

RESEARCH ARTICLE

Common species contribute little to spatial patterns of functional diversity across scales in coastal grasslands

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Abstract

1. Spatial patterns of functional diversity are important in understanding community assembly as well as spatial variation in ecosystem functioning, yet the contribution of different species to these patterns remains unclear, making it difficult to generalise. Several studies have previously used a sequential addition approach to determine the subsets of species that contribute to the spatial distribution of species richness, frequently showing the importance of common species to richness patterns. This approach, however, has not been applied to functional diversity despite the central role of species traits in community ecology.
2. Here we use a multiscale survey of plants from the Machair grassland system of the Western Isles of Scotland to ask the following questions: (i) Do functional diversity patterns correlate better with geographically common or geographically rare species?; (ii) Do their relative contributions vary with spatial scale?; and (iii) Do these patterns vary between functional diversity measures?
3. We show that while species richness patterns correlate with geographically common species, common species contribute less than expected to spatial patterns of functional diversity at frequently used spatial monitoring scales. The relative contribution of species to overall biodiversity patterns, however, can vary with spatial scale.
4. *Synthesis.* Surveying only common species may be inadequate for estimating spatial patterns of functional diversity, especially if using occurrence as opposed to percentage cover or abundance data, and spatial scale needs to be considered when designing surveys. Our approach highlights the species that may be adequate indicators of different dimensions of biodiversity and contributes to our understanding of the distribution of functional diversity in space.

KEYWORDS

commonness, distribution, functional diversity, plant diversity, rarity, traits

1 | INTRODUCTION

The spatial distribution of biodiversity components such as functional diversity is of great interest to ecologists as it reflects

community assembly as well as the variation in ecosystem functioning in space. However, we are still uncertain how the distribution patterns of individual species contribute to overall biodiversity patterns, particularly functional diversity. Functional diversity

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is an important component of biodiversity that captures the extent of ecological trait differences within a community (de Bello et al., 2021) and determines both the response of communities to their environment and the effect of the community on ecosystem functioning (Lavorel & Garnier, 2002; Violle et al., 2007). Like taxonomic and phylogenetic dimensions of biodiversity, functional diversity varies in space. For plants, environmental factors including climate (Ordonez & Svenning, 2016; Wieczynski et al., 2019) and grazing (Carmona et al., 2012; Fischer et al., 2019) contribute to spatial variation in functional diversity; however, the contribution of individual species, and their attributes, to this spatial variation is yet to be determined.

The geographical rarity of species influences the observed spatial arrangement of biodiversity, yet there is no general consensus on whether common or rare species are more important for determining observed spatial biodiversity patterns. A handful of studies have investigated the contribution of common and rare species to spatial patterns of species richness, showing differential contributions of these species to spatial patterning, often with the richness of common species showing a higher correlation with overall species richness patterns (Lennon et al., 2004, 2011; Reddin et al., 2015; van Proosdij et al., 2016). However, whether the importance of common and rare species differs in the spatial patterning of other important biodiversity components, such as functional diversity, has not yet been investigated to our knowledge.

Lennon et al. (2004) developed a method to determine the contribution of geographically rare (narrow ranged) and geographically common (widespread) species to spatial patterns of species richness by ranking species by their geographic rarity and calculating the correlation between spatial patterns of species richness of different subassemblages compared to full assemblages. This methodology has been applied across multiple taxonomic groups in different geographic regions, frequently showing that common species contribute more than rare species to species richness patterns (e.g. Bregović et al., 2019; Pearman & Weber, 2007; van Schalkwyk et al., 2019; Vazquez & Gaston, 2004). This pattern can change, however, depending on whether correlations are plotted against the size of the subassemblage, that is its richness, or the amount of information the subassemblage holds, that is the sum of the binomial variances within the subassemblage (Reddin et al., 2015). By ranking species according to geographic rarity and applying methods to determine the contribution of rare and common species to functional diversity, we investigate how patterns and processes inferred for species richness translate to additional biodiversity components.

Although rare species have often been shown to contribute disproportionately to functional diversity (Jain et al., 2014; Leitão et al., 2016), these analyses do not incorporate the spatial distribution of diversity. By incorporating space into analyses of rarity and functional diversity, not only in terms of geographic rarity, but also spatial variation in biodiversity, we can determine the types of species that may be useful indicators of different biodiversity components including functional diversity. The analysis of how rarity

contributes to the spatial distribution of functional diversity will facilitate targeted surveying and trait data collection as well as contribute to our understanding of the distribution of functional diversity in space and the functional importance of rare species.

The contribution of common and rare species to spatial patterns of species richness depends on two properties of species distributions: the species-occupancy distribution and the species richness distribution (Heegaard et al., 2013). If geographically rare species are evenly distributed across the species richness gradient, then overall species richness will be correlated with common species, whereas if rare species only occur in the richest sites, then they will show a correlation with overall species richness. The same may hold true for functional diversity, and the contributions of individual species to spatial patterns of functional diversity may depend on the relative proportion of common and rare species in areas with low functional diversity.

Unless species show true fractality in their distribution, the contribution of geographically rare and common species to spatial biodiversity patterns is likely to be scale dependent. However, as the size of the lens we look through (or sample area) increases, we are likely to sample more species, following the species-area relationship. Therefore, the area of occupancy of rare species may increase with the spatial scale investigated and appear more common, thus influencing the size of the contribution made by rare and common species as we increase the sampling unit size.

To investigate the contribution of rare and common species to spatial patterns of functional diversity, we use a multiscale survey of plants from Machair grassland on the Western Isles of Scotland. The Machair system is a globally threatened habitat that is only found on the western coasts of Scotland and Ireland. Machair is an ecologically important, partially managed grassland with a high floristic diversity resulting from livestock grazing and some areas receiving rotational management of low intensity cropping (Angus & Dargie, 2002). The combination of low intensity, rotational agricultural management and fertilisation with kelp, alongside exposure to Atlantic storms, results in substantial spatio-temporal turnover of communities in terms of both their species and traits (White et al., 2018). The high diversity of the system and spatial heterogeneity provide a unique opportunity to assess macroecological patterns of biodiversity at a local scale with a unique dataset of plant percentage cover in nested quadrats at three spatial scales: 0.04 m × 0.04 m; 0.2 m × 0.2 m; and 1 m × 1 m.

