Fig. S1 online).

118 Traits explained a larger part of the variation in species responses to elevation
119 than those to aspect and slope (Fig 3). According to the association's coefficient
120 (-0.32, SE=0.15), maximum height contributes the most in the explanation.
121 Moreover, short trees had a more positive response to elevation than those with
122 average height, and *vice versa* (Fig 4, top row fourth column). That is to say,
123 shorter-statured tree species were more common on high-altitude sites than the
124 low-altitude, while for taller-statured tree species, we could more easily find them
125 on the lower-altitude sites.

126 In addition, the association between seed mass and aspect also had a large and
127 significant coefficient (0.29, SE=0.10), so seed mass modulates the response to
128 aspect more than that to elevation and aspect. Furthermore, the association

129 between seed mass and aspect (Fig 4, the last row, the second column) indicated
130 that trees with heavy seed had a more positive response to aspect than those with
131 an average seed mass, and most trees with small seed responded to aspect
132 negatively. Thus, species with heavy seeds were more likely to be more common
133 on south-facing sites compared to north-facing slopes, while species with small
134 seeds were more likely to have the opposite response to aspect.

135 **Discussion**

136 In this study, functional traits, especially seed mass and maximum height,
137 appeared to mediate species response to topographic gradients. These findings are
138 important to reveal the role of traits in species distribution along with the
139 topographic change. Below we will discuss some of them in greater detail, with
140 limitations and suggestions of further research.

141 **Maximum height modulating species response to elevation**

142 Our results showed that shorter-statured tree species had more positive responses
143 to higher-altitude elevations than taller ones. Maximum height represented
144 several ecological strategies (Westoby, 2002). First of all, taller species have a
145 greater chance of getting light before their neighbors do (Westoby, 2002).
146 Sunshine to high mountains is less likely to be blocked by their surroundings so
147 that all plants there usually are exposed to adequate light. By contrast, plants at
148 lower altitude lose such topologic advantage and the weakness in height can
149 critically affect the chance of shorter-statured tree species reach the light, while

150 taller plants are more competitive here and distribute more. Second, growing
151 taller than its usual can be attained at the cost of the plant stem diameter growth,
152 and result in less mechanically and physiologically support to the crown (King,
153 1981; Mäkelä, 1986). However, the living condition at high mountains is usually
154 not such friendly to those thin stem plants. They are more likely to be broken by
155 strong winds or lightning strike, but those shorter and sturdy individuals are more
156 possible to survive.

157 In addition, the sink limitation hypothesis (Hoch et al., 2002; Körner, 1998) in
158 treeline formation studies may give us another perspective to understand this
159 phenomenon. Sink-limitation proposes a low-temperature restriction of tissue
160 formation at upmost stands. Specifically, cold temperatures at high elevation limit
161 the tissue formation in shoots and roots by increasing its concentration of non-
162 structural carbohydrates (NSC) (Körner, 1998; Hoch & Körner, 2009, 2012; Shi,
163 Körner, & Hoch, 2008). In other words, under cold temperature conditions,
164 instead of forming new tissue, more sugars produced in the Calvin cycle reactions
165 are directed into NSC. Studies showed that root growth was strongly and directly
166 restricted by the soil temperature when it was lower than 6 °C, because cell
167 elongation rates would be significantly reduced in that situation (Nagelmüller,
168 Hiltbrunner, & Körner, 2017). Moreover, shoot meristematic growth is slowed in
169 high elevation stands, probably because of decreasing air temperature
170 (Hendrickson, Ball, Wood, Chow, & Furbank, 2004; Körner & Hoch, 2006). To
171 understand it, we collected micro-environment data including near-surface

172 extreme cold hours via microclimate modelling and fit the trait-environment
173 model. The result showed that there was a significantly negative coefficient of
174 the association between maximum height and near-surface extreme cold hours
175 (Supplementary Table S2 online, Supplementary Fig. S3 online).

176 **Seed mass modulating species response to aspect**

177 According to our results, heavier-seeded trees responded more positively to more
178 southerly aspects than trees with lighter seeds. It can be explained by “seed mass
179 trades off seed number” (Muller-Landau, 2010). Large seeds have the advantage
180 in the tolerance of stress, while small seeds have the advantage in seed yield
181 (Muller-Landau, 2010; Westoby, 2002).

