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

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

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Abstract:
The associations between functional traits and species response to environments have aroused more and more ecologists’ interest and can provide insights into understanding and explaining how plants respond to the environment. Here, we applied a hierarchical generalized linear model to quantifying the role of
functional traits in plants response to topography. Functional traits data, including specific leaf area, maximum height, seed mass and stem wood density, together with elevation, aspect and slope were used in the model. In our results, species response to elevation and aspect were modulated by maximum height and seed mass. Shorter-statured tree species had a more positive response than taller ones to an increase in elevation. Compared to light-seeded trees, heavy-seeded trees responded more positively to more southerly aspects where the soil was drier. In this study, the roles of maximum height and seed mass in determining species distribution along elevation and aspect gradients were highlighted respectively where plants are confronted with low-temperature and soil moisture deficit conditions. This work contributes to the understanding of how traits may be associated with species responses along mesoscale environmental gradients.

**Keywords**

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

**Introduction**

Functional traits are associated with environmental conditions and can provide insights into understanding and explaining how plants respond to environments. A trait-environment association is a consistent and general pattern linking a biological attribute and an environmental gradient without considering taxonomic identity (Díaz, Cabido, & Casanoves, 1999). Trait-environment associations may
mean that only species with particular traits have the opportunity to become
abundant under certain environmental conditions. For instance, high-SLA
(specific leaf area) species that have fast growth rates and take up nutrients
quickly have an advantage in resource-rich environments (Ordoñez et al., 2009;
Westoby, Falster, Moles, Vesk, & Wright, 2002). In contrast, low-SLA species,
which have long-lived leaves and a low resource turnover rate, are more tolerant
of resource-poor conditions (Ordoñez et al., 2009; Westoby et al., 2002).

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

Plant species distributions are associated with topography at various scales,
although the effect is indirect (Elith & Leathwick, 2009; Moeslund, Arge, Bøcher,
Dalgaard, & Svenning, 2013). Topography, including elevation, aspect and slope,
controls microclimate patterns, such as soil moisture and micro-temperature, which then influence species distributions (Elith & Leathwick, 2009; Moeslund et al., 2013). For example, soil moisture and micro-temperature vary from south-facing slopes to north-facing slopes (Burnett, Meyer, & McFadden, 2008; Hais, Chytrý, & Horsák, 2016; Holden & Jolly, 2011), from high altitudes to low altitudes, as well as from steep slopes to flat slopes (Dyer, 2009). Many studies have presented the patterns of species response to topography (Lan, Hu, Cao, & Zhu, 2011; Punchi-Manage et al., 2013; Rubino & McCarthy, 2003; Sefidi, Esfandiary Darabad, & Azaryan, 2016). However, details of how plant traits modulate plant responses to topography are unknown, and the mechanisms behind them could provide a way to understand how topography influences plant distribution.

Here, we applied a model-based method to data on species traits and occurrences, and topography from a broadleaved deciduous forest in North China, to explore the role of functional traits in plant distribution along topographic gradients. We addressed this issue by asking how the response of species to topography is modulated by traits? To do so, we selected three basic topographic variables (elevation, aspect and slope), and five traits across 31 woody species, including their specific leaf area (SLA), seed mass (SM), stem wood density (SD) and maximum height (MH). These traits represent the leading dimensions of plant ecological strategic variation (Díaz et al., 2016; Westoby, 1998; Westoby et al., 2002), and influence species performance under different environmental
conditions (Díaz et al., 1999; Ordoñez et al., 2009; Pollock et al., 2012; Westoby et al., 2002). In addition, to help us understand the associations between topographic features and functional traits further, we also fitted a model with microclimatic data that estimated by microclimate modelling, while the microclimatic variable we picked here are much relevant to topology since those topographic variables were our main focus.