In this study, we extend the method developed by Lennon et al. (2004) and apply it to the Machair system to investigate the contribution of geographically common and rare species to spatial patterns of species richness and two measures of functional diversity. These measures are functional dispersion (FD_{is}; Laliberté & Legendre, 2010) and Petchey and Gaston's dendrogram-based measure of functional diversity (PGFD; Petchey & Gaston, 2002). We analyse diversity patterns across four sampling scales to see how the contribution of common and rare species to spatial diversity patterns varies with spatial scale.

We determine the contribution of commonness and rarity to spatial diversity patterns and investigate the species and community

characteristics that may underlie differing contributions. We do this by (i) calculating the sequential correlations of the diversity of subassemblages of species to overall spatial diversity patterns; (ii) determining whether the 25% most common and most rare species differ in their functional diversity from what we would expect from random; and (iii) modelling how community diversity is related to the proportion of the community consisting of the 25% most common or most rare species.

2 | MATERIALS AND METHODS

2.1 | Overview

We describe the data collection in the Machair grassland of the Western Isles of Scotland and the ranking of commonness and rarity using the area of occupancy. We calculate the species richness and functional diversity of subassemblages of species and correlate this with the diversity of the full assemblage to determine which set of species better match overall spatial patterns of diversity. To investigate the components of species and trait distributions that lead to different contributions of common and rare species, we calculate the functional diversity of the 25% most common and most rare species, and determine how the proportion of species within a community that consists of these species influences observed species richness and functional diversity.

2.2 | Data

Plant percentage cover data were obtained from 19 Machair grassland sites across the Western Isles of Scotland collected in 2008 (see White et al., 2018). Each site was sampled at three nested quadrat scales: 0.04 m × 0.04 m; 0.2 m × 0.2 m; and 1 m × 1 m. Each of these quadrat scales was part of a 5 × 5 grid so that at each of the 19 sites, 25 quadrats were sampled at each of the three scales. This gives a total of 475 quadrats sampled per spatial scale, which we now refer to as plots. Plots of 1 m × 1 m were also aggregated at each site to give a total of 19 plots at the 5 m × 5 m scale. The spatial sampling design is shown in Figure S1. There were 58 species in total at the 0.04 m × 0.04 m sampling scale, 86 at the 0.2 m × 0.2 m sampling scale and 115 at the 1 m × 1 m and 5 m × 5 m sampling scales.

2.3 | Diversity calculations

The traits used to calculate functional diversity were canopy height, seed mass, SLA, leaf size (one-sided area of leaf), pollen vector (insect, selfing or wind) and mode of reproduction (seed or vegetative). These data were obtained from BioFlor (Klotz et al., 2002) and LEDA (Kleyer et al., 2008) trait databases. These traits were chosen as they have good coverage for the species present and reflect key

vegetative traits including the leaf-height-seed trait dimensions of Westoby (1998), leaf size, which is well-correlated with disturbance (Pakeman, 2011), and two reproductive traits that are related to other trophic levels (pollen vector) or to primary means of regeneration (mode of reproduction).

We calculated two measures of functional diversity of plant communities, namely PGFD and FDis. Functional dispersion captures the dispersion of species in trait space, that is are they clustered together or functionally very different, and can be calculated using either occurrence or abundance data. We use both occurrence (presence-absence) and percentage cover data to calculate two versions of the measure to investigate how the contribution of species depends on whether occurrence or abundance-weighted measures of functional diversity are used. Petchey and Gaston's measure, on the other hand, uses occurrence data and reflects the functional richness of species within a community through their functional similarity. Rao's quadratic entropy (RaoQ) and abundance-weighted RaoQ were also calculated. However, as FDis and RaoQ are inherently linked as they both estimate species dispersion in trait space (Laliberté & Legendre, 2010), we only present the results for FDis and abundance-weighted FDis in the main text. Additional results for RaoQ can be found in the Supporting Information and broadly match those of FDis (see Figures S2 and S3). We also calculated species richness.

PGFD calculates the total minimum branch length of a functional tree linking the species within a community (Petchey & Gaston, 2002, 2006). It is a multidimensional measure of functional richness (Schleuter et al., 2010) where higher values indicate greater complementarity of trait values, that is greater differences between species in terms of their traits (Petchey & Gaston, 2002). Firstly, we used Gower distances to create a distance matrix from the species-by-trait matrix. Gower distances allowed us to use both categorical and continuous traits and weight categorical traits according to the number of levels that trait has. For example, pollen vector (which has three levels) was given the same overall weight as the mode of reproduction (two levels) so that these two traits contribute equally to the calculation of functional diversity. Secondly, species pairwise functional distances were clustered using the group average method (UPGMA) as suggested by Podani and Schmera (2006), which has been shown to outperform other clustering methods (Clark et al., 2012) to produce a functional tree. PGFD was calculated using the *treedive* function in the R package 'VEGAN' (Oksanen et al., 2019).

FDis measures the dispersion of species in functional trait space by measuring the average distance of each species to the centroid of the community, which can be weighted by species abundances (Laliberté & Legendre, 2010). Lower values of FDis, therefore, represent clustering of species in trait space, that is the species are functionally similar in terms of their traits. Unlike PGFD, FDis is not inflated by species richness and can, in fact, decrease with higher numbers of species if the additional species are functionally similar to other species present in the community (Laliberté & Legendre, 2010).

FDis was calculated using the *dbFD* function in the R package 'FD' (Laliberté et al., 2014; Laliberté & Legendre, 2010) using both occurrence data and percentage cover. As with PGFD, we used Gower distances to calculate the functional dissimilarity of species. The distance matrix was then analysed using the principal coordinate analyses and the resulting axes used as traits. The species-by-species distance matrix could not be represented in Euclidean space and so a square root correction was used.

2.4 | Contribution of common and rare species to diversity metrics

We ranked the species according to their geographic rarity from common to rare, and rare to common at each spatial scale based on the number of plots at that scale that they appeared in. This represents the area of occupancy of each species. Equally ranked species were added in a random order. From these rankings, we generated a series of species richness and functional diversity patterns for subsets of the communities within each plot with increasing numbers of species (which we call subassemblages). The diversity measures of each of these subassemblages were correlated with the diversity measures of the full assemblage using Pearson's correlations.

