**ORIGINAL
ARTICLE**

Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients

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ABSTRACT

Aim Species specialization, which plays a fundamental role in niche differentiation and species coexistence, is a key biological trait in relation to the responses of populations to changing environments. Species with a limited niche breadth are considered to experience a higher risk of extinction than generalist species. This work aims to measure the degree of specialization in the regional flora of the French Alps and test whether species specialization is related to species rarity and ecological characteristics.

Location This study was conducted in the French Alps region, which encompasses a large elevational gradient over a relatively limited area (26,000 km^2).

Methods Specialization was estimated for approximately 1200 plant species found in the region. Given the inherent difficulty of pinpointing the critical environmental niche axes for each individual species, we used a co-occurrence-based index to estimate species niche breadths (specialization index). This comprehensive measurement included crucial undetermined limiting niche factors, acting on both local and regional scales, and related to both biotic and abiotic interactions. The specialization index for each species was then related to a selection of plant typologies such as Grime strategies and Raunkiaer life-forms, and to two measurements of plant rarity, namely regional area of occupancy and local abundance.

Results Specialist species were mainly found in specific and harsh environments such as wetlands, cold alpine habitats and dry heathlands. These species were usually geographically restricted but relatively dominant in their local communities. Although none of the selected traits were sufficient predictors of specialization, pure competitors were over-represented amongst generalist species, whereas stress-tolerant species tended to be more specialized.

Main conclusions Our results suggest that co-occurrence-based indices of niche breadth are a satisfactory method for inferring plant specialization using large species samples across very heterogeneous environments. Our results are an empirical validation of the tolerance–dominance trade-off and also provide interesting insights into the long-standing question of which biological properties characterize species with narrow niche breadth that are potentially threatened by global changes in the environment.

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INTRODUCTION

The functioning of ecosystems involving complex interactions is strongly altered by ongoing global changes (Chapin *et al.*, 2000; Thuiller, 2007), and may lead to unprecedented losses of biodiversity (Pimm & Raven, 2000). However, not all species or ecosystems are expected to have the same vulnerability (Sala *et al.*, 2000). Some regions, such as alpine regions, are considered to be 'biodiversity hotspots' (Körner, 2004) because they harbour numerous rare or specialist species expected to be particularly sensitive to extinction (Pimm *et al.*, 1988; Gaston, 1997).

Species specialization, resulting from evolutionary trade-offs between a species' ability to exploit a wide range of resources and the effectiveness with which it uses each of these, may provide indicators of species response to global changes in the environment (Gregory *et al.*, 2005; Broennimann *et al.*, 2006; Winck *et al.*, 2007). Apart from rare exceptions recorded in highly arid climates where environmental changes may favour specialist species over generalist species (Attum *et al.*, 2006), species with limited environmental tolerance and resource use spectra are expected to be more sensitive to environmental changes than generalists (Evans *et al.*, 2005; Wilson *et al.*, 2008). This has recently been shown for a large range of individual taxa including plants (Thuiller *et al.*, 2004), birds (Jiguet *et al.*, 2007; Devictor *et al.*, 2008a), fish (Munday, 2004; Feary, 2007), mammals (Laidre *et al.*, 2008) and bumblebees (Williams, 2005). Conversely, generalist species are expected to dominate as a result of habitat fragmentation or anthropogenic disturbance (for an example on birds see Devictor *et al.*, 2008b).

Ecological specialization is one of the main mechanisms of niche differentiation, which in turn favours species coexistence (Chase & Leibold, 2003). A species' niche is usually defined as the *n*-dimensional environmental space occupied by a species along different environment axes (Hutchinson, 1957). As formulated in Gause's law, two species competing for the same resource cannot coexist if all other ecological factors remain constant. One scenario that may explain observed patterns of diversity is that one of the two species initially competing for similar resources escapes from competitive exclusion by specializing in a small part of the multi-dimensional ecological space. This species becomes more competitive in this restricted ecological space where it may dominate, to the detriment of other parts of the gradient where it becomes a weaker competitor and may even be excluded. Specialist species are therefore expected to have a high local relative abundance and to occur in peculiar or stressful environments such as high elevations, wetlands or xeric habitats (Thompson *et al.*, 1998; Lavergne *et al.*, 2004). These patterns would be explained by a tolerance–dominance trade-off across species (Wisheu, 1998).