**Results**

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

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

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

In addition, the association between seed mass and aspect also had a large and significant coefficient (0.29, SE=0.10), so seed mass modulates the response to aspect more than that to elevation and aspect. Furthermore, the association
between seed mass and aspect (Fig 4, the last row, the second column) indicated that trees with heavy seed had a more positive response to aspect than those with an average seed mass, and most trees with small seed responded to aspect negatively. Thus, species with heavy seeds were more likely to be more common on south-facing sites compared to north-facing slopes, while species with small seeds were more likely to have the opposite response to aspect.

**Discussion**

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

**Maximum height modulating species response to elevation**

Our results showed that shorter-statured tree species had more positive responses to higher-altitude elevations than taller ones. Maximum height represented several ecological strategies (Westoby, 2002). First of all, taller species have a greater chance of getting light before their neighbors do (Westoby, 2002). Sunshine to high mountains is less likely to be blocked by their surroundings so that all plants there usually are exposed to adequate light. By contrast, plants at lower altitude lose such topologic advantage and the weakness in height can critically affect the chance of shorter-statured tree species reach the light, while
taller plants are more competitive here and distribute more. Second, growing
taller than its usual can be attained at the cost of the plant stem diameter growth,
and result in less mechanically and physiologically support to the crown (King,
1981; Mäkelä, 1986). However, the living condition at high mountains is usually
not such friendly to those thin stem plants. They are more likely to be broken by
strong winds or lighting strike, but those shorter and sturdy individuals are more
possible to survive.

In addition, the sink limitation hypothesis (Hoch et al., 2002; Körner, 1998) in
treeline formation studies may give us another perspective to understand this
phenomenon. Sink-limitation proposes a low-temperature restriction of tissue
formation at upmost stands. Specifically, cold temperatures at high elevation limit
the tissue formation in shoots and roots by increasing its concentration of non-
structural carbohydrates (NSC) (Körner, 1998; Hoch & Körner, 2009, 2012; Shi,
Körner, & Hoch, 2008). In other words, under cold temperature conditions,
instead of forming new tissue, more sugars produced in the Calvin cycle reactions
are directed into NSC. Studies showed that root growth was strongly and directly
restricted by the soil temperature when it was lower than 6 °C, because cell
elongation rates would be significantly reduced in that situation (Nagelmüller,
Hiltbrunner, & Körner, 2017). Moreover, shoot meristematic growth is slowed in
high elevation stands, probably because of decreasing air temperature
(Hendrickson, Ball, Wood, Chow, & Furbank, 2004; Körner & Hoch, 2006). To
understand it, we collected micro-environment data including near-surface
extreme cold hours via microclimate modelling and fit the trait-environment model. The result showed that there was a significantly negative coefficient of the association between maximum height and near-surface extreme cold hours (Supplementary Table S2 online, Supplementary Fig. S3 online).

**Seed mass modulating species response to aspect**

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

Differences in the heat received between south-facing and north-facing slopes will cause the variation of water content in soil (Burnett et al., 2008; Hais et al., 2016; Holden & Jolly, 2011). Generally, the soil on south-facing sides is drier than that on north-facing sides in the northern hemisphere, and this trend had also been illustrated in our study area (Supplementary Fig. S2 online). That’s to say, trees on south-facing slopes may facing more drought stress in Baxian mountain. The drier condition is a challenge to the plants with small seed, while larger seed trees will be more possible to survive as they tend to perform better in seedling growth when facing drought and other hazards, and it is most likely because heavier seeds can produce larger seedlings (seedling-size effect) (Lloret, Casanovas, & Peñuelas, 1999; Quero, Villar, Marañón, Zamora, & Poorter, 2007). In our study, this trend was indicated by the negative coefficient of the interaction
between seed mass and soil moisture in the microclimatic data fitted model, although not very certain (Supplementary Table S2 online, Supplementary Fig. S3 online). It is consistent with most previous results regarding the relationship between seed mass and soil moisture (Hallett et al., 2011; McFadden et al., 2019; Moles & Westoby, 2004; Shipley et al., 2017).

