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ECOGRAPHY

Research article

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Ecography
2023: e06504
doi: 10.1111/ecog.06504
Subject Editor:
Catherine H Graham
Editor-in-Chief:
Jens-Christian Svenning
Accepted 10 October 2022

Beyond the local abundance of species, their functional trait distinctiveness is now recognized as a key driver of community dynamics and ecosystem functioning. Yet, since the functional distinctiveness of a species is always relative to a given species pool, a species distinct at regional scale might not necessarily be distinct at local or community scale, and reciprocally. To assess the importance of scale (i.e. the definition of a species pool) when quantifying the functional distinctiveness of species, and how it might distort the ecological conclusions derived from it, we quantified trait distinctiveness of 1350 plant species at regional, local and community scales over ca 88 000 grassland plots in France. We measured differences in functional distinctiveness of species between regional (mainland France), local (10 × 10 km cell) and community (10 × 10 m plot) scale, and tested the influence of environmental predictors (climate and nitrogen input) and contexts (environmental distinctiveness, frequency and heterogeneity) on these variations. In line with theoretical expectations, we found large variation in functional distinctiveness (in particular between regional and community scales) for many species, with a general tendency of lower distinctiveness at smaller scales. We also showed that nitrogen input – a key aspect of high land use intensity – and environmental frequency partly explained the differences between local and regional scale only. These results suggest the role played by environmental filtering on species distinctiveness at local scale, but the determinant of distinctiveness variations at community scale still need to be elucidated. Our study provides robust empirical evidence that measures of ecological originality are strongly scale-dependent. We urge ecologists to carefully consider the scale at which they measure distinctiveness, as ignoring scale dependencies could lead to biased (or even entirely wrong) conclusions when not considered at the scale of interest for the respective research question.

Keywords: community ecology, ecological originality, leaf traits, trait-based ecology

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Introduction

The dynamics and assembly of ecological communities are influenced by the abundance and the trait values of species within a given environmental context (McGill et al. 2006, Weiher et al. 2011). Similarly, ecosystem processes are partly determined by the trait values of the most abundant species (Díaz and Cabido 2001, Lavorel and Garnier 2002, Cadotte et al. 2011). Functional trait-based ecology has traditionally relied on community-aggregated properties, which tend to focus on dominant species (Grime and Society 1998, Garnier et al. 2004) as they represent optimal phenotypes in a given environment (Denelle et al. 2019).

Although the concept of trait originality is not new (Pavoine et al. 2005), recently the distinctiveness of traits held by a species has gained interest in trait-based ecology (Violle et al. 2017, Kondratyeva et al. 2019). The functional trait distinctiveness of a species (sensu Violle et al. 2017) is the degree to which the trait values of a given species differs from the trait values of the other species within an assemblage. Functionally distinct species may enhance the long-term insurance (i.e. the maintenance of ecosystem functioning against loss of functions) and resilience (i.e. the recovery of ecosystem functions after perturbation) of ecosystems undergoing environmental changes (Yachi and Loreau 1999) because those species sustain functions that are not performed by other species (Jaillard et al. 2021), and increase ecosystem functionality through complementarity mechanisms (Loreau 1998, Hooper et al. 2005, Delalandre et al. 2022). There is therefore a fundamental interest in documenting the distribution of functionally distinct species (Grenié et al. 2018, Loiseau et al. 2020) and identifying its potential determinants (Fournier et al. 2020, Kondratyeva et al. 2020).

Species functional distinctiveness has been mainly studied at global (Thuiller et al. 2015, 2020, Grenié et al. 2018, Loiseau et al. 2020) and regional scales (Echeverría-Londoño et al. 2018), but also at local scales (Mouillot et al. 2013, Rosatti et al. 2015, Chapman et al. 2018, Kondratyeva et al. 2020) without considering how the scale of study might influence the revealed patterns and conclusions. However, because species functional distinctiveness is relative to a given assemblage, its value strongly depends on the spatial scale at which this assemblage is defined (Hartley and Kunin 2003, Münkemüller et al. 2014, Kondratyeva et al. 2020). While widely recognized in community ecology (Levin 1992, Chave 2013, Münkemüller et al. 2014, Chase et al. 2018, Kondratyeva et al. 2019), this scale dependency is yet to be explicitly considered in empirical studies of functional distinctiveness. This is particularly important, considering the growing interest towards measuring and understanding patterns of functional distinctiveness across large spatial and taxonomic scales (Echeverría-Londoño et al. 2018, Loiseau et al. 2020).

To evaluate the scale-dependency of species functional distinctiveness, we consider three nested spatial scales (regional, local and community scale). Each scale has a corresponding species pool (regional pool, local pool, community) determined by the varying influence of ecological processes, following Zobel (2016). The regional pool corresponds to a set of species occurring in a particular region (i.e. the regional flora) and mainly results from evolutionary, biogeographical and historical processes. The local pool corresponds to the set of species occurring in a particular landscape that can potentially maintain viable populations because of the suitable local ecological conditions, and thus mainly results from the environmental filtering process. The community pool corresponds to the set of species observed within a plot, and results from both small-scale environmental filtering and biotic interactions (Fig. 1). Environmental filtering is expected to decrease assemblage trait dispersion between regional and local scale (Schellenberger Costa et al. 2017) (Fig. 1b – local pool A). The influence of environmental filtering on the local pool trait space can directly affect species distinctiveness measure at this scale, and different species will be differently affected depending on their situation in the regional trait space. At community scale (Fig. 1c) interspecific competition can further decrease (e.g. under hierarchical competition (Fig. 1c community B1) but also increase (e.g. under limiting similarity) trait dispersion (Kraft et al. 2008, Mayfield and Levine 2010, Paine et al. 2011), again with variable consequences on the measured species distinctiveness at community scale. Although both environmental filtering and biotic interactions drive community assembly, it is often assumed that the effect of environmental filtering is stronger at regional-to-local scales, and the effect of biotic interactions is stronger at local-to-community scales (Zobel et al. 1998). These expectations provide a basis to identify and interpret the scale dependency of species functional distinctiveness, and can help to better understand the processes governing its spatial variation. They indicate that:

1) There will be, on average, a decrease in distinctiveness with decreasing scale because environmental filtering should generally filter species with more similar traits at a lower scale (e.g. species D1 in local pool A and community B1, species D2 in local pool B, Fig. 1).
2) Depending on locations and contexts, however, a species can exhibit either an increase or decrease in distinctiveness depending on the local effect of environmental filtering on species assemblage (species D1 in local pool A versus local pool b, Fig. 1).
3) The pathways through which processes influence distinctiveness are multiple and context-dependent, and thus not predictable across large datasets and various contexts.
4) Environmental characteristics will broadly influence patterns of scale dependency of species functional distinctiveness as they indirectly influence the relative effect of different assembly processes.

