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Experiment meets biogeography: plants of river corridor distribution are not more stress tolerant but benefit less from more benign conditions elsewhere

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Abstract

Aims
Factors limiting distributions of species are fundamental to ecology and evolution but have rarely been addressed experimentally for multiple species. The conspicuous linear distribution patterns of plant species confined to river corridors in the Central European lowlands constitute an especially long-standing distribution puzzle. We experimentally tested our novel hypothesis that the tolerance of species to river corridor conditions is independent of the degree of confinement to river corridor habitats, but that species not confined to river corridors are better able to take advantage of the more benign non-river corridor conditions.

Methods
We grew 42 herbaceous species differing in their confinement to river corridors in a common garden experiment on loamy soil typical for river corridor areas and sandy soil typical for non-river corridor areas, and with and without a flooding period. For a subset of species, we grew plants of both river corridor and non-river corridor origin to test for adaptation to river corridor conditions.

Important findings
Species more confined to river corridor areas benefited less from the more benign non-flooded and non-river corridor soil conditions than species of wider distributional range did. For subsets of 7 and 12 widespread species, the response to flooding and soil origin, respectively, did not differ between plants from river corridor sites and plants from other sites, suggesting that the habitat tolerance of widespread species is due to phenotypic plasticity rather than to local adaptation. Overall, we found clear support for our novel hypothesis that species not confined to river corridors are more able to take advantage of the more benign non-river corridor conditions. Our study provides a general hypothesis on differences between species confined to stressful habitats and widespread species out for test in further multispecies comparative experiments.

Keywords: distributional patterns • edaphic factors • environmental tolerance • flooding • local adaptation • multispecies experiment • phenotypic plasticity

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INTRODUCTION

Among the long-standing fundamental questions in ecology and evolution is the one asking for factors restricting distributional species ranges (Darwin 1859; Good 1931). Based on observational and comparative studies relating environmental factors to realized species distribution, climatic, edaphic and hydrological variation and species dispersal have been suggested as main determinants of distributional ranges (Cain 1944; Walter 1954; Rajakaruna 2004). However, unequivocal experimental data are largely missing in this context, particularly so for larger numbers of species (but see Hölzel and Otte

2004). The few experiments showed niche differentiation of species (Grace and Wetzel 1981; Lenssen and de Kroon 2005; Mommer *et al.* 2006) and of genotypes within species (Lenssen *et al.* 2004) along environmental gradients, explaining a replacement of species or genotypes along these gradients.

However, such replacement patterns along environmental gradients need not be the rule. In the Central European lowlands, some plant species, many of which are threatened, have conspicuous linear distribution patterns reflecting their confinement to river corridors (Fig. 1a), which mainly consist of the water body, the river banks, the floodplain and surrounding, episodically flooded areas (Forman and Gordon 1986; Burkart 2001). At the same time, many other species occur more widely distributed both within and outside of river corridors (Burkart 2001; Fig. 1b). In contrast, hardly any species are strictly confined to areas outside of river corridors, indicating that there is no replacement of species when moving outside of the river corridors.

As potential determinants of the confinement of some species to river corridors, tolerance to climatic, edaphic and hydrological conditions of the river corridor species were suggested along with specific seed-dispersal characteristics (Burkart 2001). Climatic conditions differ between river corridor and adjacent habitats mainly in more hilly areas such as the ones neighbouring the upper courses of the river Rhine, but not in the large river systems of Central European lowland, and therefore cannot explain the river corridor distribution there. Direct effects of flooding and the disturbance caused by flooding clearly suggest that river corridors are more stressful habitats than non-river corridor habitats. Moreover, although river corridor soils are usually considered more nutrient rich than non-river corridor soils in Central European lowland, they may during dry periods also have a lower water availability as a consequences of the higher clay content (English *et al.* 2005), and maintain lower oxygen concentrations during flooding (Schwartz *et al.* 1999). Therefore, river corridor soils may frequently be less favourable for plant growth than non-river corridor soil.

It is interesting to note that most of the hypotheses put forward to explain the river corridor specificity of some species (Burkart 2001) concentrate on the tolerance of these river corridor species of the stressful environments in which they actually co-occur with more widespread species, rather than on the most peculiar characteristic of the river corridor distribution pattern, namely the absence of confined species from less disturbed non-flooded habitats. To explain the latter, we propose that the degree of confinement to river corridor habitats should be independent of the tolerance of species to river corridor conditions, but that species not confined to river corridors should be more able to take advantage of the more benign non-river corridor conditions.

