Rarity and sparseness in plant communities: impact of minor species removal on beta diversity and canonical ordination

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Abstract

Question –Among the 'minor' species present in communities, we distinguish between true 'rare' species, with infrequent occurrence (low occupancy) in a given regional data set, and 'sparse' species, which may be present over most of the study area, but with low local abundance. Do rare and sparse species play a different role in the evaluation of beta diversity and in the constrained ordination of plant community data sets?

Methods – Based on their positions in the abundance-occupancy scatterplots of six contrasted vegetation data sets, we distinguished core, rural, urban and satellite species. To disentangle the role of rarity and sparseness, we applied to each data set a progressive removal of either the least frequent or the least locally abundant species. We assessed impacts on beta diversity (q = 0, 1 and 2), and on model performance of RDA, without or after pre-transformation of absolute cover values.

Results – Multiplicative beta diversity decreased with the number of removed rare species, with slightly higher values for q = 2, whereas it increased when removing sparse species, with much higher values for q = 0. With raw data or after binary or by-site transformation, the fraction of variation explained by RDA increased only slightly when removing rare species, with a more sensible increase of the relative contribution of the first canonical axis. By contrast, progressive elimination of sparse species, which mimics a lower sampling effort within each community, negatively affected model performance. Generally, the removal of rare species clearly improved the performance of RDA after double transformation (chi-square transformation), contrary to the removal of sparse species.

Conclusions –The frequently observed positive correlation between occupancy and abundance hides profound differences with critical impacts on vegetation analysis. Providing that meaningful transformations are applied, there is no need to remove rare species prior to RDA. Focusing only on abundant species during sampling is likely to limit the performance of ecological empirical models.

Key-words: abundance-occupancy relationship; beta-diversity; core-satellite species hypothesis; minor species; rare species; redundancy analysis

Introduction

Vegetation data sets generally include many species with a low frequency of occurrence, their number depending on plot size and on vegetation heterogeneity within and among sites. They are responsible for a high proportion of zeros in the community data matrix and thus for a high inertia in the multivariate response to be explained by constrained ordination. It has been argued that such infrequent species should be removed because they add noise to the analysis and reduce model performance (Cao et al., 2001; Poos & Jackson, 2012; Jing et al., 2015; Brasil et al., 2020). However, Legendre & Gallagher (2001) argued that removal of the most infrequent species may be relevant before correspondence analysis (CA) and canonical correspondence analysis (CCA), but not before principal component analysis (PCA), after showing that these species only play minor roles in PCA, without or with data transformation.

These infrequent species often show low abundances in local communities, whereas frequent species are often locally dominant, so that there is generally a positive correlation between the frequency of occurrence of a species (also called ‘occupancy’ or ‘distribution’) throughout a data set and its average abundance in occupied plots (‘abundance-when-present’), i.e. a positive interspecific abundance-occupancy relationship (Collins et al., 1993; Gaston, 1998; Gaston et al., 2000; Blackburn et al., 2006; Borregaard & Rahbek, 2010; Eriksson, 2013; Guedo & Lamb, 2013).

In its broad sense, ‘rarity’ is often defined using the framework of Rabinowitz (1981), which considers the three axes of range size, local abundance and habitat specialism. In the British flora, Rabinowitz et al. (1986) found these three axes to be independent, whereas other studies often find high proportions of species that are rare in all three dimensions (Harrison et al., 2008). Habitat specialism, i.e. the specificity of a species to a few habitats, is more

difficult to measure than the two other dimensions and is sometimes interpreted by the availability of suitable sites for a species in the landscape, measured by the rarity of its preferred habitat (Broennimann et al., 2005). Habitat specificity can be better viewed as an underlying cause of rarity than a rarity dimension (Crisfield et al., 2024). Here, we will not consider this controversial dimension of 'rarity' and will focus on the difference between the two other dimensions.

They correspond to the conceptual distinction between regionally *rare* species with low occupancy (frequency of occurrence) in a given regional data set, and locally *sparse* species with low relative abundance (measured by density, cover, biomass or local frequency) in each local community. These sparse species are sometimes neglected during sampling, e.g. when recording dominant species only or when working on small plots, where the probability of observing an abundant species is higher. In contrast, rare species may be omitted when restricting the range of habitats in the study area, as they are expected to have introgressed from surrounding habitats. We argue that the expression *rare* species should be restricted to species with a low frequency of occurrence in a given regional community data set, although this term is often also used to refer to locally *sparse* species. A generic term for both rare and sparse species may be 'minor' species.