182 Differences in the heat received between south-facing and north-facing slopes
183 will cause the variation of water content in soil (Burnett et al., 2008; Hais et al.,
184 2016; Holden & Jolly, 2011). Generally, the soil on south-facing sides is drier
185 than that on north-facing sides in the northern hemisphere, and this trend had also
186 been illustrated in our study area (Supplementary Fig. S2 online). That’s to say,
187 trees on south-facing slopes may facing more drought stress in Baxian mountain.
188 The drier condition is a challenge to the plants with small seed, while larger seed
189 trees will be more possible to survive as they tend to perform better in seedling
190 growth when facing drought and other hazards, and it is most likely because
191 heavier seeds can produce larger seedlings (seedling-size effect) (Lloret,
192 Casanovas, & Peñuelas, 1999; Quero, Villar, Marañón, Zamora, & Poorter, 2007).
193 In our study, this trend was indicated by the negative coefficient of the interaction

194 between seed mass and soil moisture in the microclimatic data fitted model,
195 although not very certain (Supplementary Table S2 online, Supplementary Fig.
196 S3 online). It is consistent with most previous results regarding the relationship
197 between seed mass and soil moisture (Hallett et al., 2011; McFadden et al., 2019;
198 Moles & Westoby, 2004; Shipley et al., 2017).

199 In addition, plants on the north-facing slopes suffer less drought stress. Such less
200 survival stress benefits all local, while large seed plants produce less seeds than
201 the small-seed plants which would lead to a smaller population. As a result, small
202 seed plants flourish more than the big seed plants on the north-facing slopes.

203 **Limitations of this study**

204 Trees on the southerly sites are facing more drought stress than the northerly on
205 Baxian Mountain (Supplementary Fig. S2 online). Drought can lead to the xylem
206 cavitation of vascular plants (Willson & Jackson, 2006), and cavitation will
207 frequently occur when they are getting too little water, so that embolized conduits
208 will no longer be able to hold the sap, and the plants will die (Tyree & Sperry,
209 1989). Vascular plants of dry habitats are more likely to have more cavitation
210 resistance (higher hydraulic conductivity) than species living in wet conditions
211 (Peguero-Pina et al., 2011; Wubbels, 2010). In fact, hydraulic traits should be
212 more typical to represent the drought tolerance of vascular plants (Cavender-
213 Bares, Kitajima, & Bazzaz, 2004; Tyree & Sperry, 1989; Wubbels, 2010). We
214 recommend one easy-measured hydraulic trait, the xylem vulnerability to
215 embolism, either to stem or to leaf, to reflect that ability straightforwardly. It

216 represents the xylem pressure caused by cavitation when 50% of hydraulic
217 conductivity is lost (P_{50}) (Perez-Harguindeguy et al., 2016). Hydraulic traits have
218 rarely been incorporated into models (model-based methods) to explain how
219 functional traits modulating species response to environments, let alone the
220 response to soil moisture. The role of hydraulic traits in species response to
221 environments is worth considering more in the future.

222 Additionally, the trait data used in our study were collected from trait database,
223 the interspecific trait variation could be narrowed within a local landscape.
224 However, the species in our study cover a large range of families and genera, and
225 phylogeny contribute the most trait variations (Yang et al., 2019), and such fitted
226 model can still bring much inspiring results.

227 Our subsampling of large permanent plots was important for controlling bias in
228 the location and environmental conditions. Those subsamples introduced
229 variation into the estimated coefficients. We favor using the averages of these
230 models and acknowledge that future work might attend to how to describe the
231 estimates and their uncertainty in such subsampled models.

232 **Methods**

233 **Study area**

234 The species occurrence data, functional traits and environmental variables were
235 collected on Baxian Mountain National Nature Reserve (40.1836 N, 117.5464 E),
236 Northern China, at elevations between 200 and 1000 m. According to the Köppen

237 climate classification, it is within the hot summer continental climate regime
238 (Dwa) (Li, Lu, Yu, & Yang, 2018, Figure 2; Peel, Finlayson, & McMahon, 2007,
239 Figure 5). The annual average temperature is 12.9°C (<https://web.archive.org/>).
240 The warmest month is July, with an average temperature of 26.8°C, while the
241 coldest month is January, with an average temperature of -3.4°C. The annual
242 precipitation is 516 mm. The month with the highest precipitation on average is
243 July, reaching 150 mm, while the lowest month is January with an average of 3
244 mm. The reserve is a mostly deciduous broad-leaved forest, dominated by *Acer*,
245 *Quercus* and *Juglans* species.