The environmental tolerance of more widespread species may reflect high phenotypic plasticity and environmental tolerance of individuals or that the species consists of more specialized locally adapted populations, each of low environmental tolerance (Bradshaw 1965; Levins 1968; Schmid 1992; Kawecki and Ebert 2004; Leimu and Fischer 2008). Therefore, in the context of river corridors, it is very interesting to test whether

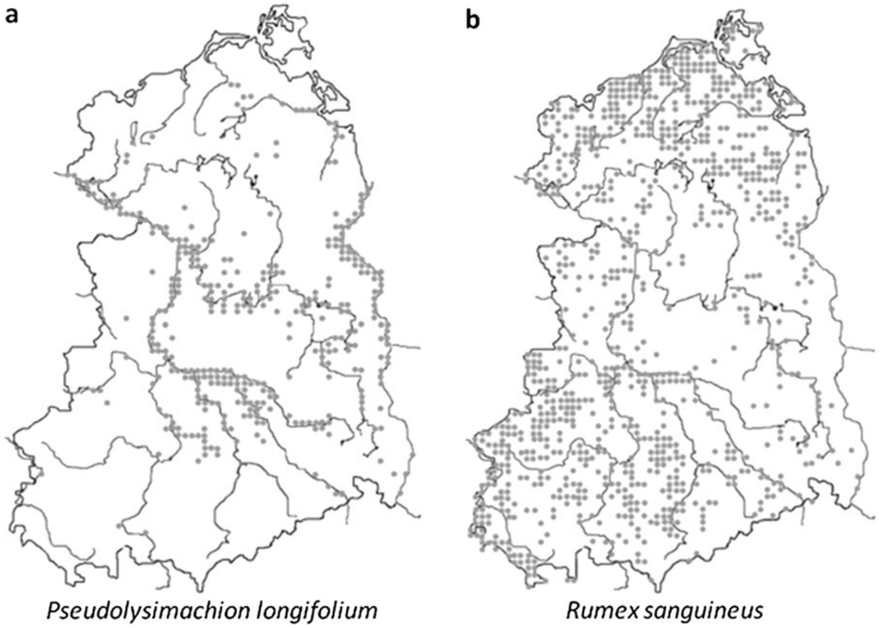

Figure 1: distribution of two of the 42 study species in eastern Germany. (a) *Pseudolysimachion longifolium* is a species that is largely confined to river corridors. (b) *Rumex sanguineus* is a species that is equally abundant within and outside of river corridor areas. The maps were redrawn from Benkert *et al.* (1996). Each grey dot indicates the occurrence of the species in a grid cell (each of size 5′ longitude by 3′ latitude; ~30 km^2). The lines within the borders of eastern Germany indicate the rivers

species occurring inside and outside of river corridor habitats show local adaptation to the conditions of these habitat types.

Clearly, because a multitude of confounded environmental factors could affect the distribution of the species in the field, the response to environmental factors differing between river corridor and other habitats needs to be assessed experimentally for a large number of species differing in their confinement to river corridors. Therefore, we sampled seeds of 42 herbaceous plant species differing in the degree of their confinement to Central European river corridors from the area of the rivers Elbe and Havel in north-eastern Germany. In a common garden experiment, we measured their biomass when grown on loamy river corridor soil and sandy non-river corridor soil, and when grown in the absence and presence of a flooding period. To test whether environmental tolerance of the widespread species reflects phenotypic plasticity or local adaptation to either river corridor conditions or non-river corridor conditions, we included for 12 of the widespread species, plants from river corridor populations and non-river corridor populations.