Adding to the confusion, abundance measured as local frequency – e.g. the fraction of small quadrats located within each site that is occupied by a given species, or the proportion of contacts with this species in a point-intercept method – can be seen as similar to regional occupancy, i.e. the fraction of large plots where a species is found, but at a finer scale (Eriksson, 2013). Thus, from this strict methodological point of view, the distinction between rare and sparse species would be dependent on the scale (grain and extent) considered in the study from which the data set was built. However, the distinction between rare and sparse species is also supported by an ecological argument: as far as each relevé corresponds to a local plant community, with strong biotic interactions and homogeneous habitat conditions (Lortie et al., 2004), species abundance results from fine-scale environmental and biotic filtering, while species occupancy depends on dispersal, biogeographical filtering, and on the range of habitats considered in the regional data set. Hence, rarity and sparseness, as well as commonness and abundance, deserve to be distinguished in order to correctly assess the role of 'minor' species in the analysis of a vegetation data set.

To put the distribution-abundance relationship in the dynamic context of metapopulation models, Hanski (1982) developed his core-satellite species hypothesis by distinguishing two main kinds of species with respect to their average local abundance N and the fraction of

occupied patches, i.e. occupancy *p*: 'core' species with large *N* and *p* (abundant and common, relatively well spaced-out in niche space), and 'satellite' species with small *N* and *p* (sparse and rare, with a narrow niche). Following Söderström (1989), Hanski (1991) further considered two other distribution types of species which he named by analogy to human populations: 'rural' species with small *N* but large *p* (sparse but common), and 'urban' species with small *p* but large *N* (rare but abundant). Urban species are supposed to have high local growth rate and low dispersal rate, leading to population concentration, contrary to rural species. Thus, for a given data set, species may be classified into core, satellite, urban and rural species according to their position in the abundance-occupancy scatterplot, revealing distinct niche patterns (Collins et al., 1993). Indeed, many data sets include urban and rural species in addition to core and satellite species that shape the popular positive distribution-abundance relationship.

Hanski's core and satellite species are somewhat equivalent to Grime's 'dominant' and 'transient' species, respectively (Grime, 1998; Gibson et al., 1999). 'Subordinate' (i.e. frequent but never dominant) species of Grime's classification can be viewed as equivalent to rural species. Real-world species removal experiments showed that subordinate plant species play an overlooked but important role in grassland biodiversity and ecosystem functioning (Mariotte, Buttler, et al., 2013; Mariotte, Vandenberghe, et al., 2013). The 'subordinate insurance hypothesis' suggests that subordinate species may assist dominant species or compensate for their loss on ecosystem functions via complex plant-soil feedbacks (Mariotte, 2014). Another typology of concepts based on abundance-occupancy patterns has been proposed recently (Avolio et al., 2019), somewhat equivalent to Hanski's classification, core species being called 'common', urban species 'restricted', satellite species 'rare', and rural species 'sparse'. In this conceptual framework, locally abundant species (either 'common' or 'restricted') may be 'dominant' or 'subordinate' depending on their impact on their surrounding environment, community and ecosystem functioning. In the absence of a consensus on vocabulary and for methodological reasons, we prefer to restrict the meaning of 'rare' and 'sparse' species to each dimension of occupancy and abundance.

Equivalences among these different concepts and theories should be considered with caution, however. Urban species are not considered in Grime's dominant-subordinate-transient classification. Grime's classification is based on frequency-abundance patterns inside a plant community, whereas Hanski's classification basically considers a metacommunity, i.e. a network of patches of the same habitat occupied by local communities at a broader spatial scale. Moreover, discussions about abundance-distribution relationships

131 often refer to macroecology and biogeography, involving a variety of habitats in a wide
132 region. Thus, as often in ecology, semantic shifts are likely to obscure the comparison of these
133 concepts.
134 The questions addressed in this paper are the following: given the potential ecological
135 roles of rare and sparse species, what are the consequences of discarding them when
136 analyzing abundance-occupancy patterns, diversity patterns and community-environment
137 relationships in vegetation science? Do rare and sparse species play the same role in these
138 analyses? Therefore, considering a variety of vegetation data sets differing in their spatial
139 extent and ecological diversity, the specific question examined in this paper is: how does a
140 progressive removal of *either* the regionally least frequent species *or* the locally least
141 abundant species affect (1) the proportion of core, rural, urban and satellite species, (2) the
142 evaluation of taxonomic β-diversity and (3) the performance of constrained ordination? In
143 addition, does the impact of species removal on RDA model performance depend on the
144 choice of the prior transformation of abundance-cover data?