To determine if these correlations using ranked subassemblages differed from what we might expect from random subassemblages, we took two randomisation approaches: one for species richness and one for the functional diversity measures. For species richness, we randomly added the species into the subassemblages 1000 times, maintaining the distribution of each species. For the functional diversity measures, we used a constrained randomisation approach—a random assembly model—where the species names were randomised in the species-by-trait matrix 500 times using the independent swap algorithm (Gotelli & Entsminger, 2003). Species were then added into the subassemblages in order from common to rare, and rare to common, and the functional diversity of each subassemblage calculated using the randomised species-by-trait matrix (i.e. 500 randomisations for each of the subassemblages in order from common to rare, and again from rare to common). This ensured that only the species traits of a species were randomised, while species richness and any trait covariances were constrained. Both randomisation approaches constrained the spatial autocorrelation of species occurrences (i.e. where species are present was not altered), which is important given the spatial structure of the data arising from the nested sampling protocol.

Unless they are ubiquitously present or absent, common and rare species, by their definition, hold different amounts of information if their range occupancy distribution is right-skewed, that is, a certain number of common species will hold more information than the same number of rare species if the common species' occupancy is closer to 50% than the rare species (Heegaard et al., 2013; Lennon et al., 2004). Therefore, emergent patterns between Pearson correlations and subassemblage richness (the number of species in the subassemblage)

may purely be a result of a statistical artefact. Using the cumulative information of species, rather than subassemblage richness, puts common and rare species on equal footing (Lennon et al., 2004; Reddin et al., 2015). We calculated the cumulative information content of each subassemblage as the sum of the binomial variance of each species presence-absence within the subassemblage $p(1-p)$, where p is the proportion of sites occupied by a species.

We plotted the Pearson correlation of the subassemblage with the full assemblage for each diversity metric against the cumulative information content for common-to-rare, and rare-to-common rankings. We used these to compare the contributions of common and rare species to spatial patterns of each of the diversity metrics so that if the common-to-rare curve increases at a higher rate than the rare-to-common curve, this shows that common species contribute more to the spatial pattern of diversity than rare species and vice versa.

2.5 | Functional diversity of most common and rare species

To determine whether common and rare species were more or less diverse in terms of their traits than expected, we identified the 25% most geographically common and geographically rare species at each spatial scale. We calculated FDis and PGFD of these species and compared this to the null distribution of FDis and PGFD of these species generated from 999 randomisations of species names in the species-by-trait matrix of all the species recorded in the surveys following the same independent swap algorithm as above. We calculated the p -values for the observed FDis and PGFD of the 25% most common and most rare species within the null probability distribution at each spatial scale to determine whether they were more or less diverse than we would expect from random using a two-tailed test, that is whether they fall outside the 2.5th percentiles of the distribution of values from the randomisations. We additionally tested this using the 33% most common and most rare species to see whether the result varied with the threshold set.

2.6 | Community composition on diversity

To test the suggestion of Heegaard et al. (2013) that the contribution of commonness and rarity to spatial diversity patterns depends on the distribution of rare species relative to the most diverse plots, we modelled diversity as a function of the proportion of the community comprising of the most common and most rare species. We calculated the proportion of the community in each plot that the 25% most common and most rare species made up. We then modelled log species richness, PGFD, FDis and abundance-weighted FDis using a Bayesian approach, with the predictor first being the proportion of the community made up of common species, and secondly the proportion of the community made up of rare species. These were included in separate models as by their calculation they are inherently linked and, therefore,

colinear. At the three smaller spatial scales, we used conditional autoregressive models which account for spatial autocorrelation within their error structure with the function *S.CARleroux* from the R package 'CARBAYES' (Lee, 2013). We used a distance matrix to identify all plots within the 5 × 5 sampling grid at each site (i.e. all plots at a particular spatial scale, at an individual site) to define the neighbourhood for the spatial weights. We set Rho to 1 for intrinsic conditional autoregressive models. Spatial priors were given a gamma distribution with shape 0.5 and scale 0.0005. At the 5 m × 5 m spatial scale, we assumed no spatial autocorrelation as there was only one 5 m × 5 m plot sampled at each site. We used the *MCMCglmm* function from the R package 'MCMCGLMM' (Hadfield, 2010) for GLMs at this scale. All models were carried out with uninformative priors and a Gaussian distribution. The chains were run for 50,000 iterations with a burn-in of 10,000. Convergence of all models was confirmed through visual inspection of the trace plots and the Geweke diagnostic.

3 | RESULTS

3.1 | Rarity distributions of Machair species

Area of occupancy and maximum percentage cover of species were similarly correlated across spatial scales with Pearson's correlation coefficients ranging from 0.44 at 5 m × 5 m to 0.52 at

0.20 m × 0.20 m (Figure S4). The frequency distributions of area of occupancy and mean percentage cover of species were both strongly right-skewed (Figure S5), that is there are more rare species than common ones. The percentage of species found only within a single plot (i.e. the most geographically rare) varied with the spatial scale of sampling: 17.2% at 0.04 m × 0.04 m; 11.6% at 0.2 m × 0.2 m; 12.2% at 1 m × 1 m; and 33.0% at 5 m × 5 m.

3.2 | Contribution of common and rare species to diversity

Across all biodiversity measures, the difference in contribution between common and rare species to overall spatial patterns appeared lowest at the 0.04 m × 0.04 m spatial scale, as at this scale the two curves increased at similar rates.