246 **Species occurrence data collection**

247 We sampled three, one-hectare plot sets along topographic gradients, including
248 100, 10 m x 10 m plots (Fig 1) in each set. Moreover, we broadly located 69, 10
249 m x 10 m plots outside those three sets along topographic gradients (Fig 1). In
250 order to avoid the many plots from the three one-hectare plot sets inducing
251 significant spatial autocorrelation, we resampled from those sets by putting a 3 *
252 3 grid on each set, and randomly picking 3 plots in each grid cell, in the end
253 comprising 150 plots ($27 * 3 + 69 = 150$) for modelling. Moran's I was measured
254 to check if the dataset spatial autocorrelation was successfully limited (Gittleman,
255 & Kot, 1990). We repeated this sampling strategy 10 times yielding 10 datasets
256 for modelling. In each plot, we recorded the occurrence of every species, and here
257 we used the data from 31 moderately common woody species. Their scientific

258 names, and corresponding abbreviations used in figures are listed in
259 Supplementary Table S1 online.

260 **Functional trait data collection**

261 We followed the Leaf-Height-Seed (LHS) scheme (Westoby, 1998), and focused
262 on SLA reflecting the fast-slow continuum of leaf economics (Reich, Wright, &
263 Lusk, 2007), MH representing the responses to the balance of productivity and
264 disturbance (Westoby et al., 2002) and SM reflecting a tolerance-fecundity trade-
265 off (Leishman, Wright, Moles, & Westoby, 2000; Muller-Landau, 2010). In
266 addition, we also selected SD to denote the trade-off between growth and survival
267 in woody plants, as the fourth trait dimension (Díaz et al., 2016).

268 For 31 woody species, we collected their functional trait data including SLA
269 (fresh area / dry mass, $\text{cm}^2 \cdot \text{g}^{-1}$), SD (dry mass / fresh volume, $\text{mg} \cdot \text{mm}^{-3}$), seed
270 mass and maximum height from TRY (Kattge, et al., 2020), China plant trait
271 database (Wang, et al., 2018), Kew Seed Information database
272 (<https://data.kew.org/sid/>), the Scientific Database of China Plant Species (DCP)
273 (<http://db.kib.ac.cn/>) and some republished papers (Marchi, Tognetti, Minnocci,
274 Borghi & Sebastiani, 2008; Knapp, Wang, Clark, Pile, & Schlarbaum, 2014;
275 Chen, Wang, Baiketuerhan, Zhang, Zhao, & von Gadow, 2014).

276 All functional traits ranged widely among the species in this study. Species
277 ranged in SLA from $5.60 \text{ m}^2 \cdot \text{kg}^{-1}$ to $45.05 \text{ m}^2 \cdot \text{kg}^{-1}$. Seed mass ranged over nearly
278 four orders of magnitude, from 0.10 mg to 9259.00 mg. The tallest species had

279 an average height of 30 m, six times that of the shortest (5 m). The stem wood
280 density ranged least, from $0.35 \text{ g}\cdot\text{cm}^{-3}$ to $0.85 \text{ g}\cdot\text{cm}^{-3}$.

281 **Environmental variables**

282 Three topographic variables on Baxian mountain nature reserve were used:
283 elevation, aspect and slope. We acquired elevation data for each plot from a 30-
284 meter resolution digital elevation model (DEM) (Resource and Environment Data
285 Cloud Platform, <http://www.resdc.cn/Default.aspx>). From this DEM, we derived
286 slope and aspect in ArcGIS (version 10.2) for each plot. For aspect, we
287 transformed the variable to degrees of south-north orientation, from 0° (facing
288 north) to 180° (facing south). Values over 180° were converted by subtracting
289 360 and multiplying by -1.

290 **Data pre-processing**

291 Considering the distributions of our original covariate data were highly skewed,
292 all traits and environmental data except aspect were log-transformed. To interpret
293 the model coefficients more easily, we centered all traits and environmental data
294 and reduced the range by twice of the standard deviation (Gelman, 2008). In this
295 way, intercepts could be explained as overall prevalence given all the mean values
296 of environments and traits, and slope terms could be interpreted as partial
297 dependencies given that other variables have mean values.