145 **Methods**

146 *Data sets*

147 We selected six contrasted vegetation data sets for which species absolute cover and
148 explanatory variables were available (Table 1), i.e. three small and homogeneous data sets
149 (hereafter called ‘vare’, ‘catgrass’ and ‘dune’) and three bigger and more heterogeneous data
150 sets (‘trufe’, ‘vltava’, ‘bryce’). Each species data set is associated with an environmental data
151 set containing explanatory variables to be used in constrained ordination.
152 We describe each original species data set by the species frequency distribution (Fig. 1)
153 and by the abundance-occupancy scatterplot (Fig. 2). According to the core-satellite species
154 hypothesis, frequency distribution is supposed to be bimodal (U-shaped), but it depends on
155 plot size and on the heterogeneity of the studied vegetation (Collins & Glenn, 1997). An
156 abundance-occupancy scatterplot represents the average relative cover of each species in all
157 occupied sites, without taking into account absences (its mean abundance-when-present, on a
158 log scale) vs. the proportion of sites occupied by the species (its frequency of occurrence). It
159 includes a regression line from the linear model explaining the logarithm of average
160 abundance-when-present by the frequency of occurrence, as well as the delimitation of core,
161 satellite, urban and rural species.

Fifty percent frequency is the threshold considered by Mariotte (2014) to first distinguish transient (i.e. satellite) from both dominant and subordinate species within a plant community. Above 50% frequency, this author suggested that species with a cumulative relative cover below 2% should be considered as transients, comprised between 2% and 12% as subordinates, and above 12% as dominants. Collins & Glenn (1997) considered as core species those present in more than 90% of the sites and as satellite species those present in less than 10% of the sites, all other species being classified as 'intermediate' without distinguishing rural and urban. To our knowledge, no clear boundaries have been specified so far to delimit these four categories. Since we consider here both mono- and multi-site data sets at various spatial scales, we retained Hanski's classification, but we adapted Mariotte's typology to delimit species groups. Therefore, we counted the number of core, satellite, urban and rural species by considering common arbitrary boundaries to delimit these four groups: 50% frequency and 5% relative cover (Fig. 2 and 3).

The Spearman rank correlation was used to measure and to test the abundance-occupancy relationship (Table 1). The heterogeneity of the species matrix was measured by (i) the multiplicative β-diversity of species richness, related to the differentiation among habitats (Whittaker, 1972; Tuomisto, 2010), (ii) the relative MacArthur's homogeneity measure, which compares communities based on the Hill-Shannon beta diversity (Jost, 2007, equation 22), (iii) the proportion of zeros in the vegetation table (species absences), and (iv) the number of species observed at only one site or plot (Table 1).

The 'vare' data set describes the understorey vegetation of boreal pine forests (Väre et al., 1995). 'varespec' (species) and 'varechem' (environmental variables) data frames are available in the R package vegan (Oksanen et al., 2024). Abundance was recorded as the average absolute cover of 44 lichen, bryophyte and vascular plant species in 15 or 10 quadrats of 1 m^2 within 24 sites. This relatively homogeneous data set shows a low β-diversity, with a high proportion of core and rural species, but no urban species. The environmental matrix is made of 14 quantitative variables: soil concentration of 11 chemical elements, bare soil cover, humus thickness and pH.

The 'catgrass' data set (Kohler, 2004) consists of 90 1-m^2 quadrats equally distributed over three experimental sites of montane pastures in the Swiss Jura Mountains, in which absolute cover of 94 vascular plant species was measured by a point-intercept method after two years of treatment (simulation of various combinations of cattle activities). This rather homogeneous data set contains few core and urban species. The environmental matrix is made

of 7 binary and semi-quantitative variables representing each factor of the treatments: site, shading, mowing, manuring, trampling, abandonment and grazing.

The 'dune' data set is a classic example of dune meadows in the Netherlands (Jongman et al., 1995). 'dune' (species) and 'dune.env' (environmental variables) data frames are available in the R package vegan. Original 9-class cover values of 30 vascular and bryophyte species recorded in 20 quadrats of 2 × 2 m^2 were transformed into mid-class percentages of absolute cover (van der Maarel, 1979; Dengler & Dembicz, 2023). β-diversity is low, with many urban and no rural species. The environmental data frame is composed of five variables: thickness of soil A1 horizon (quantitative), soil moisture and manure (semi-quantitative, treated as numeric variables instead of ordered factors to avoid overfitting in ordination analysis), management and use (qualitative).