A range of metrics for measuring niche specialization have been applied in ecological studies (Devictor *et al.*, 2010). For instance, specialization has been inferred indirectly from species distributions and environmental data (Thuiller *et al.*, 2004), from direct measurements of species performance in multiple environments (Kassen, 2002) or from detailed measurements of species diets, such as variance in prey size (Bolnick *et al.*, 2003). All these methods require the pre-selection of the main factors limiting resource acquisition (Austin *et al.*, 1984; Austin, 1985). However, niche differentiation based on a few selected resource-limiting axes does not seem to explain plant coexistence as most plants require common resources (light, water, CO_2, phosphorus, potassium and certain other mineral nutrients) and there are a limited number of ways in which they can acquire them (Silvertown, 2004). There is increasing evidence that numerous axes of niche differentiation are needed to explain species coexistence (Clark *et al.*, 2007), particularly in species-rich communities such as herbaceous habitats. Given the lack of understanding of the key environmental variables that determine each species' niche and the paucity of reliable spatial data on all potential environmental variables, the description of a species' niche is generally based on the few niche axes that are relatively easy to measure or to gather from spatial datasets (Vetaas, 2002; Chase & Leibold, 2003). To investigate niche specialization over a large set of species and a large spatial scale whilst accounting for niche axes that explain coexistence at the community scale, we chose a metric that does not require any pre-selection of environmental variables. Fridley *et al.* (2007) proposed using the co-occurring species to depict diversity across a given species' habitats. They consider that:

> Co-occurrence data offer an approach that is in effect a biological assay for 'habitat diversity' or 'niche width' that requires no assumptions about the definition of a habitat or the most critical environmental factors that control plant species distributions.
> (Fridley *et al.*, 2007, p. 708)

This indirectly accounts for numerous niche axes that may be of importance at both local and regional scales, and which may differ from one species to another.

Here we use an extensive vegetation survey across the French Alps region that encompasses a broad elevation gradient from 55 to 3200 m a.s.l., and investigate the overall pattern of plant niche specialization for more than 1200 plant species. The study region provides an optimal ecological setting for studying plant specialization as it presents steep environmental gradients over small spatial scales (Körner, 1999). We specifically address the following questions: (1) Do specialist species occur in particular habitats? (2) Is species specialization related to species geographical range and local dominance? (3) Which biological characteristics are common among specialist species?

MATERIALS AND METHODS

Data

This study was conducted over the French Alps region (Fig. 1), which covers over 26,000 square kilometres and presents a wide range of environmental conditions due to mixed continental, oceanic and Mediterranean climatic influences, with annual precipitation ranging from 522 to 2895 mm, mean annual temperatures ranging from −7 to 12.6 °C and slope
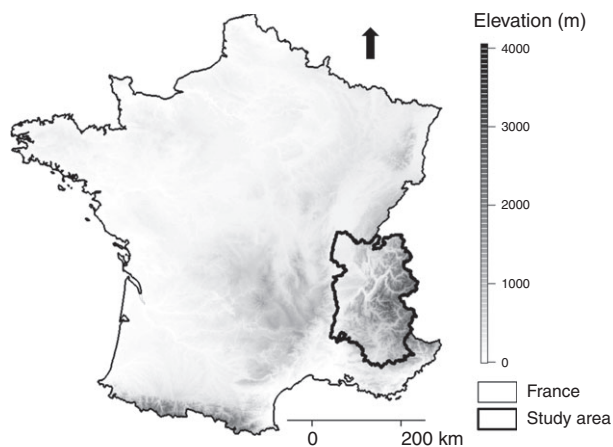
Figure 1 The study area of the French Alps region, located in south-eastern France. This area is on the edge of the Alpine region, where three climatic zones come together: the Mediterranean, continental and oceanic climates.

angle up to 78° [data extracted from the Aurelhy meteorological model (Bénichou & Le Breton, 1987), based on interpolated measurements at a resolution of 250 × 250 m]. We used a comprehensive vegetation survey of 6929 community plots sampled over large environmental gradients from 55 to 3200 m a.s.l. (from lowlands to alpine summits). For each plot the relative abundance of all present species was recorded, for a total of 2543 species overall. The National Alpine Botanic Conservatory (CBNA) provided this dataset. Plots were surveyed in a homogeneous area of 100 m^2 on average. Smaller habitats had a minimum of 10 m^2 and some forest plots were sampled up to 1000 m^2. Species nomenclature was standardized according to the *Index synonymique de la flore de France* (Kerguélen, 1993).

Each plot was assigned to one of ten habitat classes. Forests were subdivided into evergreen and deciduous forests. Six herbaceous habitats were described: meadows (including tall grass prairies, usually mown), grasslands (mostly grazed), rocks (cliffs and screes), wetlands (marshes, swamps, stream edges, peat bogs), floodplains and fields (cultivated areas). Two other classes described shrub habitats: the first represented scrubland including garrigue and heathlands (open land with low shrubs such as *Rhododendron ferrugineum* or *Vaccinium myrtillus*) and the second class contained thickets.

Studied species were assigned to different Grime ecological strategies (*sensu* Grime, 1974) for 891 species (competitor, ruderal, stress-tolerator or mixed), life span for 864 species (annual/biennial, perennial herbs, perennial woody species) and life-forms for all species (Raunkiaer's classification; Raunkiaer, 1934). This was done using the field observations of botanists from the Alpine Botanical Conservatory and two available databases: LEDA (Knevel *et al.*, 2003) and BiolFlor (Kühn *et al.*, 2004).

Methods

In order to estimate plant specialization, we used the co-occurrence index 'theta' proposed by Fridley *et al.* (2007).