Although trait mean values are known to vary with environmental gradients (Keddy 1992, Lavorel and Garnier 2002, Blonder et al. 2018, Šímová et al. 2018, Boonman et al. 2020), the environmental determinants of functional distinctiveness are less understood. First, we can expect climate and land use to affect the distinctiveness measured at different scales because their effect on trait composition and diversity varies across scales (Ordoñez et al. 2009, Borgy et al. 2017a).

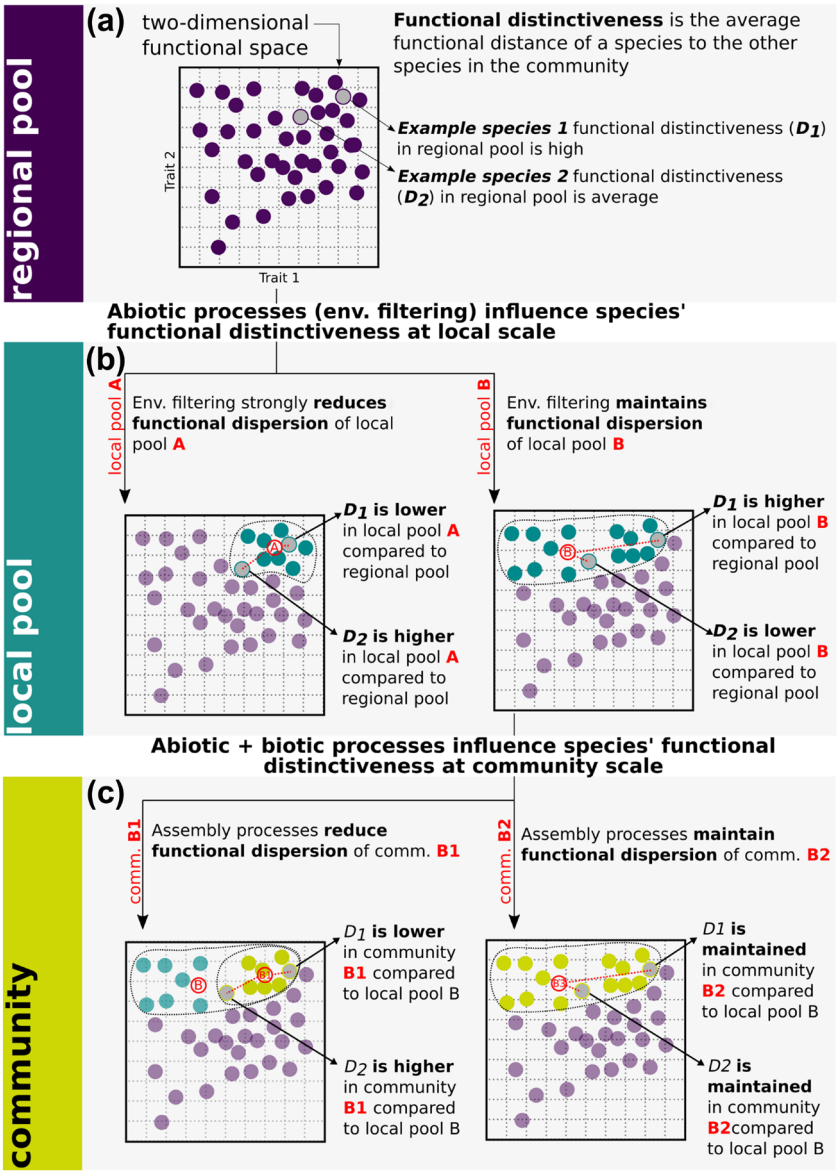

Figure 1. Theoretical expectations underpinning the scale-dependency of functional distinctiveness, with some example scenarios. In a given assemblage, species traits delineate functional space from which we can compute species functional distinctiveness as the average functional distance of the species to the other species (Grenié et al. 2017). The regional pool (purple) is mainly shaped by biogeography and evolutionary history. We assume that the local pool (green) is mainly shaped by environmental filtering that affects the trait space differently depending on the site. Between regional and local scales, species functional distinctiveness can increase or decrease depending on the functional dispersion of the local pool. The community (yellow) is mainly shaped by biotic processes. Different biotic processes (e.g. competitive dominance, limiting similarity, facilitation) and their relative weights differently affect the community trait space. Between local and community scales, species functional distinctiveness can increase, be maintained or decrease, depending on community functional dispersion.

Second, when traits are linked to resource acquisition and use, functional distinctiveness should reflect species ecological specialization to the environment (Willis et al. 2009). In this case, particular properties of the local environment such as the environmental distinctiveness (how much local environmental conditions differ from conditions in the surrounding area), environmental frequency (the rarity/commonness of the local conditions) and environmental heterogeneity (the local diversity of the environmental conditions) might also influence species functional distinctiveness differently across scale. For example, harsh environmental conditions (particularly dry, or cold or low in nutriment) might filter species with specific trait values that provide adaptation to these environments. Given those particular traits, the species can be distinct at the regional scale because they are different from other species at this scale. However, species with these similar and regionally distinct traits are filtered by harsh conditions locally, hence lowering their distinctiveness in regard to the local pool. Similarly, when such environments are distinct (i.e. different from the surrounding area) and rare (i.e. not

frequently found in the surrounding area), the distinct traits that provide adaptation to those environments can be held by a limited number of specialized species, hence strengthening the decrease in distinctiveness between regional and local (or community) scales for those species in these particular environments. To date, a single empirical study has emphasized the potential of environmental frequency and heterogeneity to explain functional distinctiveness and ecological specialization (Fournier et al. 2020). The explicit consideration of the scale-dependency of both biological and environmental features should help to clarify the environmental determinants of species functional distinctiveness.