MATERIAL AND METHODS

Study system

We first compiled a list of all herbaceous species growing in corridors of the rivers Elbe and Havel in the German federal states of Brandenburg and Saxony-Anhalt, and divided these species into three groups based on their river corridor specificity. From these three groups, we randomly chose a total of 42 species covering the whole range from species strictly confined to river corridors to ones that are equally abundant within and outside of river corridors (Table 1 and Fig. 1). We used species distribution maps of eastern Germany (Benkert *et al.* 1996) to calculate for each of the species a river corridor-specificity index by dividing the proportion of occupied river corridor cells (each of size 5′ longitude by 3′ latitude; $\sim 30\ \text{km}^2$) by the sum of the proportion of occupied river corridor cells and the proportion of occupied non-river corridor cells. River corridor-specificity indices ranged between 0.47 (indicating species for which the proportion of occupied river corridor grid cells almost exactly equals the proportion of occupied non-river corridor grid cells) and 1.00 (indicating species that are entirely confined to river corridors) and did not differ between the 16 annual and the 26 perennial species (two-sided t-test; $n = 42$; $t = 1.65$; $P > 0.1$). Because the grid cells of the distribution maps are relatively large ($\sim 30\ \text{km}^2$), we cannot exclude the possibility that some of the river corridor cells included some non-river corridor habitats and *vice versa*. Therefore, we also asked *a priori* three expert botanists (Volker Kummer, Michael Ristow and one of the authors, M.B.) to score the species regarding their river corridor specificity using a scale from 1 (not restricted to river corridors) to 5 (restricted to river corridors). The scores of the experts were highly correlated with the river corridor index that we calculated from the distribution maps (all Spearman $r > 0.869$, $P < 0.001$). Therefore, we are confident that our river corridor index is accurate.

Table 1: List of the 42 study species, and their life forms, sorted according to their river corridor-specificity index

Taxa	Life form	River corridor-specificity index
Epilobium hirsutum[a]	Perennial	0.47
Phragmites australis var. *australis*	Perennial	0.49
Geum urbanum[a]	Perennial	0.49
Sonchus arvensis[a]	Perennial	0.49
Tripleurospermum perforatum[a]	Annual	0.49
Achillea millefolium[a]	Perennial	0.50
Cirsium arvense[a]	Perennial	0.50
Rumex crispus[a]	Perennial	0.50
Carex hirta	Perennial	0.50
Tanacetum vulgare[a]	Perennial	0.50
Agrostis stolonifera var. *stolonifera*	Perennial	0.51
Gnaphalium uliginosum	Annual	0.52
Phalaris arundinacea[a]	Perennial	0.53
Bromus tectorum	Annual	0.53
Lactuca serriola[a]	Annual	0.54
Echinochloa crus-galli[a]	Annual	0.54
Erysimum cheiranthoides	Annual	0.54
Rumex sanguineus	Perennial	0.55
Armeria maritima subsp. *elongata*	Perennial	0.55
Rumex thyrsiflorus	Perennial	0.59
Juncus compressus[a]	Perennial	0.61
Chenopodium polyspermum	Annual	0.61
Leontodon saxatilis	Perennial	0.63
Thalictrum flavum	Perennial	0.65
Teucrium scordium	Perennial	0.66
Chenopodium ficifolium	Annual	0.76
Sanguisorba officinalis	Perennial	0.77
Senecio paludosus	Perennial	0.78
Limosella aquatica	Annual	0.81
Portulaca oleracea subsp. *oleracea*	Annual	0.86
Pseudolysimachion longifolium	Perennial	0.87
Gratiola officinalis	Perennial	0.88
Pulicaria vulgaris	Annual	0.88
Allium angulosum	Perennial	0.90
Leonurus marrubiastrum	Annual	0.95
Cardamine parviflora	Annual	0.96
Mentha pulegium	Perennial	0.97
Bidens radiata	Annual	0.99
Euphorbia lucida	Perennial	0.99
Achillea salicifolia	Perennial	1.00
Amaranthus blitum subsp. *emarginatus*	Annual	1.00
Eragrostis albensis	Annual	1.00

An index of 0.5 indicates that the species has a proportion of occupied river corridor grid cells that equals the proportion of occupied non-river corridor grid cells, and an index of 1 indicates that the species is entirely confined to river corridors.

[a] For these species, seeds were collected in a river corridor site and a non-river corridor site.

In 2003, we collected seeds of each species in corridors of the rivers Elbe and Havel in the German federal states of Brandenburg and Saxony-Anhalt. For 12 of the widely distributed species (i.e. species with low river corridor specificity index; mean ± 1 SE = 0.51 ± 0.011; Table 1), we collected additional seeds in non-river corridor areas. The latter allowed us to test whether the response of plant species to soil conditions and flooding reflects phenotypic plasticity or local adaptation of river corridor and non-river corridor genotypes. Seeds were collected from up to 15 maternal plants per site, but for some species only three plants were available resulting in a median of 10 maternal plants per site.