The overall method relies on the assumption that the species found in many different habitats (i.e. generalists) have a relatively high rate of species turnover across the plots in which they occur. Reciprocally, specialist species, regardless of their frequency in the data set, should have a low species turnover in their plots because they consistently occur within the same set of species (Fridley *et al.*, 2007). The general idea is very similar to indirect species ordination such as (detrended) correspondence analysis (DCA; ter Braak, 1987). However, this recently developed method makes it possible to include a re-sampling procedure that accounts for differences in species frequencies in the dataset and makes it possible to select the appropriate underlying distance and turnover (beta) diversity metrics. This last point seems crucial given the recent literature on the estimation of beta diversity (de Bello *et al.*, 2010; Tuomisto, 2010a,b; Anderson *et al.*, 2011). To ensure the method is comprehensive, we provided a comparison of species niche breadth estimates using the theta index (Fridley *et al.*, 2007), an indirect gradient ordination, DCA (ter Braak, 1988) and a direct gradient ordination, outlying mean index (OMI, Dolédec *et al.*, 2000) (see Appendix S1 in the Supporting Information).

The overall frequency of a species in the sampled plots results from both the vegetation survey sampling strategy and that species' niche specialization. Following the framework proposed by Fridley *et al.* (2007), we removed the effects of the sampling design in the dataset by applying a randomization procedure. We randomly chose a fixed number of plots containing the focal species before calculating the turnover among these plots, thereby keeping the plot frequency constant between species. For each species we applied the randomization 100 times. Theta is the resulting average turnover. We also calculated the standard deviation of turnover from these 100 repetitions.

The number of selected plots for each randomization had to be determined arbitrarily, based on the number of species present in the vegetation database but also on the minimum number for species occurrence. Setting the threshold too high (e.g. > 40 plots) removed too many species with few occurrences, whereas setting the threshold too low affected the relevance of the measure. We selected a threshold of 10 plots after having checked that the results were consistent for 5, 10 and 15 plots (see Appendix S1). Furthermore, we decided to only calculate theta for species occurring in more than 20 plots in order to be able to resample the plots for all the species analysed. However, species occurring in fewer than 20 plots were kept in the community data to compute the theta value for all other species. The specialization index was thus computed for 1216 plant species.

The most critical point of this approach is the estimation of the species turnover among the sampled plots. Fridley *et al.* (2007) originally proposed using the additive beta measure, $\beta = \gamma - \mu(\alpha)$, where γ is the total number of species in the 10 sampled plots and $\mu(\alpha)$ is the mean species richness of these 10 plots. This choice was recently criticized on the grounds that this beta measure 'is dependent on the

size of [the] species pool at the position of species optima' (Zelený, 2009, p. 10). Another set of possible measurements was then proposed including the Jaccard index, two other indices based on Simpson or Sørensen for multiple sites (Baselga *et al.*, 2007) and one based on R. H. Whittaker's decomposition. Based on the recommendations, we could still use several indices according to what we aim to measure. In the recent literature, several authors have attempted to gather all these beta-diversity indices into a more comprehensive framework in order to guide ecologists in their choices (Jost, 2006, 2007; de Bello *et al.*, 2010; Tuomisto, 2010a,b; Anderson *et al.*, 2011). In the light of all these discussions, we chose an index that estimates the proportional species turnover between plots and generalizes the methodological framework, allowing the inclusion of species abundances and functional or phylogenetic dissimilarities between species if available. This index is based on Rao's quadratic entropy formula (Rao, 1982):

$$Q = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_i p_j \qquad (1)$$

where S is species richness, d_{ij} is the dissimilarity between each pair of species i and j (equal to 1 when $i \neq j$ or 0 else) and p_i, p_j are the relative abundance of species i and j in each sample. When d_{ij} is composed of 0 and 1 as in our case, Rao's quadratic entropy is equal to the Gini–Simpson diversity index and is related to the *true diversity D* (Jost, 2007; Tuomisto, 2010a) and the Jost 'number equivalents' (Jost, 2007; de Bello *et al.*, 2010):

$$(a)\, D_\gamma = \frac{1}{1 - Q_\gamma}, \quad (b)\, D_\beta = \frac{1}{1 - Q_\beta} \quad \text{and} \quad (c)\, D_\alpha = \frac{1}{1 - \overline{Q}_\alpha}. \qquad (2)$$

The true β-diversity component D_β is 'the number of communities that have no diversity overlap' (de Bello *et al.*, 2010, p. 995) and Q_β represents 'the proportion of diversity accounted for by the differentiation between communities' (de Bello *et al.*, 2010, p. 996). In Tuomisto (2010a, p.12) Q_β corresponds to the 'proportional effective species turnover' with an order of diversity $q = 2$. The turnover formula is thus:

$$Q_a = \frac{D_\gamma - D_\alpha}{D_\gamma} = \frac{Q_\gamma - \overline{Q}_\alpha}{1 - \overline{Q}_\alpha} \qquad (3)$$

where $\overline{Q}_\alpha$ is the mean quadratic entropy of the selected plots, and Q_γ is the quadratic entropy including all species from the selected plots. To calculate Q_α, $p_i = p_j = 1/S_x$ when the species is present (S_x is the species richness of the xth plot) and $p_i = p_j = 0$ when the species is absent. To calculate Q_γ, p_i is the mean across all plots x of all p_{ix} (de Bello *et al.*, 2010).