Here, we address this challenge by studying the variation in species functional distinctiveness between the regional scale (at which it is commonly considered) and the local scale or the community scale, and identifying their main environmental determinants. We specifically addressed the following two questions:

Q1. How does species functional distinctiveness vary between regional, local and community scales?
Q2. How much of this variation is related to environmental conditions (climate and land-use intensity) and environmental distinctiveness, frequency and heterogeneity?

To do so, we focused on grassland plant species across mainland France, which we considered as the 'regional scale' (~550 000 km^2, Fig. 2). We combined a comprehensive plant species occurrences database (4447 cells of 10 × 10 km, i.e. the 'local scale'), with an extensive vegetation plot database (87 991 vegetation plots of varying area between 5 × 5 m and 10 × 10 m, i.e. the 'community scale'). We calculated functional distinctiveness for a large number of species (n = 1350) based on five functional traits (specific leaf area, leaf area, leaf dry matter content, maximum plant height and seed mass) summarizing plant ecological strategies (Díaz et al. 2016). We then assessed the effects of five environmental predictors describing the climate (growing season length), the management intensity (nitrogen inputs), the environmental distinctiveness, frequency and heterogeneity on the variation in plant functional distinctiveness across scales. Growing season length and nitrogen inputs represent climatic and nutrient stress gradients for plants, and are known to have strong interacting effects on leaf traits. In European grasslands, long growing season length and high nitrogen input have been linked to the predominance of species with high resource acquisition (high Specific Leaf Area (SLA), high Leaf Nitrogen Content (LNC) and low Leaf Dry Matter Content (LDMC)) via relaxation of climatic and nutrient constraints (Borgy et al. 2017a). Further analyses (Borgy et al. 2017a) indicated that grasslands under high nitrogen inputs and growing season length had a reduced species compositional turnover.

Material and methods

Vegetation data across assemblages

We defined the community scale as the set of species present in a vegetation plot. We used community vegetation data (occurrences) on 96 183 botanical plots of varying area (5 × 5–10 × 10 m) located in permanent grasslands in France (DIVGRASS database) (Violle et al. 2015). These vegetation data include permanent grasslands composed of 'perennial or self-seeding annual forage species which may persist indefinitely' which are managed but not cultivated or seeded (Allen et al. 2011, Violle et al. 2015). The dataset covers a broad extent of the climate space covered by European grasslands (Borgy et al. 2017a). Focusing on grassland plant species allows us to study a consistent set of species and, in particular, avoids our results being influenced by the dichotomy existing between two functional hotspots (woody plants mainly found in forest versus herbaceous plants mainly found in grasslands) (Díaz et al. 2016).

We retained a set of 1350 species (of the original 2648 species) for which we could gather trait information (see next section). The rarity/commonness did not differ among the selected and non-selected species, and the species functional distinctiveness and species commonness were not related within the set of selected species (see Supporting information for details of species distinctiveness and commonness). We excluded communities with fewer than eleven species to avoid undersampled communities and limit numeric

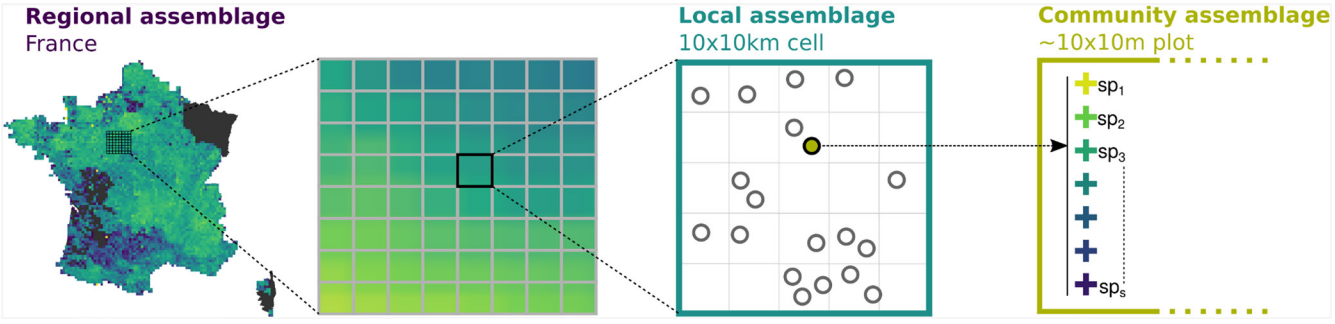

Figure 2. Definition of organizational and spatial scales proposed to study the scale-dependency of plant functional distinctiveness in France, and how variation in functional distinctiveness is defined across scale. In the map (left), color scale shows the completeness of the Siflore floristic inventory in each 10 × 10 km cell: the lighter, the more complete (Just et al. 2015). Community assemblage data came from the Divgrass botanical survey (Violle et al. 2015) with varying sizes from 5 × 5 m to 10 × 10 m.

stochasticity while keeping a large number of communities. Vegetation plots were geolocated with a precision of 1000 m on average (97.8% of plots are geolocated with a precision of 704 or 1137 m). We excluded communities for which geolocation information appeared incorrect or with a precision coarser than 5 km. This selection provided a final set of 87 991 community plots (Fig. 2).

We defined the local scale assemblage as the set of species present in a 10 × 10 km cell (10 000 km^2). We defined the local scale assemblage as the set of species present in a 10 × 10 km cell (10 000 km^2). We used data (list of species) from the electronic atlas of the French flora (http://siflore.fcbn.fr, Just et al. 2015) for our 1350 species to get local assemblages. These atlas data, for which the original scale of recording is the administrative territory of a municipality, are aggregated at a resolution level of 10 × 10 km in order to capture environmental conditions at landscape level and to accommodate the uncertainty of community geolocalization. We excluded grid cells with fewer than 150 species as they were considered as undersampled (Just et al. 2015). This selection provided a final set of 4456 (out of 5252 before filtering) 10 × 10 km grid cells covering most of the French territory (Fig. 2).

We defined the regional assemblage as the entire set of 1350 plant species considered in the study covering mainland France (~550 000 km^2).