Common garden experiment

During 11–13 May 2004, 20 seeds, if available, per maternal plant (i.e. per seed family) were sown into trays (19 × 14 × 5 cm) filled with a 1:2 mixture of sand and commercial potting compost in a non-heated greenhouse of the Botanical Gardens in Potsdam, Germany (latitude 52°24′N, longitude 13°01′E). Germination rates were not related to river corridor specificity ($F_{1,38} = 0.11$, $P > 0.05$) or life form ($F_{1,38} = 0.14$, $P > 0.05$). When seedlings were large enough to be transplanted, we planted seven seedlings per seed family into separate 1-l pots (totalling 2606 pots), three filled with loamy soil from a typical river corridor site (dry weight of soil per pot: mean ± SE = 846.6 ± 18.5 g, $n = 5$) and four with sand from a typical non-river corridor site (dry weight of soil per pot: mean ± SE = 1027.2 ± 11.8 g, $n = 5$). In our study region, all species restricted to river corridors are found on loamy soil, while species not restricted to river corridors are also found on sandy soil. Pots were assigned to random positions within a garden plot close to the greenhouse. All seedlings were transplanted between 1 June and 19 August 2004. One of the four seedlings per seed family planted into sand-filled pots was assigned to the flooding treatment (i.e. we had up to 15 plants per species in the flooding treatment). However, for nine species, we did not have enough seedlings to include them in the flooding treatment. For the flooding, we used two inflatable basins that were 27 cm deep and filled with water from the Havel river. Flooding lasted from 28 June to 15 July 2004. In our study regions, flooding events are most frequent in spring, but they can also occur in summer. The water of the river Havel moves very slowly, and during flooding it is almost stagnant, like in our basins. We harvested plants above ground at the time of peak biomass for each species, and dried them to constant mass at 70°C. All plants were harvested from 10 August to 19 October 2004. Of the 2606 plants in the experiment, 68 plants, all of them in the flooding treatment, died during the experiment, and accordingly were assigned a biomass of zero.

Analyses

We analysed variation in aboveground biomass (after log10 transformation) with mixed-model analysis of covariance (ANCOVA; type I SS). Effects of soil origin and flooding were tested in two separate analyses. We included life form (annual and perennial), seed origin (river corridor area and non-river corridor area) and treatment (sand, loamy soil or flooded and non-flooded) as fixed factors, species (nested within life form) and seed family (nested within species) as random factors and river corridor-specificity index as a covariate. We also ran the analyses with time to germination and time to planting as covariates, but as this did not change the results, we only report results without these covariates.

Because the analyses above do not correct for phylogenetic relatedness between the species, we additionally tested for correlations between river corridor-specificity index of species and their average difference in biomass production between the river corridor treatments and non-river corridor treatments (i.e. river corridor soil versus non-river corridor soil and flooded versus non-flooded) with phylogenetically independent contrasts using the CAIC software (Purvis and Rambaut 1995). For these analyses, we used the phylogeny of the German flora (Durka 2002). As there is no information on the branch lengths of this phylogeny, we assigned equal lengths to them (Purvis and Rambaut 1995). The difference in biomass between treatments was log10-transformed for these analyses.

To test for potential local adaptation to soil and flooding conditions within the species that had been collected in a river corridor and a non-river corridor site, we analysed aboveground biomass (after log10 transformation) with mixed-model ANCOVAs (type I SS) similar to the ones above, but excluded the covariate river corridor-specificity index. For the test of local adaptation to soil conditions, we had data on 12 species, and for the test of local adaptation to flooding conditions, we had data on seven species.

RESULTS

Averaged over all study species, plants produced 98% more biomass on sandy non-river corridor soil than on loamy river corridor soil ($F_{1,36} = 70.20$, $P < 0.001$). Moreover, for the 33 (of 42) species that we had included in the flooding treatment, plants produced on average 262% more biomass when they had not been flooded than when they had experienced a 17-day flooding period ($F_{1,29} = 116.93$, $P < 0.001$). This clearly supports the idea that abiotic conditions are less stressful outside of than within river corridors.