We measured the Rao beta-diversity index using the 'disc' function in the 'ade4' R software package (Rao, 1982). The values were then multiplied by 100 and therefore range from 0 (no turnover) to 100 (complete turnover). A comparison with other indices is included in Appendix S1. In our case the chosen index is very similar to the Jaccard index used in a similar study (Manthey *et al.*, 2011), because there are neither abundance data nor distances between species (Pearson's product–moment correlation coefficient between the two indices = 0.9944, see Appendix S1).

In order to compare the observed values to the random expectations for theta distribution we performed a null model analysis that assumed there to be no niche constraint or dispersal limitation. We computed the turnover among 10 plots randomly selected in the dataset 999 times. This allowed us to estimate the potential range of theta across the study region, for the same number of sampling sites.

A species' niche breadth has often been seen as a property of a species related to species rarity (Rabinowitz *et al.*, 1986). Here we explored the relationship between the specialization index, which measures the ecological range of a species, and two facets of species rarity at regional and local spatial scales (Gaston, 1997). The regional rarity referred to each species' area of occupancy in the study region. This area was estimated by a convex hull, which is the smallest polygon containing all line segments between each pair of species occurrences. This method is relatively widely used in ecology to measure area (for a recent example see Cornwell *et al.*, 2006). We used the function 'calcConvexHull' in the R package 'PBSmapping' (for the algorithm, see Eddy, 1977). This function computed the convex hull polygon from a set of points. The local rarity referred to local abundance. It was measured from the average local relative abundance of a given species across all sample sites. This measurement therefore captures the mean dominance of each species within the communities where it occurs (Kunin & Gaston, 1993; Kunin, 1997). To describe the relationship between the specialization and the two rarity measurements, we used generalized least squares regressions that account for heterogeneous variance in the residuals (Durbin–Watson test for homogeneity rejected: P-values < 0.01). We used the function 'gls' in the R package 'nlme', with the variance increasing or decreasing as a power of the absolute fitted values. The proportion of variance explained was estimated by the adjusted R^2 of the regression between observed and predicted theta values.

All comparisons between plant specialization and ecological characteristics (life span, Raunkiaer life-forms and Grime strategies) were made using Fisher tests or the Kruskal–Wallis nonparametric test of means when variances were too heterogeneous between groups. All statistical analyses were carried out using R 2.11 software (R Development Core Team, 2010).

RESULTS

Overall patterns of species specialization

The 1216 species analysed showed a skewed distribution of theta ranging between 35 and 80. For all species, the specialization index was lower than random expectation (ranging from 81 to 90; Fig. 2a), which implies strong niche differentiation in the plant communities investigated (plant species did not co-occur randomly). This comparison with the null model ensured that the ecological range of the study area