298 **Trait-environment model**

299 The trait-environment model we used was a hierarchical generalized linear model,
300 or generalized linear mixed-effect model (GLMM). It was proposed by Pollock
301 et al. (2012) to represent the modulation by traits of the relationship between
302 species occurrence and environmental gradients. We added site identifier as a
303 random effect to account for non-independence (Jamil et al., 2013), and assumed:

$$\text{Logit}(p_{ij}) = \alpha + a_j + (\beta_1 + b_j)X_i + \beta_{12}Z_j X_i + c_i,$$
$$i = 1, 2, \dots, n, \quad j = 1, 2, \dots, m,$$

306 where p_{ij} is $Pr(y_{ij} = 1)$, referring to the probability of species j occurrence in site
307 i . X is a matrix of quantitative environmental data for n sites. Z is the trait matrix
308 for m species. α, β_1 and β_{12} are fixed effect terms. α gives the overall prevalence
309 of species across sites given the mean value of each trait for all species and the
310 mean value of each environmental variable for all sites. β_1 refers to the average
311 response to each environmental variable given average trait values for all species.
312 β_{12} denotes the trait-environment association, indicating how traits modulate
313 species response to environmental variables. a_j, b_j and c_i are the random effect
314 terms, where a_j and c_i respectively show the deviations in prevalence at species
315 and site levels. b_j describes the response of every species to each environmental
316 variable. Not fully following the model proposed by Jamil et al. (2013) and
317 recommended by Miller *et al.* (2019), in our study, functional traits have only
318 been incorporated into our model as “trait-environment” interactions rather than
319 fixed effect terms. It means functional traits influence species occurrence through

320 modulating their response to environments rather than influence their occurrence
321 directly.

322 We used *blme* (Chung, Rabe-Hesketh, Dorie, Gelman, & Liu, 2013) package to
323 fit our model in a Bayesian setting, which allowed us to specify a particular form
324 of weak prior to getting an approximate Bayesian maximum posterior estimation.
325 The prior distribution for the species covariance of random effects was an inverse
326 Wishart distribution with $df = 8$ and a 4×4 diagonal variance-covariance matrix,
327 and the variance was 2. The prior distribution for the site covariance of random
328 effects was an inverse gamma distribution with shape and scale parameters 0.5
329 and 100, respectively (default). The prior distribution for fixed effects was a
330 normal distribution with $\mu = 0$ and $sd = 1$. We evaluated model performance by
331 the area under the receiver operating characteristic curve (AUROC) and the area
332 under the Precision-Recall curve (AUPRC) since the input data of our model are
333 highly skewed (Boyd, Costa, Davis, & Page, 2012; Sofaer, Hoeting, & Jarnevich,
334 2019). AUROC and AUPRC were calculated using R package *PRROC* (Grau,
335 Grosse, & Keilwagen, 2015; Keilwagen, Grosse, & Grau, 2014). In addition, we
336 calculated the values of AUPRC/prevalence for each species, where prevalence
337 here is equal to AUPRC of a random classifier (Saito & Rehmsmeier, 2015), to
338 show how many times the model's prediction is better than a random classifier.
339 We fitted the model with four traits (Fig 2) of 31 species and three topographic
340 variables from 150 plots. Based on the 10 datasets from grid sampling process,
341 we built up 10 topographic models, and averaged the coefficients for each fixed

342 effect terms for visualization (Supplementary Fig. S1 online). Additionally, to
343 help us to understand the associations between topographic variables and
344 functional traits, we fitted this trait-environment model with microclimatic
345 variables predicted by microclimate modelling, which was considered directly
346 associated with plant occurrence underlying the effect of topography, and some
347 results from this model will be mentioned in the discussion part and the details
348 can be found in Supplementary methods (see Supplementary methods online for
349 more details).

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569

570

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578 **Authors' contributions**

579 LLT, WKM, PAV and FCS conceived and designed the study. LLT, MZ and FCS

580 undertook the fieldwork. LLT, WKM and PAV analyzed the data. LLT, WKM

581 and PAV wrote the manuscript; other authors provided editorial advice.

582 **Competing interests**

583 The authors declare no competing interests.

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590 **Figure legends**

591 Fig. 1 Baxian Mountain National Nature Reserve and plot sites. Three black
592 square boxes in the second map show the location of three plot sets, and each of
593 them has one hundred 10 m x 10 m plots. Those red dots in 100 plots set are
594 plots we sampled and picked.

595 Fig. 2 Effect of environmental variables on the occurrence of 31 species given
596 their traits. Species names were shortened following Supplementary Table S1
597 online.

598 Fig. 3 The explanatory power of traits for the response of species occurrences to
599 topographic variables. First, we calculated the variance of species responses to
600 environmental variables. The model's fixed effect coefficients caught all the
601 variance of species response to the environment. Then, from the model we built,
602 we extracted the residual standard deviation by eliminating the modulation from
603 traits. The difference among these two standard deviations was the variation
604 explained by traits, which was shown as the light grey area.