Biomass response of species differing in river corridor specificity

When grown on non-river corridor soil under non-flooded conditions, among the 42 study species the ones that are rather confined to river corridors produced less aboveground biomass than the species for which the proportion of occupied river corridor grid cells equals the proportion of occupied non-river corridor grid cells (Fig. 2). However, when plants were grown on river corridor soil, these differences in biomass production largely declined (Fig. 2a), and even disappeared when plants had been flooded for 17 days (Fig. 2b). This was reflected in significant interactions of river corridor confinement with soil

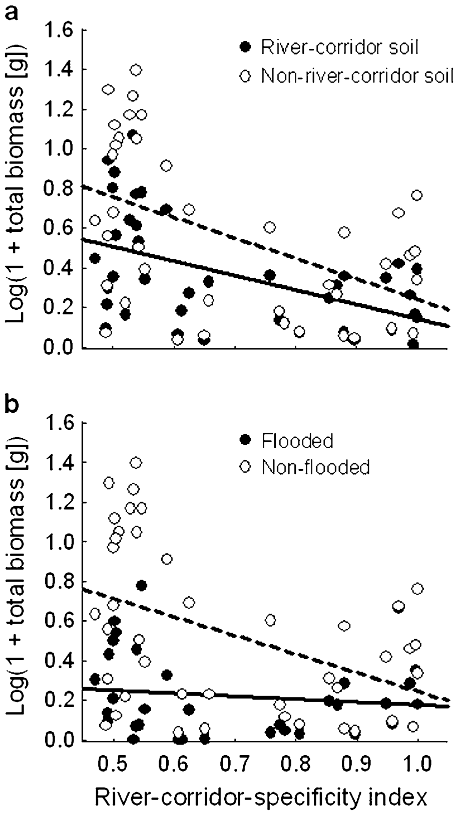

Figure 2: plant performance in relation to river corridor specificity of species. (a) Aboveground biomass production on river corridor soil and non-river corridor soil. (b) Aboveground biomass production with and without a 17-day flooding period. An index of 0.5 indicates that the species has a proportion of occupied river corridor grid cells that equals the proportion of occupied non-river corridor grid cells, and an index of 1 indicates that the species is entirely confined to river corridors

origin ($F_{1,36} = 7.33$, $P = 0.010$) and with flooding ($F_{1,29} = 29.38$, $P < 0.001$).

After correction for phylogenetic relatedness among species, differences in biomass production under river corridor and non-river corridor conditions were still negatively correlated with the river corridor-specificity index of species, and this was significant with regard to flooding (soil: $r_{\mathrm{PIC}} = -0.248$, $F_{1,38} = 0.59$, $P = 0.447$; flooding: $r_{\mathrm{PIC}} = -1.224$, $F_{1,31} = 11.00$, $P = 0.002$).

Biomass responses of plants of widespread species from river corridor sites and other sites

The subsets of species with similar proportions of occupied river corridor grid cells and non-river corridor grid cells, for which we had planted both plants from river corridor origin and from non-river corridor origin, grew much better without flooding and on non-river corridor soil, indicating strong phenotypic plasticity of growth in response to the different soil and flooding treatments (Fig. 3). Averaged over the two soil treatments, plants from the non-river corridor populations produced slightly more biomass than plants from the river corridor populations ($F_{1,10} = 5.66$, $P = 0.039$; Fig. 3a). On the other hand, such a difference was not apparent when biomass production was averaged over the two flooding treatments ($F_{1,10} = 2.10$, $P > 0.05$; Fig. 3b). Most interestingly, however, plants from river corridor sites and non-river corridor sites did neither outperform the others on their local soils nor under their local flooding conditions (soil: $F_{1,10} = 1.25$, $P > 0.05$; flooding: $F_{1,5} = 0.83$, $P > 0.05$; Fig. 3), not suggesting any local adaptation to river corridor conditions.