is large enough to capture the ecological limits of most study species. The average standard deviation per species was 2.9 (6% of the total range of theta for all species in the study). This sta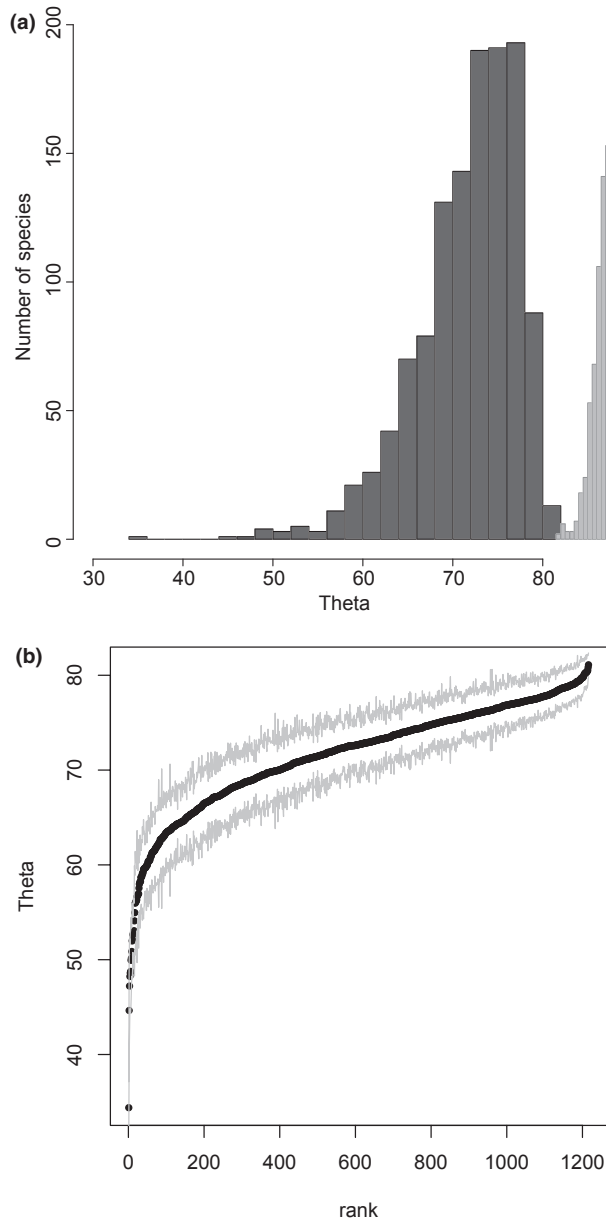ndard deviation was negatively correlated with the theta estimate (see Fig. 2b), indicating that generalist species tend to yield theta estimates with a lower standard deviation. This relationship has already been observed and seems to be inherent to the method (see Fridley et al., 2007). We were able to draw out a group of super-specialist species with theta values under 60. These species were found in various habitats, but most of them preferentially occurred in wetland, dry scrublands or alpine habitats (Fig. 3). The three most specialist were typical peat bog species (*Scheuchzeria palustris*, *Carex limosa* and *Drosera rotundifolia*). Other highly specialized species were alpine marsh species (*Carex maritima* and *Carex microglochin*) and alpine grassland species from windy crests (*Minuartia recurva*) or late-melting snow-beds (*Pedicularis ascendens*). Species associated with dry Mediterranean scrublands were also highly specialized (*Ruta angustifolia*, *Rosmarinus officinalis*, *Fumana thymifolia*, *Coris monspeliensis*, *Lonicera implexa* and *Globularia alypum*). Only one scree species (*Viola cenisia*) was found among the highly specialized species. Finally, some specialists were associated with habitats disturbed by humans (*Setaria pumila*, *Digitaria sanguinalis*, *Panicum capillare* and *Setaria viridis*).
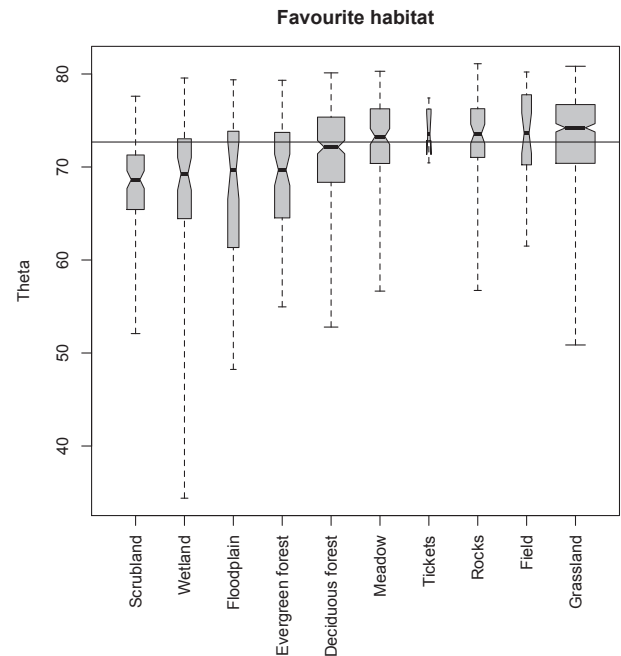

Figure 2 Specialization index distribution for 1216 French alpine plants. (a) Distribution of the specialization index and its associated null model. The specialization index theta ranges from 0 (specialist) to 100 (generalist). The light grey histogram represents 999 random turnovers of species across 10 plots of the area studied. The dark grey histogram contains the mean observed values for 10 plots containing each focal species. All the random values are above the mean observed values by species. (b) Specialization index and standard error around the estimator. The black dots indicate the specialization index (theta). Two grey lines are plotted at theta ± standard deviation. Species are ranked according to their specialization index.

Figure 3 Specialization index among 1216 French alpine plants grouped according to their favourite habitats. Box plots show extremes values and quartiles. The horizontal line indicates the median theta for all species. The black dots represent the most specialized species. Widths are proportional to the square root of the number of species in each class. If the notches for two plots do not overlap then the medians are significantly different at $\alpha = 0.05$. The theta index ranges from 0 (specialist) to 100 (generalist). The means for each group are significantly different (Kruskal–Wallis rank sum test: *P*-value $< 2.2 \times 10^{-16}$).