Plant trait data

We calculated species mean trait values using information from several databases and local datasets (including the TRY database (Kattge et al. 2020; see Thuiller et al. 2014, Violle et al. 2015 and Borgy et al. 2017b for details of trait compilation) for specific leaf area (m^2 kg^{-1}), maximum plant height (m), seed mass (g), leaf area (mm^2) and leaf dry matter content (mg g^{-1}). These traits are linked to resource acquisition, survival and reproduction (Violle et al. 2007), and have proved useful to capture variation in plant ecological strategies (Díaz et al. 2016). Specific leaf area and leaf dry matter content inform about the plant strategy regarding resource capture, usage and availability, i.e. the trade-off between resource uptake efficiency and lifespan (Wilson et al. 1999). Seed mass informs about the trade-off between fecundity and energy invested per offspring individual. Plant height is related to competitive ability for the light resource and avoidance of environmental stress (Westoby et al. 2002, Violle et al. 2009). Leaf area informs about the strategy of response to environmental stress (in particular drought) (Wright et al. 2017). We did not retain other potentially useful traits in order to increase species coverage. We log-10 transformed and scaled trait distributions once for further analyses (i.e. not scaling within each scale).

Species functional distinctiveness at different scales

We computed the functional distinctiveness of each species at each scale (regional, local, community) as the average functional distance (based on Euclidean distance of the transformed/scaled trait values using the *dist()* R function (www.r-project.org) of the focal species to the other species in the assemblage, following Grenié et al. (2017). Variation in species distinctiveness was mainly driven by variation in seed mass and leaf area, and to a lesser extent by plant height. Note that the species functional distinctiveness measure does not take the species abundance into account because 1) our study focused on the distinctiveness of traits regardless of the species abundance; and 2) even if abundance data were available at community scale as relative coverage, this measure is irrelevant and absent for the local scale. Since species functional distinctiveness and its variation were not correlated with species and the functional richness of the local or community scales (Pearson's product-moment correlation ranged between 0.0 and 0.19), we did not control distinctiveness values for species or functional richness of the assemblage.

Environmental predictors

We considered five environmental predictors. First, two predictors described environmental conditions known to affect the trait structure of herbaceous plant communities (Borgy et al. 2017a), growing season length (GSL) and nitrogen input. GSL depicts climatic influence on the growth of grassland species, and corresponds to the number of days in the year for which mean daily temperature is above 5°C and for which the ratio between soil available water content (mm) and soil water-holding capacity is > 20%. Total nitrogen input (kg ha^{-1}) depicts the intensity of grassland management, and corresponds to the sum of organic fertilization, mineral fertilization and nitrogen deposition. Organic fertilization is estimated from national surveys of the amount of nitrogen excreted by herbivores, mineral fertilization from statistics of the fertilization industry sector and nitrogen atmospheric deposition is provided by the European Monitoring and Evaluation Program (https://emep.int/mscw/mscw_moddata.html). We used raster data from Borgy et al. (2017a) at 5 × 5 km grid cells, aggregated at 10 × 10 km resolution or downscaled at 2 × 2 km resolution to match both local and community scales.

Three other predictors describing the distinctiveness, frequency and heterogeneity of environmental conditions were computed from ten uncorrelated bioclimatic variables and four soil variables. For the bioclimatic variables, we used mean annual Temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, annual precipitation, precipitation seasonality, precipitation of wettest quarter and precipitation of driest quarter from CHELSA (Karger et al. 2017) at a 30′ resolution (~ 655 m at 45° latitude, averaged for the period 1979–2013). We selected four soil variables (averaged between 0 and 60 cm depth) that we assumed to be relevant for plant establishment and growth via nutrient and water retention, extracted from the SoilGrid dataset at 250 m resolution (Hengl et al. 2017): cation exchange capacity of soil (cmol kg^{-1}), soil pH (× 10 KCl), available soil water capacity (volumetric fraction) and soil organic carbon stock (tons ha^{-1}). Bioclimatic and soil variables were reprojected to

Lambert 93 projection and were aggregated at 10 km resolution (local scale) and 2 km (community scale) resolutions through averaging. The latter resolution was chosen to match the weak GPS precision of the DIVGRASS vegetation plots (1 km in average). First, we performed a principal component analysis (PCA) on a correlation matrix (i.e. variables standardized to mean = 0 and variance = 1) on these 14 environmental variables. For each scale, we kept the first four axes (representing 83% of the total variance at regional scale). The 'regional environmental space' was defined by the four PCA axes of all 10 × 10 km cells in France. The 'local environmental space' was defined for each 10 × 10 km cell by the 25 subcells of 2 × 2 km included within each 10 × 10 km cell.

At the local scale, the environmental distinctiveness was calculated as the Euclidean distance between the environmental conditions of the cell and those of all the other cells of the regional environmental space. The environmental frequency was calculated as the density of environmental conditions of the cell within the regional environmental space. The environmental heterogeneity was calculated as the mean Euclidean distance between the environmental conditions of the 25 (2 × 2 km) subcells included in the cell following (Fournier et al. 2020).

At the community scale, the environmental distinctiveness was calculated as the Euclidean distance between the environmental conditions of the 2 × 2 km subcell (corresponding to a given community) and those of the other 25 subcells included in the 10 × 10 km cell. The environmental frequency was calculated as the density of environmental conditions of the subcell within the local environmental space. The environmental heterogeneity at community scale was the same as the environmental heterogeneity at local scale, as we consider that the heterogeneity of the landscape should be determinant for the community scale distinctiveness.

The five environmental predictors were not strongly correlated (Pearson's product moment correlation ranged from −0.02 to 0.48; see Supporting information for steps and computation of environmental predictors).

Analyses

To show how species distinctiveness varied across the scale of observation (Q1), we first represented the relationship between the regional distinctiveness of the 1350 species to their distinctiveness at the local and community scales, and computed the correlation between regional and local, and between regional and community scales. Second, we computed the difference between local and regional species distinctiveness for each of the 4456 cells and the difference between community and regional distinctiveness for each of the 87 991 plots. In order to map the spatial distribution of differences between scales, we averaged the difference between local and regional distinctiveness within each cell, and the difference between community and regional distinctiveness within each community.