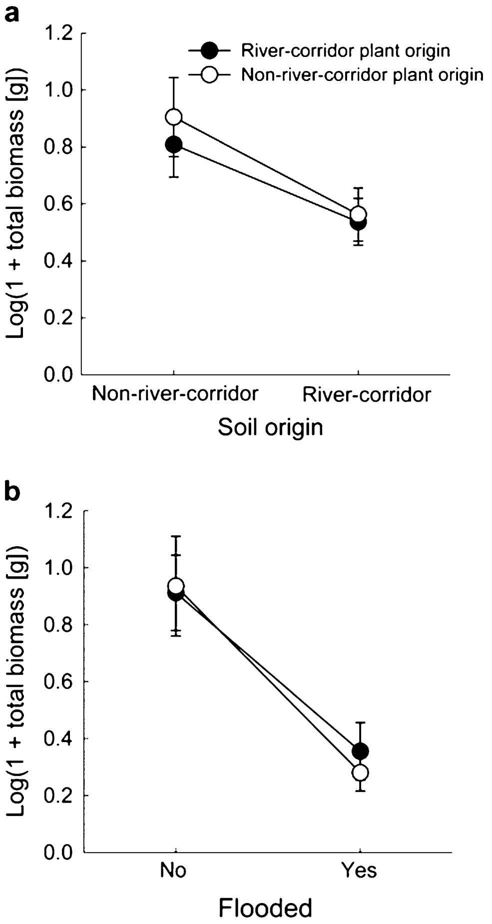

Figure 3: performance of genotypes of river corridor and non-river corridor origin. (a) Aboveground biomass production on river corridor soil and non-river corridor soil of genotypes of river corridor and non-river corridor origin for 12 species. (b) Aboveground biomass production with and without a 17-day flooding period of genotypes of river corridor and non-river corridor origin for seven species

DISCUSSION

Our common garden experiment showed that among 42 species the ones that are more confined to river corridor areas benefited less from the more benign non-river corridor conditions than species for which the proportion of occupied river corridor grid cells equals the proportion of occupied non-river corridor grid cells. This demonstrates that river corridor plants do not take advantage of the edaphic and flooding conditions typical for river corridors when compared with more widely distributed species, but that they are less able to take advantage of more benign conditions typical for non-river corridor habitats.

Despite their absence or limited occurrence outside of river corridors, our study shows that species rather confined to river corridors grew well under non-river corridor conditions. This indicates that the realized niche of these species poorly reflects their fundamental niche (Grace and Wetzel 1981). Probably, the species rather confined to river corridors do not realize their fundamental niche because they are outcompeted outside the river corridors by the widespread species that have a larger biomass gain under non-river corridor conditions.

Within the subset of 12 widespread species, the biomass response to flooding and to soil differences did not differ between plants from river corridor sites and plants from other sites. This suggests that the habitat tolerance of the widespread species is due to phenotypic plasticity and environmental tolerance of individuals rather than to local adaptation of populations (Bradshaw 1965; Levins 1968; Schmid 1992). Probably gene flow between river corridor populations and non-river corridor populations of these species is high enough to prevent local adaptation (Slatkin 1985) and to result in the evolution of generalist genotypes.

One other potential explanation of the confinement of some species to river corridors is that their dispersal might be restricted to the corridors (Loew 1879). However, although many species might be more likely to disperse within the river corridors than out of them, it could not explain the occurrence of species in different river corridors (Burkart 2001). Furthermore, molecular genetic analysis of the river corridor species *Corrigiola litoralis* did not support the idea of migration along the river corridor (Durka 1999). Moreover, our study shows that even if seeds of species confined to river corridors would reach non-river corridor areas, they would be likely to be outcompeted by the other species, which on sandy non-river corridor soil and in the absence of flooding events grow much larger than species confined to river corridors.

Another potential limiting factor for the distribution of river corridor species could be slightly colder climate outside the river corridors (Burkart 2001). A previous study on 42 species from the hilly northern Upper Rhine river area—where climatic conditions differ more between river corridor and non-river corridor habitats than in the completely flat sampling area in the East German lowlands—did, however, not find evidence that river corridor confinement is associated with temperature requirements for germination (Hölzel and Otte 2004). This suggests that climatic tolerance, at least with regard to germination, is not a main driver of species distribution patterns in the Central European lowland region.

CONCLUSIONS

Our study shows that species confined to river corridors do not benefit to the same extent as species that are not confined to river corridors from the absence of flooding and the more benign soil conditions outside river corridors. This highlights that understanding distributional patterns of apparent specialists of stressful habitats requires not only concentrating on the question why they are able to occur in stressful habitats, but also why they are absent from more benign habitats. The nonability of taking advantage of more benign conditions may well represent a general pattern distinguishing specialist species confined to more stressful habitats—such as nutrient-deficient, acidic, dry, high-elevation, cold, shady or highly disturbed ones or habitats with strong competition, herbivory or pathogen load—from generalist species not confined to such habitats. This should be tested in further comparative experiments.

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