For species richness, the common-to-rare curve consistently fell within the 95% confidence intervals generated from the randomisations, that is the Pearson correlation between species richness calculated using the subassemblage and the full assemblage did not differ from what you would expect from random for any level of cumulative information (Figure 1). At the 0.2 m × 0.2 m scale and 1 m × 1 m scale, although common species appeared to contribute more to spatial patterns of species richness when added first (left end of yellow lines in Figure 1), when added to subassemblages already containing rare species, the observed

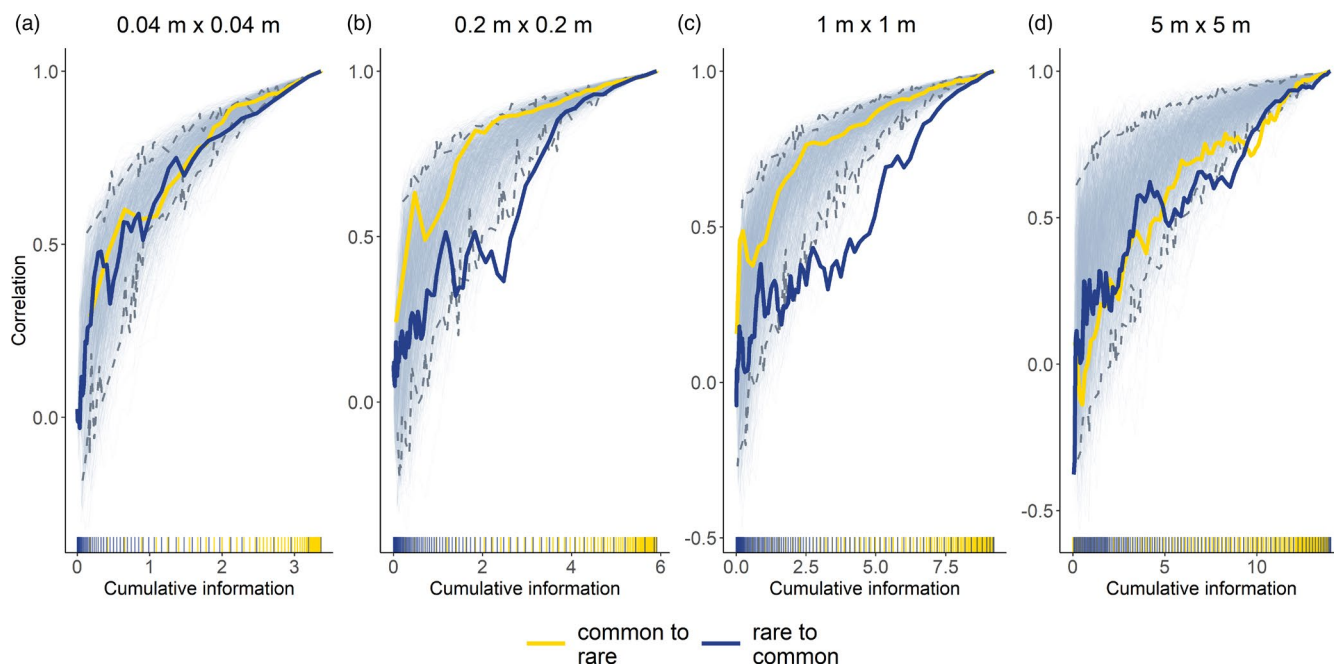


FIGURE 1 Sequential Pearson correlation coefficients between subassemblages and the full assemblage species richness at (a) 0.04 m × 0.04 m, (b) 0.2 m × 0.2 m, (c) 1 m × 1 m and (d) 5 m × 5 m. Species were added sequentially by rank from geographically rarest to geographically most common (dark blue line) and geographically most common to geographically rarest (yellow line). Blue-grey lines show 1000 randomisations with species added into subassemblages randomly and dashed lines indicate the 95% confidence intervals generated from the randomisations. Correlations are plotted against the cumulative information of the subassemblage calculated as the cumulative sum of the binomial variance of species within the subassemblage, $\sum p_i(1 - p_i)$, where p_i is the proportion of the study plots occupied by species, i . Rug plots indicate the distribution of data points for each curve

spatial pattern was less correlated than random (right end of blue line in Figure 1).

For the two measures of functional diversity that used occurrence data (FDis and PGFD), rare species gave closer approximations of spatial patterns of functional diversity than common species, particularly at the $1 \text{ m} \times 1 \text{ m}$ scale. Common species at the $0.2 \text{ m} \times 0.2 \text{ m}$ and $1 \text{ m} \times 1 \text{ m}$ scales for these two measures contributed to spatial patterns substantially less than expected from random as their correlation curves increased at a much slower rate (Figures 2 and 3). The curve fell below the 95% confidence interval for the subassemblages up to and including the 22 most common species at the $0.2 \text{ m} \times 0.2 \text{ m}$ scale for PGFD and FDis, the 29 most common species for PGFD at the $1 \text{ m} \times 1 \text{ m}$ spatial scale and 30 most common species for FDis at the $1 \text{ m} \times 1 \text{ m}$ spatial scale. When FDis was weighted by the percentage cover of species, the difference between the curves decreased and at the larger two spatial scales the common-to-rare curve lay above the rare-to-common curve indicating higher correlations with overall abundance-weighted FDis (Figure 4).

Generally, the 25% most common species fell to the left of the null distribution of functional diversity indicating that they were less functionally diverse than expected from random (negative standardised effect sizes), and the 25% rarest species fell to the right indicating they were more functionally diverse than expected from random (positive standardised effect sizes; Table 1). A two-tailed significance test showed this was only significant at the 5% level for PGFD at the $1 \text{ m} \times 1 \text{ m}$ spatial scale. Conversely, the 25% rarest

species were less functionally dispersed in trait space than you would expect from random at the $0.04 \text{ m} \times 0.04 \text{ m}$ scale. We additionally tested the functional diversity of the 33% most common and most rare species and found similar results in that only rare species at the $1 \text{ m} \times 1 \text{ m}$ spatial scale differed from random.

Diversity measures mostly showed a negative relationship with the proportion of common species that made up the community in each plot, and a weaker positive relationship with the proportion of rare species that made up the community in each plot. However, this result was not consistent at the $5 \text{ m} \times 5 \text{ m}$ spatial scale (Table 2).