To identify the environmental determinants that could explain variation in species distinctiveness across scales (Q2), we tested the effect of environmental predictors on the difference between local and regional scale distinctiveness (local model) and between community and regional scale distinctiveness (community model). Each model was a linear mixed effect model, where species distinctiveness differences were regressed against our five environmental determinants. The environmental determinants (growing season length, nitrogen input, environmental distinctiveness, environmental frequency and environmental heterogeneity) were calculated at the corresponding scale (see section "Environmental descriptors" above) and treated as fixed effects. The model was run using the *lmer()* function from the 'lme4' R package (Douglas Bates et al. 2015). Species ID was considered as a random effect on the intercept, to account for non-independence of values between species. We scaled and normalized the explanatory variables to facilitate comparisons between predictors. We checked the models' residuals for spatial patterns and deviation from normality, and did not find any clear spatial correlation nor strong deviation from normality (see Supporting information for model residuals). Marginal and conditional r-squared were computed using the function *r.squaredGLMM()* from the 'MuMIn' R package (www.r-project.org).

We also ran linear models based on cell- and community-averaged values of distinctiveness differences (Fig. 3) with similar fixed effect structure using the *lm()* function in order to test the effect of environmental descriptors while buffering the interspecific variability in distinctiveness differences within cell or community.

Results

Q1 | Species functional distinctiveness varies between scales

Regional scale and local scale species functional distinctiveness were strongly correlated (Fig. 3a, Pearson's correlation coefficient = 0.98), while regional and community scale distinctiveness were moderately correlated (Fig. 3b, Pearson's correlation coefficient = 0.77). The differences in distinctiveness between regional and local scales were moderate and ranged between −0.56 and 0.53 (Fig. 3c), corresponding to −28% and 19% in percentage of variation in their regional distinctiveness value. Differences between regional and community scales were stronger and ranged between −2.35 and 1.99 (Fig. 3d), corresponding to −95% and 192% in percentage of variation in their regional distinctiveness value.

Species functional distinctiveness was higher in the regional than in the local pool in 82.6% of the species/cell pairs (Fig. 3c), and higher in the local pool than the community in 79.3% of the species/plot pairs (Fig. 3d). Beyond this average decrease, there was a strong variability between species within a given cell or a given plot (see Supporting information for standard deviation of differences).

Averaging differences within cells revealed a clear spatial structure in (cell-averaged) differences between regional and

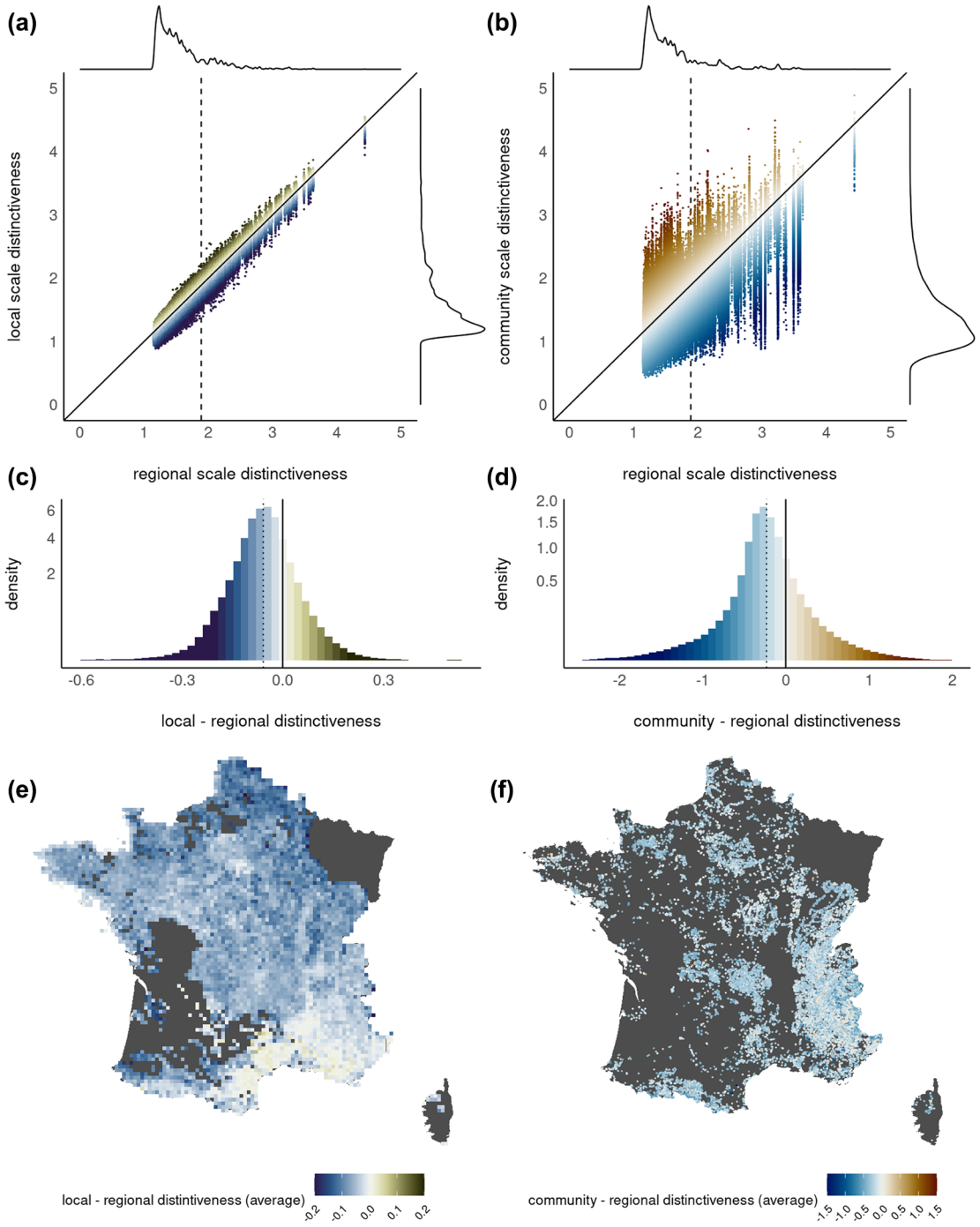

Figure 3. Variation in species functional distinctiveness between scales. (a and b) Scatterplots showing the relationship between regional and local (a) or community (b) species distinctiveness for the 1350 species. Point color shows the difference in distinctiveness values between regional and local or community scales, respectively, following values in (c) and (d). Marginal density distributions (black lines) plotted along the x and y axes show the distribution of values along the x and y axes, respectively. First bisector (one-one line) is represented by a solid black line. Vertical dashed blacklines represent the 1.88 regional distinctiveness value above which species are considered as part of the 10% most regionally distinct species. (c and d) Distribution of species functional distinctiveness differences between (c) local and regional scales (blue = decrease, green = increase) and (d) between regional and community scales (blue = decrease, brown = increase). One sample t-test showed that the distribution of distinctiveness differences was significantly lower than 0 for both local–regional ($t = -1163.1$, $df = 1\,785\,249$, p-value < 2.2e-16) and community–local ($t = -582.17$, $df = 860\,194$, p-value < 2.2e-16). (e and f) Spatial distribution of cell-averaged difference between (e) local and regional scale and (f) between community and regional scales. Black background shows French territory. Note that axis and color scales have different ranges between a–c–e and b–d–f. In both cases, grey zones correspond to missing vegetation data.