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

**Limitations of this study**

Trees on the southerly sites are facing more drought stress than the northerly on Baxian Mountain (Supplementary Fig. S2 online). Drought can lead to the xylem cavitation of vascular plants (Willson & Jackson, 2006), and cavitation will frequently occur when they are getting too little water, so that embolized conduits will no longer be able to hold the sap, and the plants will die (Tyree & Sperry, 1989). Vascular plants of dry habitats are more likely to have more cavitation resistance (higher hydraulic conductivity) than species living in wet conditions (Peguero-Pina et al., 2011; Wubbels, 2010). In fact, hydraulic traits should be more typical to represent the drought tolerance of vascular plants (Cavender-Bares, Kitajima, & Bazzaz, 2004; Tyree & Sperry, 1989; Wubbels, 2010). We recommend one easy-measured hydraulic trait, the xylem vulnerability to embolism, either to stem or to leaf, to reflect that ability straightforwardly. It
represents the xylem pressure caused by cavitation when 50% of hydraulic conductivity is lost (P50) (Perez-Harguindeguy et al., 2016). Hydraulic traits have rarely been incorporated into models (model-based methods) to explain how functional traits modulating species response to environments, let alone the response to soil moisture. The role of hydraulic traits in species response to environments is worth considering more in the future.

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

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

**Methods**

**Study area**

The species occurrence data, functional traits and environmental variables were collected on Baxian Mountain National Nature Reserve (40.1836 N, 117.5464 E), Northern China, at elevations between 200 and 1000 m. According to the Köppen
climate classification, it is within the hot summer continental climate regime (Dwa) (Li, Lu, Yu, & Yang, 2018, Figure 2; Peel, Finlayson, & McMahon, 2007, Figure 5). The annual average temperature is 12.9°C (https://web.archive.org/). The warmest month is July, with an average temperature of 26.8°C, while the coldest month is January, with an average temperature of -3.4°C. The annual precipitation is 516 mm. The month with the highest precipitation on average is July, reaching 150 mm, while the lowest month is January with an average of 3 mm. The reserve is a mostly deciduous broad-leaved forest, dominated by *Acer*, *Quercus* and *Juglans* species.

**Species occurrence data collection**

We sampled three, one-hectare plot sets along topographic gradients, including 100, 10 m x 10 m plots (Fig 1) in each set. Moreover, we broadly located 69, 10 m x 10 m plots outside those three sets along topographic gradients (Fig 1). In order to avoid the many plots from the three one-hectare plot sets inducing significant spatial autocorrelation, we resampled from those sets by putting a 3 * 3 grid on each set, and randomly picking 3 plots in each grid cell, in the end comprising 150 plots (27 * 3 + 69 = 150) for modelling. Moran’s I was measured to check if the dataset spatial autocreation was successfully limited (Gittleman, & Kot, 1990). We repeated this sampling strategy 10 times yielding 10 datasets for modelling. In each plot, we recorded the occurrence of every species, and here we used the data from 31 moderately common woody species. Their scientific
names, and corresponding abbreviations used in figures are listed in Supplementary Table S1 online.

**Functional trait data collection**

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

For 31 woody species, we collected their functional trait data including SLA (fresh area / dry mass, cm²•g⁻¹), SD (dry mass / fresh volume, mg•mm⁻³), seed mass and maximum height form TRY (Kattge, et al., 2020), China plant trait database (Wang, et al., 2018), Kew Seed Information database (https://data.kew.org/sid/), the Scientific Database of China Plant Species (DCP) (http://db.kib.ac.cn/) and some republished papers (Marchi, Tognetti, Minnocci, Borghi & Sebastiani, 2008; Knapp, Wang, Clark, Pile, & Schlarbaum, 2014; Chen, Wang, Baiketuerhan, Zhang, Zhao, & von Gadow, 2014).

All functional traits ranged widely among the species in this study. Species ranged in SLA from 5.60 m²•kg⁻¹ to 45.05 m²•kg⁻¹. Seed mass ranged over nearly four orders of magnitude, from 0.10 mg to 9259.00 mg. The tallest species had
an average height of 30 m, six times that of the shortest (5 m). The stem wood
density ranged least, from 0.35 g\cdot cm^{-3} to 0.85 g\cdot cm^{-3}.