605 Fig. 4 The relationships between environmental responses and species traits at
606 species (points) and mean (line) levels. These partial dependence plots show the

607 estimated response given the trait, with all other traits and environmental
608 variables held at their means. The environmental variables were centered, so
609 species with values above zero have positive responses to environmental
610 variables. Species names were shortened following Supplementary Table S1
611 online. For a better illustration, the values of seed mass were log transformed.

612 **Tables**

613 Table 1 Summary of the fixed effects and random effects from our topographic model.

Fixed effect	Coefficient	SE	<i>p</i> -value
Intercept	-2.23	0.22	<0.001 ***
Elevation	0.27	0.19	0.14
Slope	-0.15	0.16	0.34
Aspect	0.34	0.16	0.03*
SLA: Elevation	0.13	0.13	0.31
SLA: Slope	0.07	0.09	0.39
SLA: Aspect	-0.02	0.09	0.76
SM: Elevation	-0.14	0.15	0.33
SM: Slope	0.18	0.10	0.07
SM: Aspect	0.29	0.10	0.004**
SD: Elevation	-0.08	0.15	0.61
SD: Slope	-0.12	0.10	0.22
SD: Aspect	0.04	0.11	0.68
MH: Elevation	-0.32	0.15	0.03*
MH: Slope	-0.06	0.10	0.58
MH: Aspect	-0.18	0.11	0.09
Random effect		SD	
Site (Intercept)		1.32	
Species (Intercept)		1.01	
Species (Elevation)		0.70	
Species (Slope)		0.40	
Species (Aspect)		0.42	