4 | DISCUSSION

Spatial patterns of functional diversity based on occurrence data appear more accurately represented by geographically rare species than geographically common species as the sequential addition of species from rare to common often increased correlations with overall functional diversity faster than from common to rare. This, however, was not consistent across spatial scales or when percentage cover data were used. Previously, the importance of common species to species richness patterns (e.g. Kreft et al., 2006) has led authors to suggest that the comparison of species richness between areas with standardised sampling can be carried out using only common species (van Schalkwyk et al., 2019), allowing for rapid surveys. Our results, however, suggest that surveying common species only is

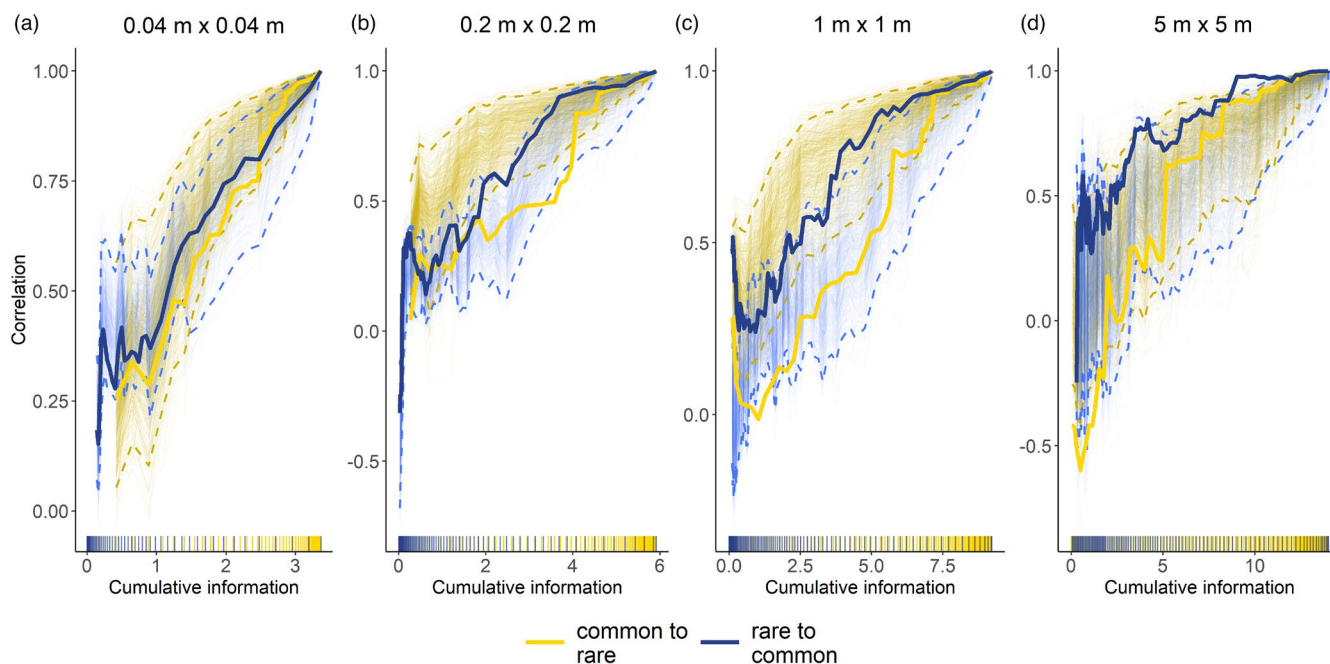


FIGURE 2 Sequential Pearson correlation coefficients between Petchey and Gaston's dendrogram-based measure of functional diversity of subassemblages and the full assemblage at (a) $0.04 \text{ m} \times 0.04 \text{ m}$, (b) $0.2 \text{ m} \times 0.2 \text{ m}$, (c) $1 \text{ m} \times 1 \text{ m}$ and (d) $5 \text{ m} \times 5 \text{ m}$. Species were added sequentially by rank from geographically rarest to geographically most common (dark blue line) and geographically most common to geographically rarest (dark yellow line). Light blue lines and gold lines show correlations where species were added in from rare to common and common to rare, respectively, where the species-by-trait matrix had been randomised 500 times, and dashed lines indicate the 95% confidence intervals generated from the randomisations. Correlations are plotted against the cumulative information of the subassemblage as in Figure 1

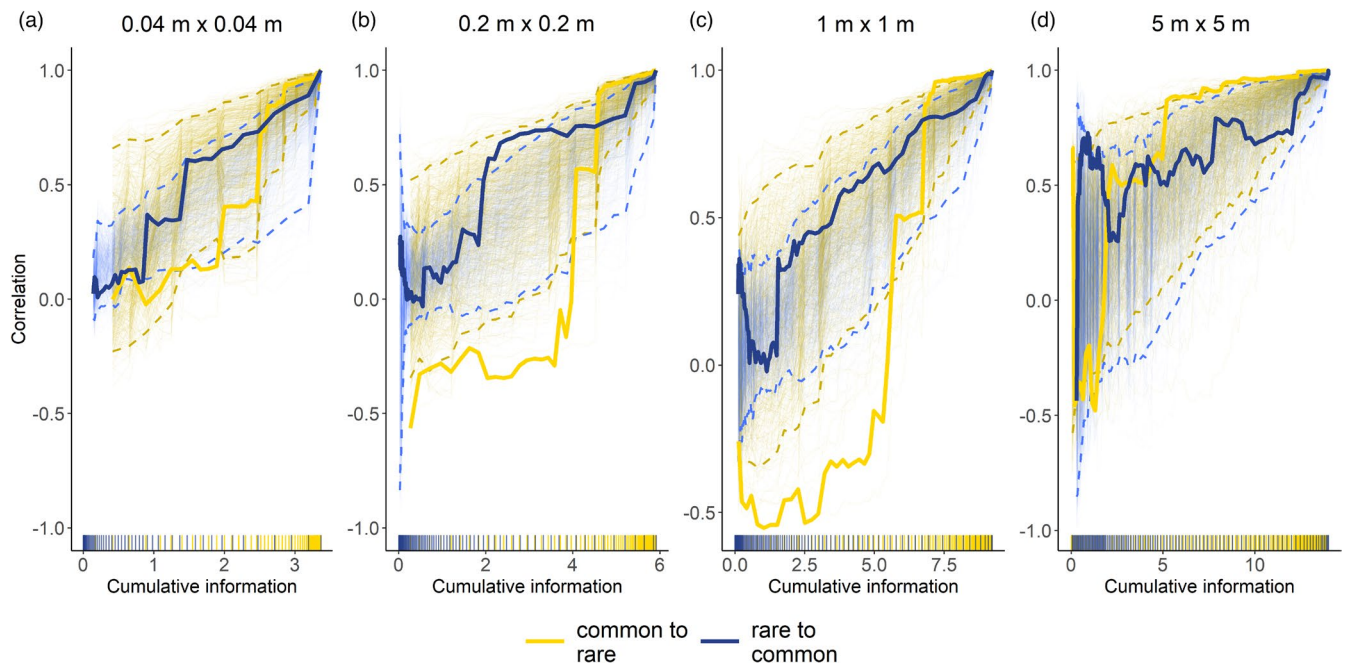


FIGURE 3 Sequential Pearson correlation coefficients between the functional dispersion of subassemblages and the full assemblage at (a) $0.04 \text{ m} \times 0.04 \text{ m}$, (b) $0.2 \text{ m} \times 0.2 \text{ m}$, (c) $1 \text{ m} \times 1 \text{ m}$ and (d) $5 \text{ m} \times 5 \text{ m}$. Species were added sequentially by rank from geographically rarest to geographically most common (dark blue line) and geographically most common to geographically rarest (dark yellow line). Light blue lines and gold lines show correlations where species were added in from rare to common and common to rare where the species-by-trait matrix had been randomised 500 times, and dashed lines indicate the 95% confidence intervals generated from the randomisations. Correlations are plotted against the cumulative information of the subassemblage as in Figure 1