Specialization and rarity

The specialization index was correlated with our two rarity measures. The comparison between specialization and species geographical ranges showed a positive trend, indicating that generalist species are usually widespread whilst specialist species tend to be geographically restricted (Fig. 4a). The
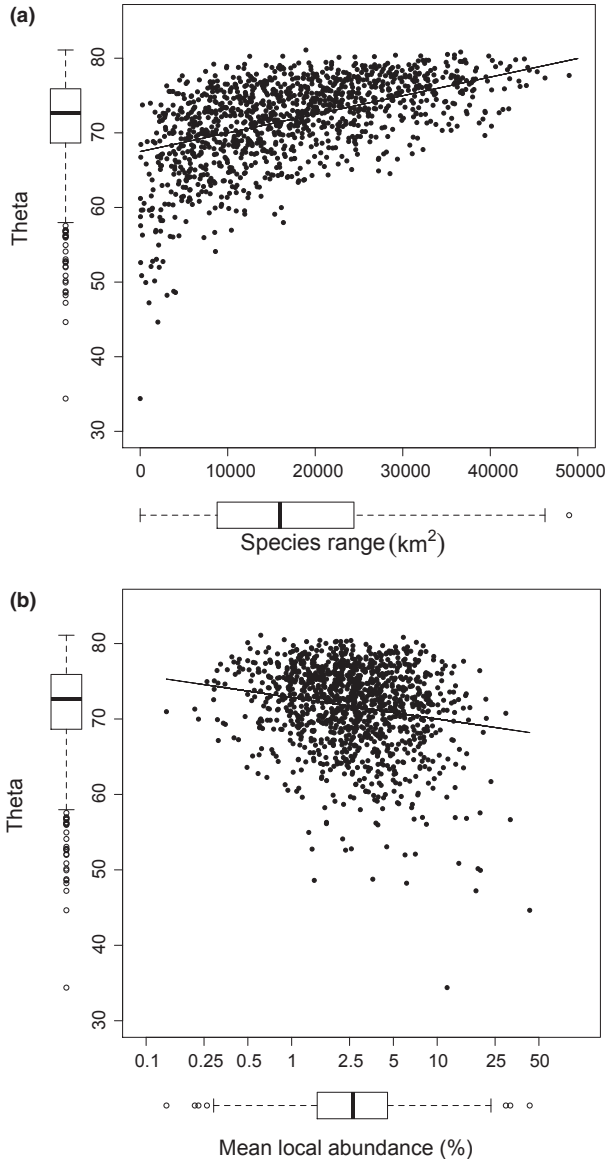
generalized least squares regression slope was significantly different from zero (P-value < 0.001) and the variance explained was meaningful (adjusted R^2 = 30.3%). However, some generalist species were detected even among species with
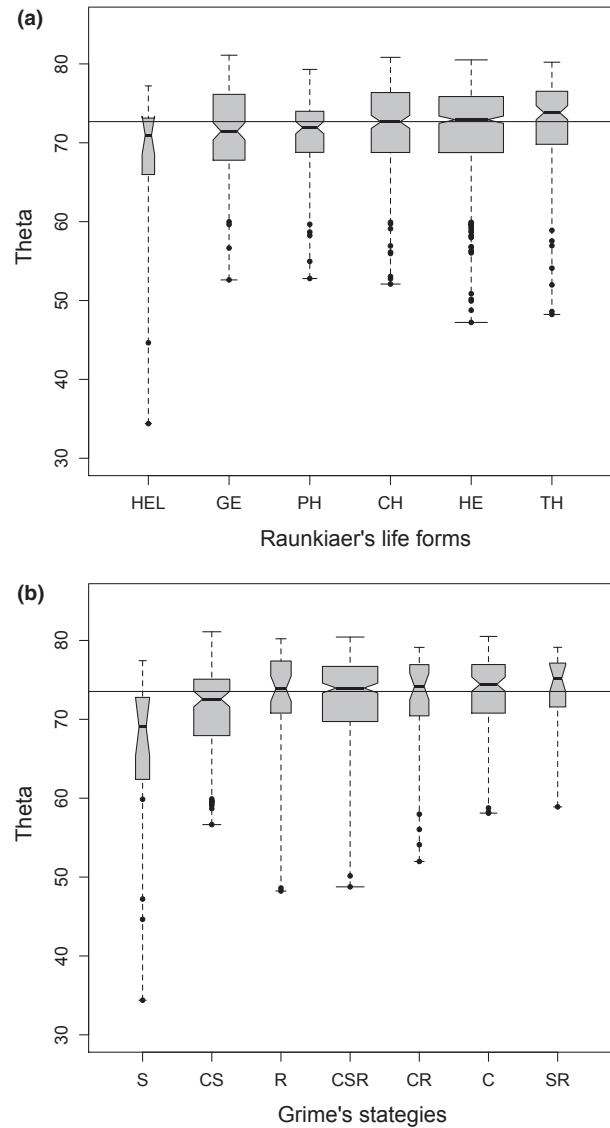

Figure 4 Specialization index of 1216 French alpine plants as a function of two different measures of rarity. Box plots along each axis show extreme values and quartiles. The middle line indicates the median value for all species. (a) Specialization as a function of the regional area of occupancy (km^2). The solid lines indicate the generalized least squares regression fit. The slope is significantly different from zero (P-value < 2×10^{-16}). Adjusted R^2 = 30.3%. (b) Specialization as a function of the logarithm of the mean relative abundance in the community plots where the species occurs. The solid lines indicate the generalized least squares regression fit. The x-axis is log-scaled. The slope is significantly different from zero (P-value < 2.2×10^{-16}). Adjusted R^2 = 4.5%.