local scale, with negative differences in most of the study area, but null or positive differences in the south-east, i.e. Mediterranean area (Fig. 3e). However, we did not detect any clear spatial structure for the plot-averaged local to community variation (Fig. 3f).

We observed qualitatively similar patterns when focusing on the 10% most regionally distinct species (Supporting information). Differences between local and regional distinctiveness were more centered around 0, with only 66.2% of the species/cell pairs showing a decrease in distinctiveness; concerning the differences between community and regional distinctiveness, 84.5% of species/plot pairs showed a decrease in distinctiveness. The spatial distribution of cell-averaged and plot-averaged differences was also similar to the pattern described for the full set of species.

Q2 | Environmental drivers of scale dependency

A small part of the difference in species distinctiveness between local and regional scales was explained by the environmental predictors (local model, marginal $r^2 = 0.07$, conditional $r^2 = 0.45$). Species distinctiveness decreased more within cells with higher environmental frequency and nitrogen input, while it was the opposite for environmental heterogeneity (Fig. 4a). The explanatory power of environmental predictors (fixed effects) was relatively low compared to random effects because of the high variability of distinctiveness differences between species within a given cell. The explanatory power of the linear model based on cell-averaged values of distinctiveness differences was higher ($r^2 = 0.34$; see Supporting information for model based on cell averaged values).

The decrease in species distinctiveness between regional and community scale was not substantially related to our set of environmental predictors, as the explanatory power of the community model was very low (community model, marginal $r^2 = 0.01$, conditional $r^2 = 0.47$), even when considering community averaged values ($r^2 = 0.014$; see Supporting information for models based on cell average values).

Discussion

Our study highlights that species functional distinctiveness is scale dependent, and that many species exhibit substantial

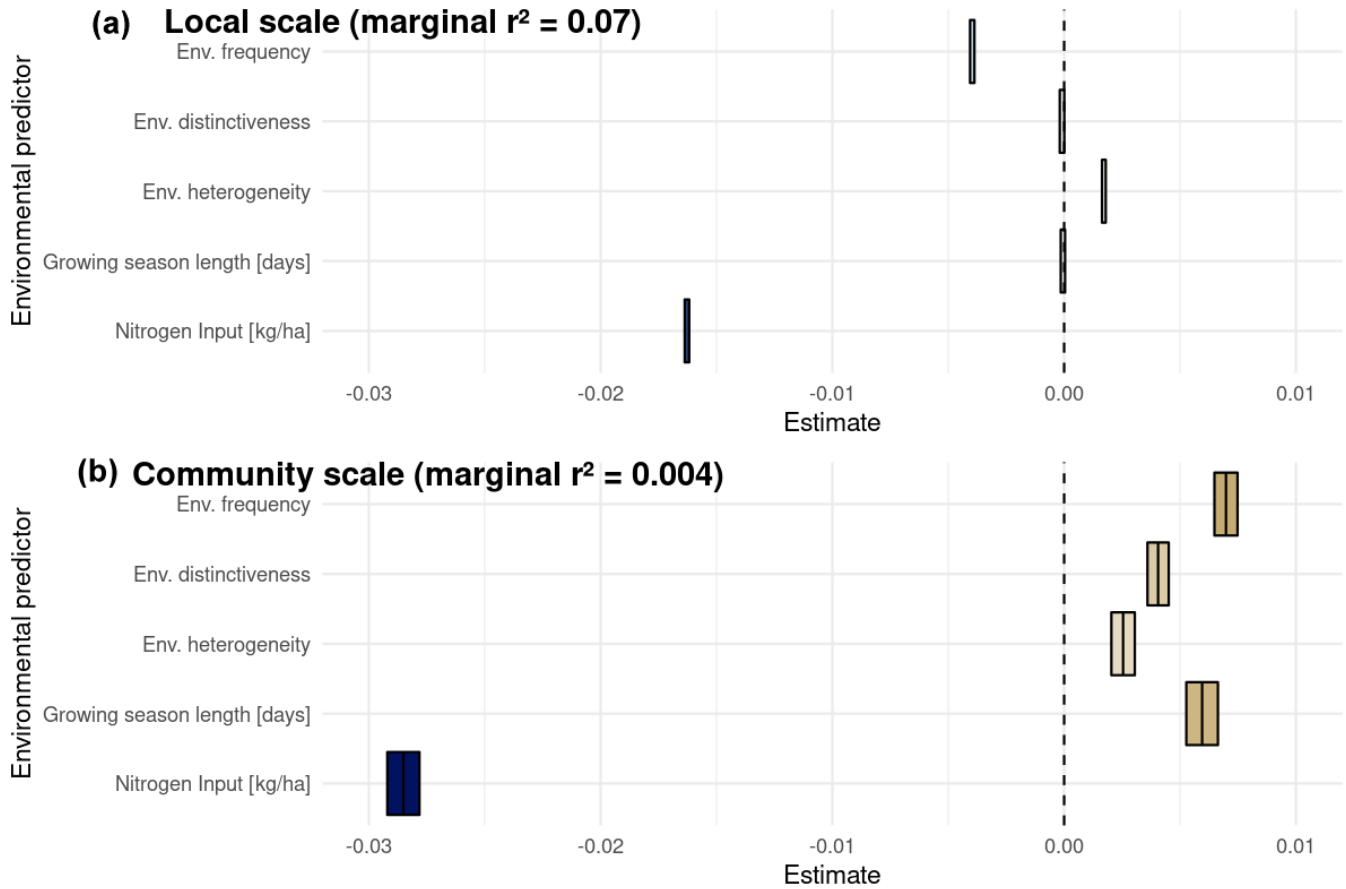

Figure 4. Environmental determinants of the scale dependency of species functional distinctiveness. Effect size for linear mixed effect models (x-axis) measuring the difference in species functional distinctiveness between local and regional scale (a) and community and regional scale (b), in response to environmental predictors (y-axis). Crossbars show model estimates (middle line) with 95% confidence intervals. See Supporting information for all details of model outputs.