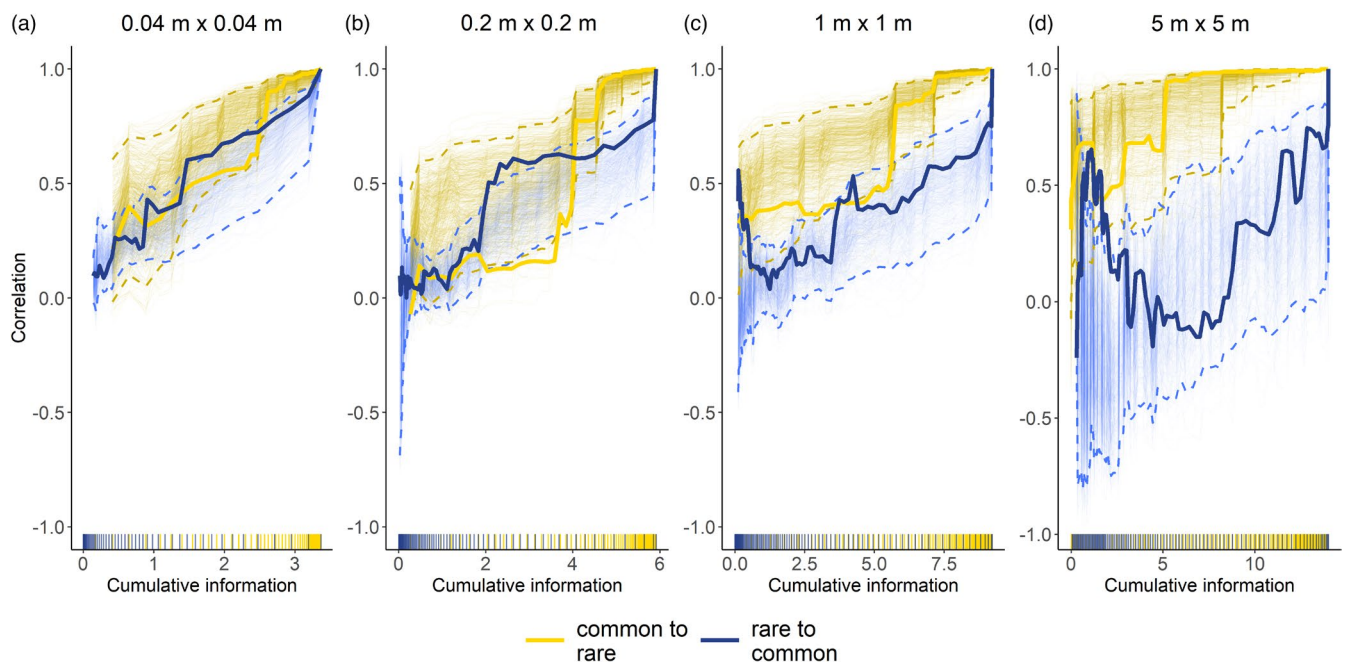


FIGURE 4 Sequential Pearson correlation coefficients between the abundance-weighted functional dispersion of subassemblages and the full assemblage at (a) $0.04 \text{ m} \times 0.04 \text{ m}$, (b) $0.2 \text{ m} \times 0.2 \text{ m}$, (c) $1 \text{ m} \times 1 \text{ m}$ and (d) $5 \text{ m} \times 5 \text{ m}$. Species were added sequentially by rank from geographically rarest to geographically most common (dark blue line) and geographically most common to geographically rarest (dark yellow line). Light blue lines and gold lines show correlations where species were added from rare to common and common to rare where the species-by-trait matrix had been randomised 500 times, and dashed lines indicate the 95% confidence intervals generated from the randomisations. Correlations are plotted against the cumulative information of the subassemblage as in Figure 1

TABLE 1 The standardised effect size of Petchey and Gaston's functional diversity (PGFD) and functional dispersion (FDis) of the 25% most common and 25% most rare species, generated from a null distribution of 999 randomisations of the species-by-trait matrix. The *p*-value for the location of the observed functional diversity within the null distribution was calculated following Swenson (2012). Instances where the observed functional diversity differed significantly from random following a two-tailed significance test (i.e. $p \leq 0.025$ or $p \geq 0.975$) are shown in bold

Diversity	Scale	Most common		Most rare	
		Standardised effect size	<i>p</i> -value	Standardised effect size	<i>p</i> -value
PGFD	0.04 × 0.04	0.279	0.618	-1.087	0.152
	0.2 × 0.2	-1.032	0.165	0.057	0.526
	1 × 1	-1.312	0.095	1.962	0.980
	5 × 5	-1.552	0.077	0.228	0.563
FDis	0.04 × 0.04	-0.157	0.421	-2.061	0.024
	0.2 × 0.2	-0.277	0.395	0.556	0.716
	1 × 1	-0.417	0.334	1.516	0.936
	5 × 5	-0.522	0.305	0.998	0.857

TABLE 2 The median estimates and upper and lower credible intervals from MCMC models of species richness, Petchey and Gaston's functional diversity (PGFD), functional dispersion (FDis) and functional dispersion using plant percentage cover (abundance-weighted FDis) with the proportion of the community made up by the 25% most common species and the proportion of the community made up by the 25% rarest species. Instances where the credible intervals do not cross zero are shown in bold. CI, confidence intervals; DIC, deviance information criterion