614

Figures

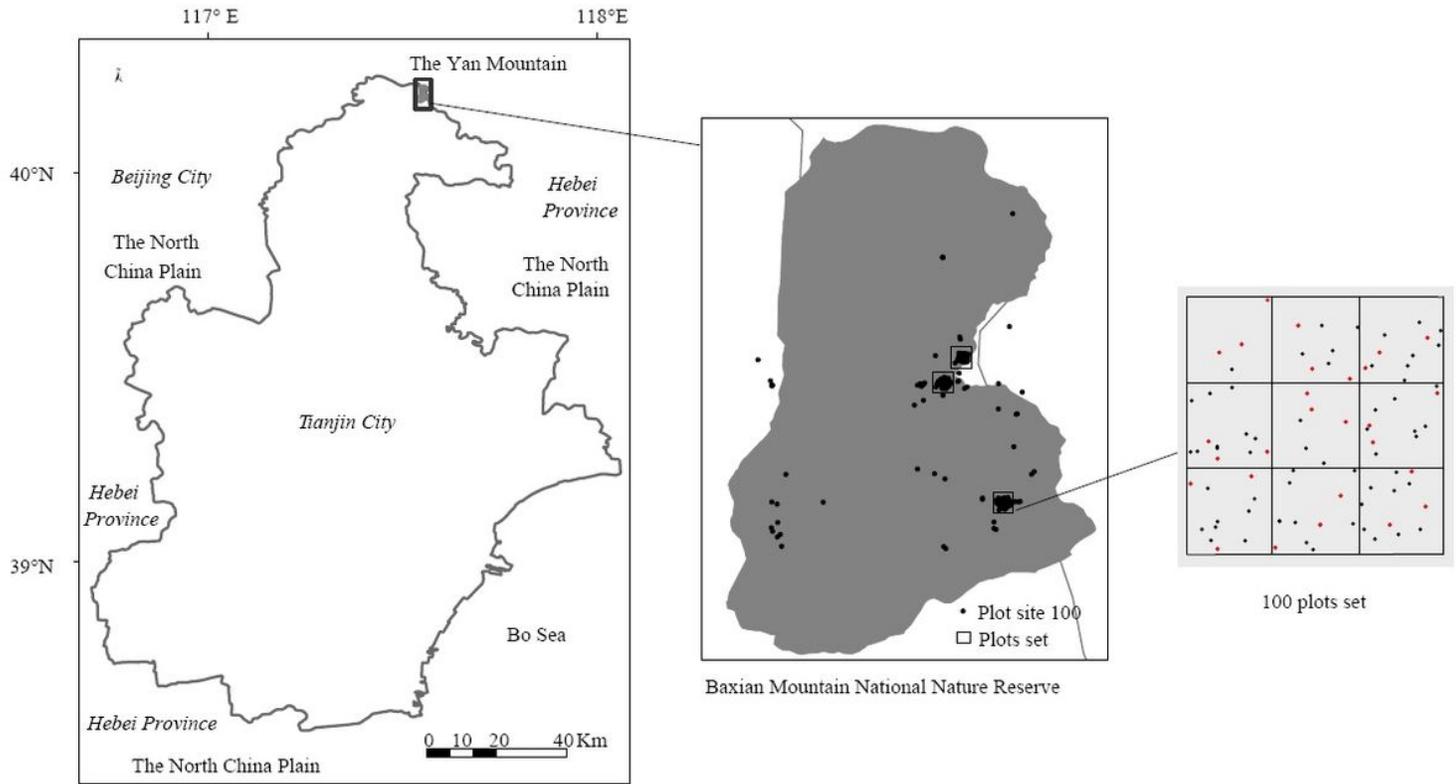


Fig. 1

Figure 1

Baxian Mountain National Nature Reserve and plot sites. Three black square boxes in the second map show the location of three plot sets, and each of them has one hundred 10 m x 10 m plots. Those red dots in 100 plots set are plots we sampled and picked.

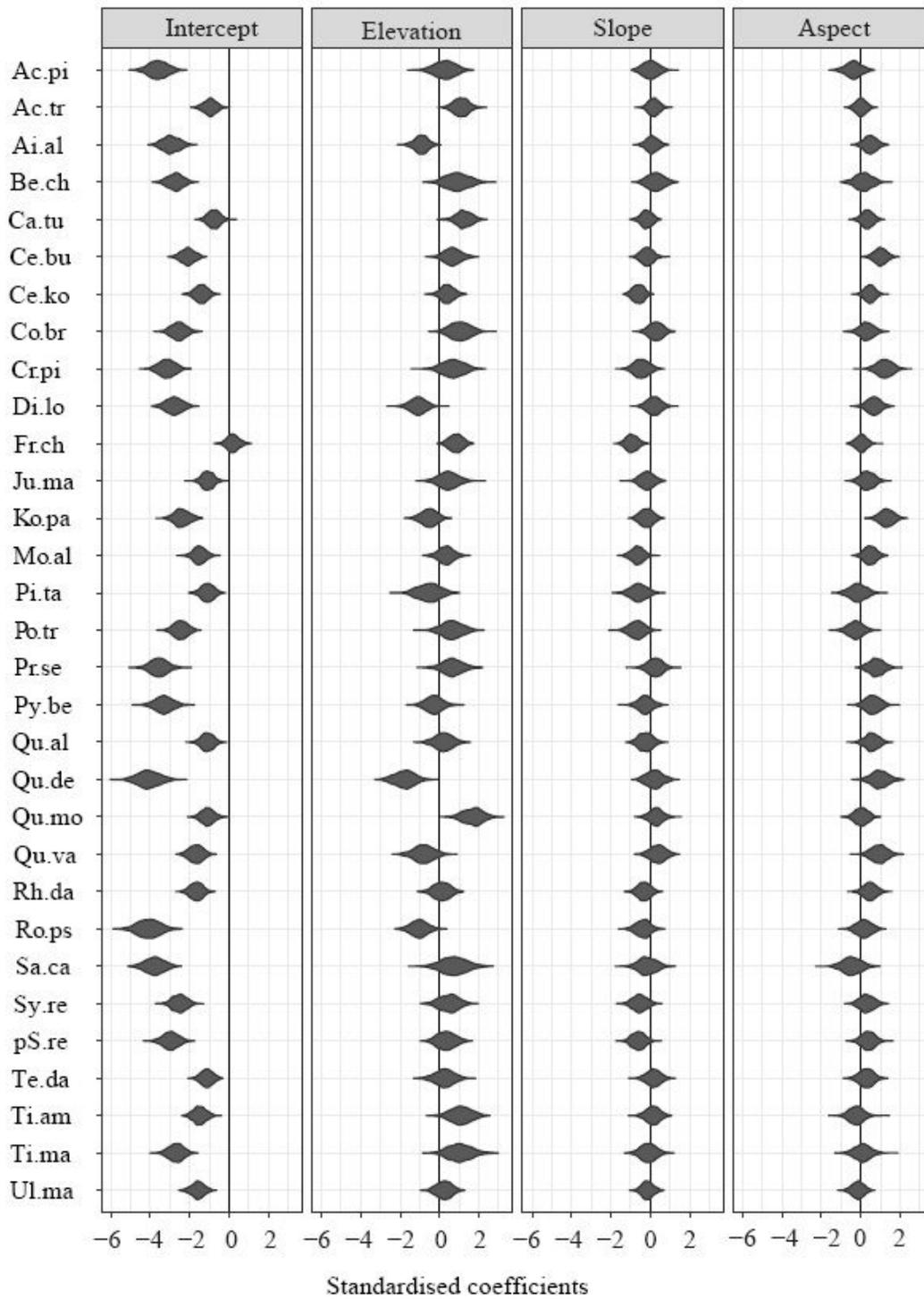


Fig. 2

Figure 2

Effect of environmental variables on the occurrence of 31 species given their traits. Species names were shortened following Supplementary Table S1 online.