variation in functional distinctiveness depending on the scale at which it is measured and reported. As expected from predictions in Fig. 1, we showed that species functional distinctiveness could either increase or decrease when transitioning from one scale to another. The direction of the change depends on the local context (e.g. species 1 in Fig. 1). We also revealed a general tendency towards a decrease in distinctiveness with decreasing scale, with stronger decreases in species distinctiveness for community than for local scale. This observation is in line with Kondratyeva et al. (2020), showing a strong variability with an overall decrease in species distinctiveness between regional and community scale in an urbanization context. We further showed that differences in species distinctiveness between scales were mainly influenced by nitrogen input at a local scale. This result is likely to be linked to the homogenizing trend of grassland previously related to high nitrogen input in Europe (Wesche et al. 2012, Buhk et al. 2017).

Variation in species distinctiveness between scales

The magnitude of distinctiveness differences represented up to a 27% decrease in the species regional values at local scale and up to a 94% decrease at community scale. These results indicate that, for many species, the scale-dependent nature of functional distinctiveness can directly affect whether a species is considered distinct or not, depending on the scale considered. Although we focus on results across all species and discuss general patterns of variation, our results and interpretations were consistent when focusing on the 10% most regionally distinct species, which are generally the focus of conservation biogeography studies (Grenié et al. 2018, Loiseau et al. 2020). On average, the 10% most distinct species at regional scale were not particularly distinct in 10.2% of the cells at local scale, and in 41.7% of the plots at community scale (see Supporting information for 10% most regionally distinct species).

Species-specific patterns of variation brought further insights on our understanding of functional distinctiveness (Supporting information). Again, we described many species-specific variation pathways, in line with theoretical expectations described in Fig. 1. In general, species largely distributed across the study area showed spatially structured distinctiveness differences at local scale, with the Mediterranean Basin consistently sheltering strong negative or positive variations. The distinctiveness of many species with low regional values tended to increase at local scale (compared to the regional scale) in the Mediterranean area, e.g. *Cichorium intybus* and *Helminthotheca echioides* (Supporting information). Some species with high regional values showed marked decreases in distinctiveness within Mediterranean local assemblages, e.g. *Carex humilis*, while others showed marked increase in distinctiveness e.g. *Asplenium ceterach* (Supporting information). This pattern is probably due to the biogeographic history and environmental conditions of the Mediterranean Basin (Myers et al. 2000) which lead to local assemblages with particular set of traits in this area. In turn, broadly distributed species appear more distinct in the Mediterranean local assemblages, and species mainly present in the Mediterranean basin appear less distinct elsewhere. Beyond this spatial structure, differences between regional and local scale distinctiveness were weaker than differences between regional and community scale, which partly results from the fact that 10 × 10 km is a quite large area to define a 'local scale'. Although it allows us to describe clear environmental gradients and fits the definition of species pools used here (Zobel 2016), the list of grassland species present in 10 × 10 km cells generally represents between 10% and 50% of the regional pool. Interestingly, looking at species-specific differences at the community scale also revealed spatial patterns for many species, e.g. following altitudinal gradients like *Minuartia verna* and *Silene nutans* (Supporting information).

Environmental predictors of functional distinctiveness variation

Overall, environmental predictors appeared to be weakly linked to the variation in species distinctiveness between regional and local or community scale. The first explanation lies in the fact that we focused on species-specific changes of distinctiveness across scales, while environmental determinants are measured for the whole assemblage. Within a local context, the effect of local environmental conditions on the distinctiveness differences of each species depends on the regional distinctiveness of the species and on the species environmental sensitivity and requirements. Hence, the strong idiosyncrasy observed in the species responses to local context limits the explanatory power of local and community scale environmental predictors. The effect of abiotic processes (environmental filtering) on the functional space at local scale can have contrasted effects on species distinctiveness depending on their regional distinctiveness and their trait values (Fig. 1). In our case, the decrease in species distinctiveness between regional and local scale mainly resulted from species with low to average regional distinctiveness situated in local pools with low functional dispersion (close to example species D2 in local pool A, Fig. 1), while most species situated in a local pool with high functional dispersion generally maintained their distinctiveness.

Beyond these species-specific responses, averaging distinctiveness differences across species within each cell clearly substantially increased the deviance explained by the model (see Supporting information for models based on cell averaged values). Nitrogen input had the strongest effect, with differences of species functional distinctiveness between regional and local scale decreasing more in localities with lower nitrogen input. Borgy et al. (2017a) showed that nitrogen input locally favors species with high resource acquisition (high SLA, high LNC and low LDMC). This environmental filtering on species traits tends to lower dispersion of species' trait values observed in cells with high nitrogen input (not shown), hence reducing the distinctiveness of species with high resource acquisition because they coexist locally with species having similar strategies. Overall, this result suggests an influence of

nitrogen input on species distinctiveness at local scale, and more generally on the functional composition of local assemblages in grasslands. High nitrogen input is a signature of intensely managed grasslands as this nutrient enrichment has the potential to increase net primary productivity (Elser et al. 2007, Stevens et al. 2015). In European grasslands, high nitrogen input is known to favour a few strongly competitive and generalist plants at the expense of many other specialized species, which enhance floristic homogenization and changes in trait composition (Walker et al. 2009, Wesche et al. 2012). Our study supports the view that nitrogen enrichment may reduce the diversity of terrestrial vegetation across scales through favoring common, fast-growing species adapted to high nutrient availability (Stevens et al. 2004, Suding et al. 2005, Hautier et al. 2014). Given the important role played by functionally distinct species on ecosystem functioning and stability at a local scale, further investigation of the consequence of eutrophication on the loss of unique functions and ecosystem functioning is needed.