Diversity	Proportion of common species					Proportion of rare species			
	Scale (m)	Median	2.5% CI	97.5% CI	DIC	Median	2.5% CI	97.5% CI	DIC
Species richness	0.04 × 0.04	-0.735	-0.939	-0.525	35.99	0.730	0.206	1.249	253.23
	0.2 × 0.2	-0.607	-0.796	-0.411	-202.93	0.751	0.239	1.267	-157.39
	1 × 1	-0.611	-0.837	-0.399	-553.64	0.753	0.125	1.375	-527.68
	5 × 5	-0.706	-1.525	0.120	-17.29	0.051	-1.586	1.648	-13.87
PGFD	0.04 × 0.04	-0.500	-0.683	-0.298	-21.85	0.436	-0.001	0.872	7.57
	0.2 × 0.2	-0.723	-0.915	-0.529	-203.43	1.219	0.702	1.740	-162.12
	1 × 1	-0.811	-1.198	-0.477	-113.32	1.610	0.566	2.653	-93.99
	5 × 5	-4.885	-8.862	-0.871	42.78	6.261	-1.710	14.038	46.29
FDis	0.04 × 0.04	-0.034	-0.059	-0.010	-1872.95	0.105	0.049	0.161	-1879.29
	0.2 × 0.2	-0.044	-0.058	-0.030	-2699.31	0.060	0.022	0.097	-2665.95
	1 × 1	-0.019	-0.034	-0.006	-3247.02	0.015	-0.028	0.058	-3236.62
	5 × 5	-0.071	-0.152	0.010	-105.21	0.196	0.069	0.320	-110.89
Abundance-weighted FDis	0.04 × 0.04	-0.075	-0.107	-0.044	-1635.01	0.071	-0.002	0.145	-1615.59
	0.2 × 0.2	-0.072	-0.100	-0.044	-1992.04	0.101	0.028	0.174	-1971.01
	1 × 1	-0.042	-0.074	-0.011	-2314.20	0.014	-0.082	0.109	-2306.55
	5 × 5	-0.024	-0.214	0.168	-72.80	0.100	-0.243	0.436	-73.17

not sufficient for discerning spatial patterns of functional diversity, as common species often correlate less than we would expect from random with the overall spatial patterns of functional diversity. This result held when both categorical traits were included in the analyses, as well as excluded (Figures S7 and S8).

Using a randomisation approach that swapped the species names in the species-by-trait matrix, we maintained trait covariances and species richness within sites while randomising the trait values associated with those species. Rather than rare species disproportionately contributing to patterns of functional diversity, the

rare-to-common curve often fell within the 95% confidence intervals of the randomisation, that is their contributions did not differ from random, while the common-to-rare curve for FDis and PGFD at the 0.2 m × 0.2 m and 1 m × 1 m spatial scales frequently correlated more weakly than expected from random. In many instances when only common species were included in the subassemblages, there was a negative correlation with the overall spatial distribution of functional diversity. Surveying only common species for spatial patterns of functional diversity is therefore likely to be misleading and supports the call that widespread species should not necessarily

be used as indicators of general biodiversity patterns (van Proosdij et al., 2016), particularly if occurrence data are being used.

In contrast to the curves for functional diversity, the common-to-rare curves for species richness fell within the 95% confidence intervals generated from the randomisation and above the rare-to-common curve at the $0.2 \text{ m} \times 0.2 \text{ m}$ and $1 \text{ m} \times 1 \text{ m}$ spatial scales, showing that common species contribute more to spatial patterns of species richness than rare species. This also matches previous investigations across multiple taxa that have showed a greater contribution of common species than rare species to the spatial distribution of species richness (e.g. Lennon et al., 2004; Pearman & Weber, 2007), and may be a result of the consistency across common species of important drivers of distributions compared to rare species (Kreft et al., 2006; Vazquez & Gaston, 2004), although this needs more investigation. This result, combined with our results for functional diversity, indicates that common species hold more information in terms of species richness distributions than they do for functional diversity.

The sequential correlations of common and rare species with species richness are, in part, a result of the range frequency distributions of species (Heegaard et al., 2013). Strongly right-skewed distributions are thought to lead to higher correlations of geographically rare species with overall species richness (van Proosdij et al., 2016). At all scales, the range frequency distributions of species in our surveys were right-skewed; however, at $0.2 \text{ m} \times 0.2 \text{ m}$ and $1 \text{ m} \times 1 \text{ m}$, common species showed a stronger correlation with species richness than rare species. This may be a result of the interaction of the range frequency distribution with the overall distribution of species richness across the sites (Heegaard et al., 2013; see Supporting Information). Šizling et al. (2009) suggest that a larger influence of geographically common species on species richness patterns is almost mathematically inevitable because of the importance of the sum of richnesses of sites at which a species occurs to the correlation of species occupancy with species richness. However, the overlapping curves for common-to-rare and rare-to-common species richness correlations at the $0.04 \text{ m} \times 0.04 \text{ m}$ and $5 \text{ m} \times 5 \text{ m}$ spatial scales suggest this may not necessarily be the case.

With functional diversity there is another component in addition to the range frequency distribution of species that contributes to the observed spatial patterns. Species richness and PGFD showed similar distributions across all sites at the $0.2 \text{ m} \times 0.2 \text{ m}$ and $1 \text{ m} \times 1 \text{ m}$ sampling scales (Figure S6) yet showed different contributions of common and rare species to their spatial patterns. This is because, unlike species richness where every species contributes equally to the measure (i.e. the addition of a species to a site will always increase the species richness by one), different species can affect functional diversity measures by different amounts as a result of their functional distinctiveness, that is how similar are their trait values to other species within the community.

The contribution of rare species to functional diversity patterns ties in with previous findings that rare species are often functionally unique or distinct from each other as well as more common species (Jain et al., 2014; Leitão et al., 2016). Therefore, the lack of

information held by common species in terms of spatial functional diversity patterns, may, in part, be a result of their lack of distinctiveness from each other. Although we found that the 25% most common species were only less functionally diverse than expected from random (in terms of PGFD) at the $1 \text{ m} \times 1 \text{ m}$ scale, plots with a high proportion of geographically common species showed lower functional and taxonomic diversity at all scales except the largest. This may explain the negative correlation sometimes observed for FDis and PGFD when only common species were included in the subassemblages as towards the left-hand end of these curves, common species make up 100% of the community across their distribution. Conversely, plots with a high proportion of geographically rare species showed higher diversity. There was only weak support for this, however, at the $5 \text{ m} \times 5 \text{ m}$ sampling scale and for abundance-weighted FDis. Additionally, the models containing the 25% most common species performed better than the models containing the 25% rarest species as they had a lower DIC. This supports our observation that, in many instances, the common-to-rare curve initially falls below the 95% confidence intervals generated from our randomisations, as the absence of rare species from the functional diversity calculations means the most functionally diverse plots are not being well-estimated.