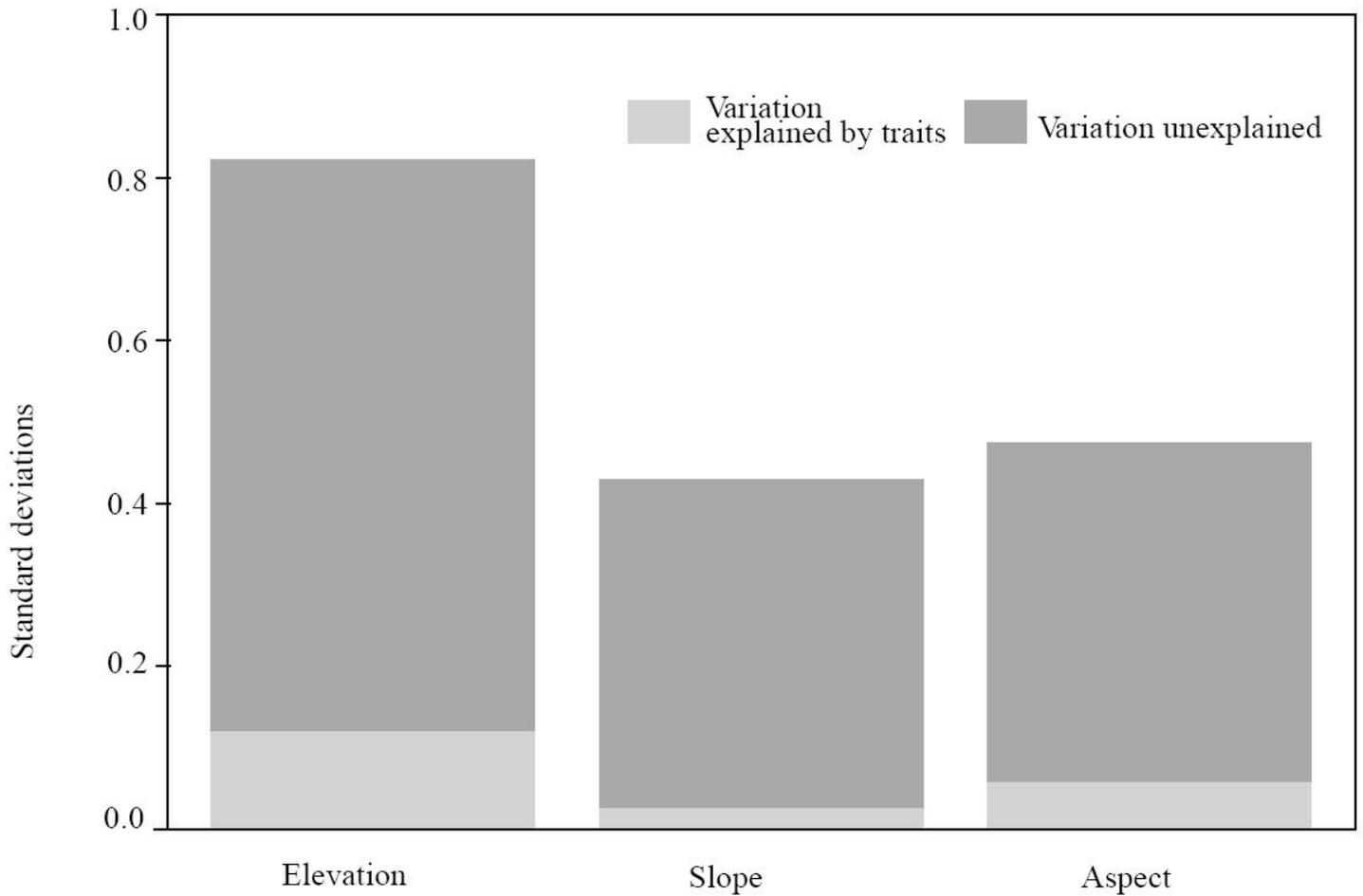


Fig. 3

Figure 3

The explanatory power of traits for the response of species occurrences to topographic variables. First, we calculated the variance of species responses to environmental variables. The model's fixed effect coefficients caught all the variance of species response to the environment. Then, from the model we built, we extracted the residual standard deviation by eliminating the modulation from traits. The difference among these two standard deviations was the variation explained by traits, which was shown as the light grey area.