The growing season length, however, was not related to the difference between local and regional distinctiveness, which was surprising given the strong structuring effect of this integrative climatic variable on the variation in average leaf trait composition (Borgy et al. 2017a). Beyond the structuring effect of nitrogen input, environmental frequency had a weak negative effect, with species distinctiveness decreasing more between regional and local scales in localities with rare environmental conditions. The general expectation is that more common environments should shelter higher proportions of regionally distinct species because 1) common environments increase the likelihood of locating suitable patches for species specialized on particular resources, and 2) indistinct/generalist species have competitive advantages in a broad range of environmental conditions (Ohlemüller et al. 2008, Denelle et al. 2020). This expectation is supported by empirical evidence of a positive relationship between the frequency of climatic conditions and functional diversity (Fournier et al. 2020). However, we here tested the influence of the environment on the difference of species distinctiveness between scales. In this case the distinctiveness difference is determined by the interaction between the species functional distinctiveness at the regional scale and the dispersion of species traits values in the local pool (or in the community). If more distinct species are more likely to occur in common environments, then assemblages in common environments tend to be more functionally diverse and dispersed (Fournier et al. 2020). The fact that species distinctiveness variation is itself linked to the assemblage functional dispersion is likely to underpin the negative relationship reported between environmental frequency and species distinctiveness differences.

At community scale, distinctiveness differences were not related to the characteristics of the local environment. This absence of explanatory power from environmental determinants likely results from the limited definition of environmental variables used at community scale. Indeed, the 2 × 2 km resolution of environmental variables (imposed by the lack of precision in the geolocation of DIVGRASS data) might be too coarse compared to the size of the vegetation plots (10 × 10 m). Indeed, environmental conditions within 10 × 10 m vegetation plots can largely vary within a given 2 × 2 km cell, in particular in montane landscapes. It should, nevertheless, be noted that a previous study quantifying trait–environment relationships on the same study system and data showed a clear environmental signal on leaf traits (Borgy et al. 2017a). A second potential bias lies in the use of species trait values averaged from global databases. Indeed, local abiotic and biotic contexts are known to affect trait expression at a local scale. This substantial variability reported between regional average and local-scale leaf trait measures (Baraloto et al. 2010, Paź-Dyderska et al. 2020) was not taken into account in our study and might blur the scale-dependence signal measured here. This intraspecific trait variation leads to challenging issues when applying species-averaged trait values in a local context (Albert et al. 2011). However, Borgy et al. (2017b) showed that this issue had low impact in our study system, as interspecific ranking based on leaf traits was conserved between species-averaged values based on global database and local measurements.

Note that several alternative determinants could also affect species distinctiveness at local and community scales. In a metacommunity perspective, differences in the size, history and connectivity of grasslands are likely to affect species dispersal and functional diversity (Plue et al. 2019), hence impacting the local distinctiveness of species. Examples include the presence of transient species in the community (Umaña et al. 2015, Snell Taylor et al. 2018), or the influence of long-term environmental stability (Ordonez and Svenning 2016, Blonder et al. 2018, Gaüzère et al. 2020). We did not incorporate these potential determinants in our study because of the absence of data (e.g. no abundance information for local pools) and/or because exploratory analyses showed weak support for potential effects of these determinants (see Supporting information for alternative determinants).

This said, the contrasted magnitude of environmental effects observed between local and community scale differences could be due to the relative effects of ecological processes acting at different scales. Indeed, at the local scale, environmental filtering is expected to prevail in structuring the local species pool, while internal filtering due to biotic interactions further drives community assembly and might – at least to some extent – blur the signal of environmental conditions on the scale dependency of functional distinctiveness (HilleRisLambers et al. 2012, Kraft et al. 2015).

Conclusion

Our study calls for consideration of scale dependency when studying functional distinctiveness. This consideration might have important implications because 1) functionally distinct species can play a unique and important role for ecosystem processes depending on the environment (Delalandre et al. 2022); and 2) the effect of functional distinctiveness on ecosystem processes should be mostly

relevant at local or community scales where the traits affect ecosystem processes (Walker et al. 1999, Yachi and Loreau 1999, Mouillot et al. 2013, Chapman et al. 2018). In the light of recent works suggesting the inclusion of ecological rarity when selecting or emphasizing (species-based) priority conservation areas (Grenié et al. 2018, Cooke et al. 2019, 2020, Loiseau et al. 2020), our results indicate that the local context and the spatial scale at which processes occur must be considered before actions or recommendations are taken based on a metric of species functional distinctiveness and functional rarity, otherwise choices might be strongly biased. Furthermore, our study paves the way for a better understanding of species functional distinctiveness across scales. In particular, the environmental filtering on species traits induced by high nitrogen input appeared as a structuring process in the perceived species distinctiveness at local scale, and calls for a thorough evaluation of the impact of nitrogen input on grasslands. The loss of important functions induced by land use intensity could have important consequences for grassland ecosystems functioning and stability. More generally, these patterns described in grassland ecosystems might be observed in other systems where strong and selective environmental filtering influence local trait combinations in regard to the regional pool (e.g. aridity in tropical forests) (de Oliveira et al. 2020). These insights are particularly important given the growing interest in understanding the role of species with distinct traits in community assembly, ecosystem dynamics and functioning, and in developing conservation strategies that preserve the most functionally distinct species.

Funding – This research was supported by the Fondation pour la Recherche sur la Biodiversité (FRB) and Electricité de France (EDF) in the context of the CESAB project 'Causes and consequences of functional rarity from local to global scales' (FREE).

Author contributions

Pierre Gaüzère: Conceptualization (lead); Formal analysis (lead); Writing – original draft (lead); Writing – review and editing (equal). **Benjamin Blonder**: Writing – review and editing (equal). **Pierre Denelle**: Writing – review and editing (equal). **Bertrand Fournier**: Writing – review and editing (equal). **Matthias Grenié**: Writing – review and editing (equal). **Léo Delalandre**: Writing – review and editing (equal). **Tamara Münkemüller**: Writing – review and editing (equal)**. Francois Munoz**: Writing – review and editing (equal). **Cyrille Violle**: Conceptualization (supporting); Writing – review and editing (equal). **Wilfried Thuiller**: Conceptualization (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/ecog.06504.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.9s4mw6mm3 (Gaüzère et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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