The difference between the common-to-rare and rare-to-common curves for FDis generally decreased when percentage cover data were used, as common species showed higher correlations when the measure was abundance-weighted. At the smallest spatial scales, rare species can make up a substantial proportion of vegetation cover in any single plot, that is a single individual may cover the entire $0.04 \text{ m} \times 0.04 \text{ m}$, and therefore overwhelm the abundance-weighted measures of functional diversity within that plot. This explains the similarity of the common-to-rare and rare-to-common curves for the abundance-weighted measure of FDis at this scale. At larger spatial scales, it is unusual for geographically rare species to have significant cover, the effect of which we can observe in the larger two spatial scales for the abundance-weighted FDis where the rare-to-common curve falls below that of the common-to-rare curve, that is common species are contributing more to abundance-weighted FDis.

We acknowledge that trait selection can impact studies of functional diversity. We took an approach to trait selection with the aim of minimising collinearity between traits and representing the intrinsic dimensionality of plant traits (Laughlin, 2014). To test whether trait selection affected our general conclusions, we ran our original analyses a second time including only continuous traits, that is excluding pollen vector and mode of reproduction. This analysis further supported our conclusions that common species contributed less than expected to spatial patterns of functional diversity, and the gap between the rare-to-common curve and common-to-rare curve was even larger when categorical traits were excluded for both PGFD and FDis (Figures S7 and S8).

Although the spatial scales under investigation in this study were small, they were relevant for the Machair system where there are no large woody species. Many plant surveys, particularly

in grassland systems, are carried out at the 1–2 m² spatial scale or below; however, our results and approach can be applied across systems where sampling scales with the size of the individuals in that system. The observed variation with spatial scale highlights that surveys need to be carried out at appropriate scales and support the notion that biodiversity patterns are scale dependent (McGlenn et al., 2019). The mechanisms underlying community assembly are scale dependent, as reflected in the functional diversity–area relationship (Smith et al., 2013), and may explain the variation in our results with spatial scale. However, at the local scales investigated here, commonness and rarity are likely to be the result of niche differences and competition (Heegaard et al., 2013), rather than where the surveys lie in relation to the species' overall extent, which may be the case at broader spatial scales (Hengeveld & Haeck, 1982). Furthermore, the assembly processes at different spatial scales may vary between geographically rare and common species, and investigation into the different environmental drivers of these subsets of species (e.g. Lennon et al., 2011) will provide further information on their distribution.

Similar to assembly processes, the classification of what is 'rare' and what is 'common' will vary with spatial scale. At all scales, we observed right-skewed distributions of rarity both in terms of area of occupancy (geographic rarity) and percentage cover of species. The skew for area of occupancy was not as strong at the 5 m × 5 m scale, however, with 23.5% of the species found in more than 50% of the plots. Therefore, at this larger scale, we may label fewer species as 'rare' than at smaller scales. Plotting against the cumulative information rather than the number of species in each subassemblage accounts for this and allows us to compare the shapes of sequential common-rare curves across spatial scales without having to set arbitrary thresholds of what is classed as 'rare' or 'common'.

The Machair grassland provides an ideal system to investigate spatial biodiversity patterns due to its high diversity and spatial heterogeneity at a local scale. Similar to the investigation of the importance of commonness and rarity to spatial patterns of species richness, our approach can be applied across taxonomic groups and systems to investigate the generality of our results, as well as across spatial scales. The previously demonstrated functional distinctiveness of rare species compared to common in many systems (Jain et al., 2014; Leitão et al., 2016) may contribute to similar general patterns that we observe in the Machair, that is common species contribute less than rare species to spatial patterns of functional diversity, and future macroecological research into the distribution of functional diversity will benefit from applying the approach we present here across different taxa and ecosystems.

Together, our results show that when functional diversity is calculated using occurrence data (presence–absence), common species will perform worse than random at capturing the spatial distribution of functional diversity. To estimate the spatial patterns of functional diversity accurately, therefore, we ideally need data on the distribution of rare species, consistent trait data across species and abundance/percentage cover data. These will facilitate more accurate estimates of both functional richness and occurrence-based

measures (e.g. PGFD) in addition to measures of the weighted distribution of species in trait space (e.g. abundance-weighted FDis). When carrying out field surveys, rare species are often missed, for example due to decreased detectability, yet this could seriously obscure apparent patterns of functional diversity. Using rarefaction methods that estimate expected functional diversity based on sample size may improve mapping of functional diversity in space across large spatial scales (Ricotta et al., 2010, 2012; Walker et al., 2008). We also need to address the deficit of rare species in trait databases (Violle et al., 2015) so that accurate assessments of functional diversity can be made. This would allow the inclusion of more traits that are potentially important for spatial partitioning or community assembly into the analyses, but where data are currently a limiting factor, such as chemical or root traits (Laughlin, 2014; Sonnier et al., 2012).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

H.J.W. led the conceptual design of the study with support from Y.M.B. and R.J.P.; The Machair data are curated by H.J.W. and R.J.P.; Trait data were collated by H.J.W. and R.J.P.; H.J.W. led the analyses and writing of the paper; Y.M.B. and R.J.P. contributed critically to drafts and gave final approval of the manuscript.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13858>.

DATA AVAILABILITY STATEMENT

Plant survey data are available from the Data Dryad Repository <https://doi.org/10.5061/dryad.n08sv> (White et al., 2017). Plant trait data are freely available from BioFlor: <https://wiki.ufz.de/bioflor/index.jsp> (Klotz et al., 2002) and LEDA <https://uol.de/en/landeco/research/leda> (Kleyer et al., 2008) trait databases. R code for the analyses can be downloaded from <https://doi.org/10.5281/zenodo.6025921> (White, 2022).

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