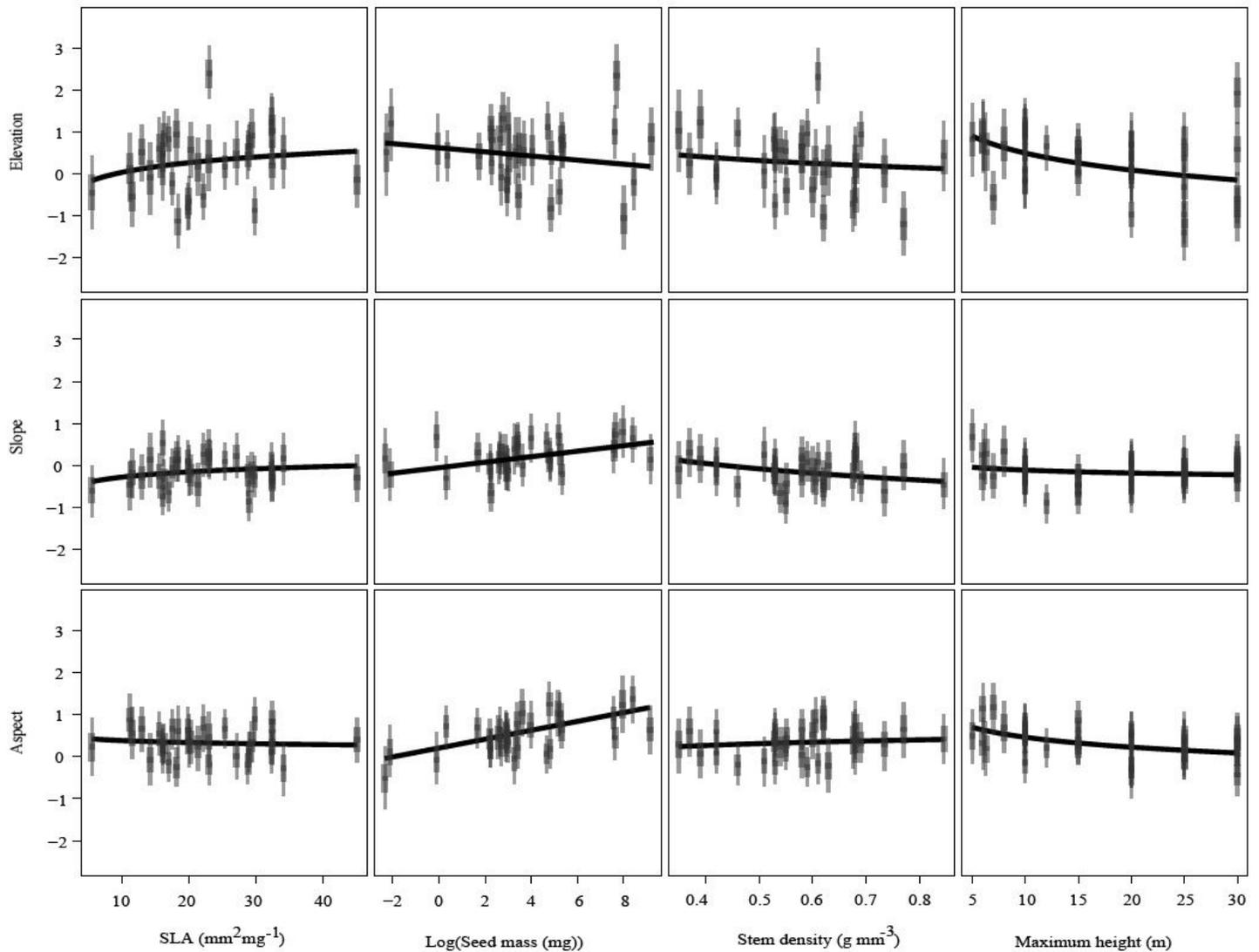


Fig. 4

Figure 4

The relationships between environmental responses and species traits at species (points) and mean (line) levels. These partial dependence plots show the estimated response given the trait, with all other traits and environmental variables held at their means. The environmental variables were centered, so species with values above zero have positive responses to environmental variables. Species names were shortened following Supplementary Table S1 online. For a better illustration, the values of seed mass were log transformed.

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