**Environmental variables**

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

**Data pre-processing**

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

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

\[
\text{Logit}(p_{ij}) = \alpha + a_j + (\beta_1 + b_j)X_i + \beta_{12}Z_jX_i + c_i,
\]

\[i = 1, 2, \ldots, n, \quad j = 1, 2, \ldots, m,\]

where \(p_{ij}\) is \(Pr(y_{ij} = 1)\), referring to the probability of species \(j\) occurrence in site \(i\). \(X\) is a matrix of quantitative environmental data for \(n\) sites. \(Z\) is the trait matrix for \(m\) species. \(\alpha, \beta_1\) and \(\beta_{12}\) are fixed effect terms. \(\alpha\) gives the overall prevalence of species across sites given the mean value of each trait for all species and the mean value of each environmental variable for all sites. \(\beta_1\) refers to the average response to each environmental variable given average trait values for all species. \(\beta_{12}\) denotes the trait-environment association, indicating how traits modulate species response to environmental variables. \(a_j, b_j\) and \(c_i\) are the random effect terms, where \(a_j\) and \(c_i\) respectively show the deviations in prevalence at species and site levels. \(b_j\) describes the response of every species to each environmental variable. Not fully following the model proposed by Jamil et al. (2013) and recommended by Miller et al. (2019), in our study, functional traits have only been incorporated into our model as “trait-environment” interactions rather than fixed effect terms. It means functional traits influence species occurrence through
modulating their response to environments rather than influence their occurrence directly.

We used `blme` (Chung, Rabe-Hesketh, Dorie, Gelman, & Liu, 2013) package to fit our model in a Bayesian setting, which allowed us to specify a particular form of weak prior to getting an approximate Bayesian maximum posterior estimation. The prior distribution for the species covariance of random effects was an inverse Wishart distribution with $df = 8$ and a $4 \times 4$ diagonal variance-covariance matrix, and the variance was 2. The prior distribution for the site covariance of random effects was an inverse gamma distribution with shape and scale parameters 0.5 and 100, respectively (default). The prior distribution for fixed effects was a normal distribution with $\mu = 0$ and $sd = 1$. We evaluated model performance by the area under the receiver operating characteristic curve (AUROC) and the area under the Precision-Recall curve (AUPRC) since the input data of our model are highly skewed (Boyd, Costa, Davis, & Page, 2012; Sofaer, Hoeting, & Jarnevich, 2019). AUROC and AUPRC were calculated using R package `PRROC` (Grau, Grosse, & Keilwagen, 2015; Keilwagen, Grosse, & Grau, 2014). In addition, we calculated the values of AUPRC/prevalence for each species, where prevalence here is equal to AUPRC of a random classifier (Saito & Rehmsmeier, 2015), to show how many times the model’s prediction is better than a random classifier. We fitted the model with four traits (Fig 2) of 31 species and three topographic variables from 150 plots. Based on the 10 datasets from grid sampling process, we built up 10 topographic models, and averaged the coefficients for each fixed
effect terms for visualization (Supplementary Fig. S1 online). Additionally, to help us to understand the associations between topographic variables and functional traits, we fitted this trait-environment model with microclimatic variables predicted by microclimate modelling, which was considered directly associated with plant occurrence underlying the effect of topography, and some results from this model will be mentioned in the discussion part and the details can be found in Supplementary methods (see Supplementary methods online for more details).

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Authors' contributions

LLT, WKM, PAV and FCS conceived and designed the study. LLT, MZ and FCS undertook the fieldwork. LLT, WKM and PAV analyzed the data. LLT, WKM and PAV wrote the manuscript; other authors provided editorial advice.

Competing interests

The authors declare no competing interests.

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**Figure legends**

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

**Fig. 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** 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.

**Tables**

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

| Fixed effect     | Coefficient | SE  | p-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|
Figures

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.
Figure 2

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