Figure 5 Specialization index among 1216 French alpine plants grouped according to their traits. Box plots show extreme values and quartiles. The horizontal line indicates the median theta for all species. The black dots represent the most specialist species. Widths are proportional to the square root of the number of species in each class. If the notches for two plots do not overlap then the medians are significantly different at α = 0.05. The theta index ranges from 0 (specialist) to 100 (generalist). (a) Specialization index among Raunkiaer's life-forms. CH, chamaephytes; GE, geophytes; HE, hemicryptophytes; HEL, helophytes; PH, phanerophytes; TH, therophytes. The means for each group are significantly different (Kruskal–Wallis rank sum test: P-value = 0.02934). (b) Specialization index among Grime's strategies, for herbaceous species only (S, stress tolerator; C, competitor; R, ruderal). The means for each group are significantly different (Kruskal–Wallis rank sum test: P-value = 3.766×10^{-5}).

narrow geographical ranges, suggesting that high theta is not a mere by-product of a species' regional area of occupancy. Conversely the local abundance was negatively correlated with the specialization index (Fig. 4b), implying that specialist species (low theta) are more often dominant in their communities than generalist species (high theta). The linear regression slope was significantly different from zero (P-value < 0.001) while the model's goodness of fit was relatively low but still significant (adjusted R^2 = 4.5%).

Ecological characteristics and plant specialization

There was no significant relationship between species life span and species specialization, nor was there any significant difference in terms of specialization between the three broad life-history classes (Kruskal–Wallis rank sum test: P-value = 0.1238). However, the group of highly specialist species appeared in herbaceous classes only.

There were significant differences in species specialization between Raunkiaer life-forms (Kruskal–Wallis rank sum test: P-value = 0.02934, Fig. 5a). Therophyte species were mainly generalists, while helophytes, phanerophytes and geophytes were generally specialists.

As expected, there was a significant relationship between species specialization and their Grime classification (Kruskal–Wallis rank sum test: P-value = 3.766×10^{-5}, Fig. 5b). Stress-tolerant and stress-tolerant competitor species (S and CS, respectively) were more specialized. Pure competitors (C) were mostly generalists. There was no difference in the degree of specialization for ruderal and ruderal competitor species (R and CR) and for species with mixed strategies (CSR) in comparison with the mean specialization.

DISCUSSION

In this paper we aimed to use an extensive vegetation survey across the French Alps region, which encompasses a wide elevational gradient, to investigate the overall pattern of plant specialization. With regard to our first objective, we have indeed shown that specialized species tend to be found in specific habitats located on the edges of environmental gradients, namely xeric Mediterranean scrublands, wetlands or alpine grasslands. We have also demonstrated that specialist species appear to be over-represented in the hydrophyte and geophyte life-form classes, and are mainly associated with Grime's stress-tolerant strategy. Our analysis shows that habitat specialization positively correlates with a species' area of occupancy, and to a lesser extent inversely correlates with the species' local dominance.

An integrated index of specialization

The unbiased measurement of species specialization in a sample with a large number of species has always seemed problematic. The approach we use was shown by Fridley et al. (2007) to be unbiased with respect to the number of

occurrences for each species (Fridley et al., 2007). The same applies to our study, where the correlation between the specialization index and the frequency of occurrence is weak (adjusted R^2 = 4.6%, see Appendix S2) whilst the variance of this frequency of occurrence within the dataset increases with increasing species theta, which means that there are no specialist species with a high number of occurrences in the dataset (Appendix S2).

More generally, the use of an integrated index of specialization is appealing as it is intended to include numerous species niche axes, as well as factors that may explain species coexistence on the local community scale. Fridley's theta framework is particularly interesting because of the re-sampling procedure that accounts for differences in species frequencies. Another advantage of this framework is that it is more flexible on the underlying distance measurements, for instance when compared to an indirect gradient analysis such as DCA. Although both approaches produce highly correlated results (Pearson correlation with theta = 0.7, see Appendix S1), the DCA is based on a chi-square distance, which is not entirely comparable to turnover as measured by Rao, multiple Simpson or Jaccard indices.

A species-based niche breadth estimate is particularly useful in detecting local environmental effects, or niches axes that are only relevant for some species. For large-scale datasets, other methods based on species distributions and environmental data cannot include the local environment because this information is not usually documented in vegetation databases and it cannot be inferred from large-scale environmental data. Although high-resolution climatic data and land-cover variables are increasingly available (Hijmans et al., 2005), they are usually interpolated or modelled data with uncertainties inherent in the process and are therefore unable to capture local information or even landscape heterogeneity. We show that using a direct ordination method (the OMI) with six topographic and climatic variables results in a similar species ordination (Pearson's correlation with theta = 0.45, see Appendix S1). This result is not entirely surprising because we pre-selected six variables that explain most of the environmental variation across the entire study area but probably fail to describe the local environmental conditions that explain species coexistence and species-specific requirements. By using species as indirect indicators of the environment we are able to take local conditions into account. With the same approach, Manthey et al. (2011) suggest that some microenvironmental factors that are usually not taken into account may have led to overestimating the effect of competition between species. We also reveal the importance of the local environmental conditions defined by the vegetation structure. For instance, Juncus subnodulosus makes dense tussocks that may exclude other species in the community, creating a very specific habitat. Another example of the effect of vegetation structure is the impact of forest trees on the herbaceous plant undergrowth. In dark forests such as beech–fir (Fagus–Abies) forests we found a large proportion of specialist species, which could be explained by the effects of trees on herbaceous species (e.g. limiting light

availability, retaining soil moisture). Furthermore, the canopy, which provides various levels of resource-related stress, is known to change competitive relationships between species (Maestre *et al.*, 2009).

Which species are more likely to be specialized?

Theoretically, specialist species are confined to a small part of the ecological space where they can locally outcompete species belonging to the competitor strategy class, which are less adapted to a specific habitat (Wisheu, 1998). Our findings corroborate this hypothesis, as most specialist species are preferentially dominant in the communities where they occur (Fig. 4b). Specialist species are indeed mainly located in stressful habitats and co-occur with the few other species adapted to the extreme local conditions. Consequently, they tend to have high relative abundance. On the other hand, generalist species may be found in very rich communities where competition is intense, leading to high species evenness.

There is a positive correlation between the specialization index theta and the geographical range (P-value $< 2.2 \times 10^{-16}$, $R^2 = 30.3\%$). We did, however, observe that generalist species are not necessarily widespread because variance in the geographical range increases with increasing theta of a species. This pattern could be explained by a high level of environmental heterogeneity across the region and the landscape mosaics, implying that species experience a wide range of environmental conditions over a restricted territory. Although the spreading of species across 20,000 km^2 with a fairly low theta value has been observed, the more specialist the species are, the smaller their geographic range. This is certainly due to the main climatic gradients that are spatially autocorrelated (e.g. temperature). In this context, specialist species are more likely to be restricted to a small area due to their narrow tolerance of environmental conditions. However, some specific wetland specialized species, for instance, should be less sensitive to these gradients, implying relative independence between the geographical range and the ecological range. The observed spatial restriction of specialist species may relate to the effect of distance decay. As the species niche breadth is estimated from species co-occurrence, a wetland species may have high theta if it occurs in two distant sites that differ in species composition due to historical legacies and dispersal limitation.

In order to test whether some specialist species are hidden among generalists, we measured the number of distinct habitats used for every species, a commonly used measurement of niche breadth (Devictor *et al.*, 2010), and related it to theta. Although the habitats have been roughly defined, the two measures are consistent (Appendix S3; Kruskal–Wallis rank sum test: P-value $< 2.2 \times 10^{-16}$). In particular, species occurring in only one type of habitat have the lowest theta values. We therefore consider that theta is a satisfactory surrogate for

estimating plant specialization for numerous species occurring in a wide range of habitats.

These two results challenge the established macroecological rule which stipulates that regional distribution and local abundance are positively related (Gaston & Lawton, 1990), by showing that this relationship does not hold (and indeed tends to be inversed) for specialist species (Fig. 4) that are located in habitats that turn out to be peculiar on the regional scale. However, it is difficult to generalize such patterns because they are sensitive to the study scale and to the measures of regional and local abundances that are used.

Longevity attributes do not distinguish generalists from specialists. Nevertheless, specialist species are not randomly distributed across life-form classes. Therophytes are over-represented amongst generalist species, which may be explained by the fact that they are opportunistic and pioneering annual plants capable of colonizing bare ground after a disturbance, which could occur in very different habitats. However, some of these species may occur in very specific habitats with sandy or acid soils. Conversely, helophytes are disproportionately represented amongst specialist species, which may be due to the particular adaptations required by wetland habitats. The geophytes class also contains numerous specialist species, which could be explained by the fact that they invest resources in bulbs or rootstock which allows them to resist dryness or grazing (Hadar *et al.*, 1999; Jutila, 1999; Noy-Meir & Oron, 2001). This resistance mechanism implies a trade-off that limits the potential of species to adapt to a large range of habitats.

The comparison of the specialization index with Grime's strategies corresponded to expected trends. Pure competitors are overrepresented among generalists, whereas species classified as stress-tolerant tend to be specialists. Once again this may be viewed as an empirical validation of the tolerance–dominance trade-off (Wisheu, 1998). Species that are generally weak competitors may have found refuge and adapt at the extreme end of environmental gradients, where generalist species may fail to become dominant. On the other hand, competitive lotteries may allow pure competitors to become locally dominant over a wider range of habitats within the limits of their physiological tolerances, thus making them appear to be more generalist species.

CONCLUSIONS

In this paper we estimate niche specialization for a large number of plant species using an approach that makes it possible to account indirectly for various factors that either explain species coexistence on both regional and local community scales, or are only relevant for some specific species. Our results are an empirical validation of the tolerance–dominant trade-off, showing that specialist species are not strong competitors (*sensu* Grime's strategies), and generally find refuge on the stressful edges of environmental gradients, in communities where they tend to dominate.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Sensitivity analyses using several beta-diversity measures between plots and two ordination techniques.
Appendix S2 Specialization index for 1216 French alpine plants, according to the number of occurrences in the dataset.
Appendix S3 Specialization index for 1216 French alpine plants, according to the number of habitats in which a species occurs in the dataset.

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BIOSKETCH

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Author contributions: I.B., S.L. and W.T. designed the study; L.G and J.V.E. collected the data and helped to interpret it; I.B. ran the analyses and wrote the paper, with substantial contributions from W.T. and S.L.

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