The 'trufe' data set was obtained from a systematic sampling of the herb layer by 110 quadrats of 1 m^2 within a 1-ha area of heterogeneous wood-pasture at La Sagne in the Swiss Jura Mountains (Béguin, 2007). Original 6-class Braun-Blanquet dominance values of 111 vascular plant species were transformed into mid-class percentages of absolute cover. The community data set encompasses a high proportion of satellite and rural species. The environmental data frame is made of 6 quantitative variables: slope, eastern aspect, shrub cover, mean soil depth, soil depth variance and yearly potential sunshine hours.

The 'vltava' data set is made of 97 forest plots of 10 × 15 m^2 arranged in transects across the Vltava river valley in the Czech Republic (Zelený & Chytrý, 2007). The transects were perpendicular to the map contour lines and the river course but the plots along the transects were rectangles parallel to the contour lines. Within each plot, the absolute cover of vascular plant species was recorded separately for each of the three layers of the forest vegetation (herbs, shrubs and trees). Cover was estimated using the 9-class ordinal Braun-Blanquet scale and these codes were consequently transformed into mid-point percentages of cover classes. The data are available at https://www.davidzeleny.net/anadat-r/doku.php/en:data:vltava. The β-diversity is high with very few core and rural species. The environmental data frame is made of 12 quantitative or binary variables: elevation, slope, aspect, heat load, landform shape (2 variables), soil type (4 dummy variables), soil depth and pH.

Finally, the 'bryce' data set is another large-extent, heterogeneous vegetation data set from the Bryce Canyon National Park in Utah (USA). The 'bryceveg' (species) and 'brycesite' (environmental variables) data frames are included in the R package labdsv (Roberts, 2023). Absolute cover of the herbaceous species was recorded in various vegetation types (badlands, savannas and forests) using an 8-class dominance scale in 145 circular plots of 375 m^2 and

229 transformed into mid-point percentages. The β-diversity is very high with very few species
230 occurring in more than half of the sites. The environmental data frame is a selection of 7
231 quantitative or qualitative variables: elevation, soil depth, topographic position, annual and
232 growing-season solar radiation, slope and aspect. 15 sites with missing values for soil depth
233 were removed from the original data set.

234 Data sets 'vare', 'dune' and 'trufe' show a bimodal frequency distribution, due to their
235 relative homogeneity, whereas 'vltava', 'bryce' and 'catgrass' show a unimodal distribution
236 (Fig. 1). However, the modes of the distribution do not always correspond to a clear
237 opposition between satellite and core species.

238

239 Table 1. Characteristics of the six vegetation data sets. Unique species are those observed in only one plot.
240 Abundance/occupancy correlation is estimated by the Spearman rank correlation coefficient between species
241 mean absolute cover and frequency of occurrence. Alpha and gamma diversities were calculated from raw
242 absolute cover data as Hill numbers for q = 0, 1 and 2. Relative McArthur homogeneity measure was deduced
243 from Hill numbers for q = 1. More explanations in text.

Data set	vare	catgrass	dune	trufe	vltava	bryce
Plot size (m^2)	10 to 15	1	4	1	150	375
Number of plots	24	90	20	110	97	145
Number of core species	7	4	7	4	3	1
Number of rural species	17	16	0	19	3	1
Number of urban species	0	5	10	12	22	36
Number of satellite species	20	69	13	76	246	128
Proportion of zeros	41.9%	69.7%	67.2%	75.4%	90.0%	91.7%
Number of unique species	0	9	3	9	55	29
Abundance/occupancy correlation	0.495	0.577	0.497	0.351	0.448	0.233
αN_0 (mean number of species)	25.6	28.5	9.9	27.4	27.4	13.8
αN_1 (alpha Hill-Shannon diversity)	5.8	12.3	4.2	11.0	13.2	4.2
αN_2 (alpha Hill-Simpson diversity	3.8	7.2	2.9	7.0	7.0	2.4
γN_0 (total number of species)	44	94	30	111	274	166
γN_1 (gamma Hill-Shannon diversity)	11.7	25.9	16.3	36.6	70.0	31.9
γN_2 (gamma Hill-Simpson diversity)	8.4	10.5	13.1	18.7	33.0	12.3
βN_0 (beta species richness diversity)	1.72	3.30	3.05	4.06	10.00	12.02
βN_1 (beta Hill-Shannon diversity)	2.02	2.11	3.86	3.34	5.30	7.53
βN_2 (beta Hill-Simpson diversity)	2.25	1.46	4.53	2.68	4.74	5.14
Relative MacArthur homogeneity	0.474	0.469	0.220	0.293	0.180	0.127

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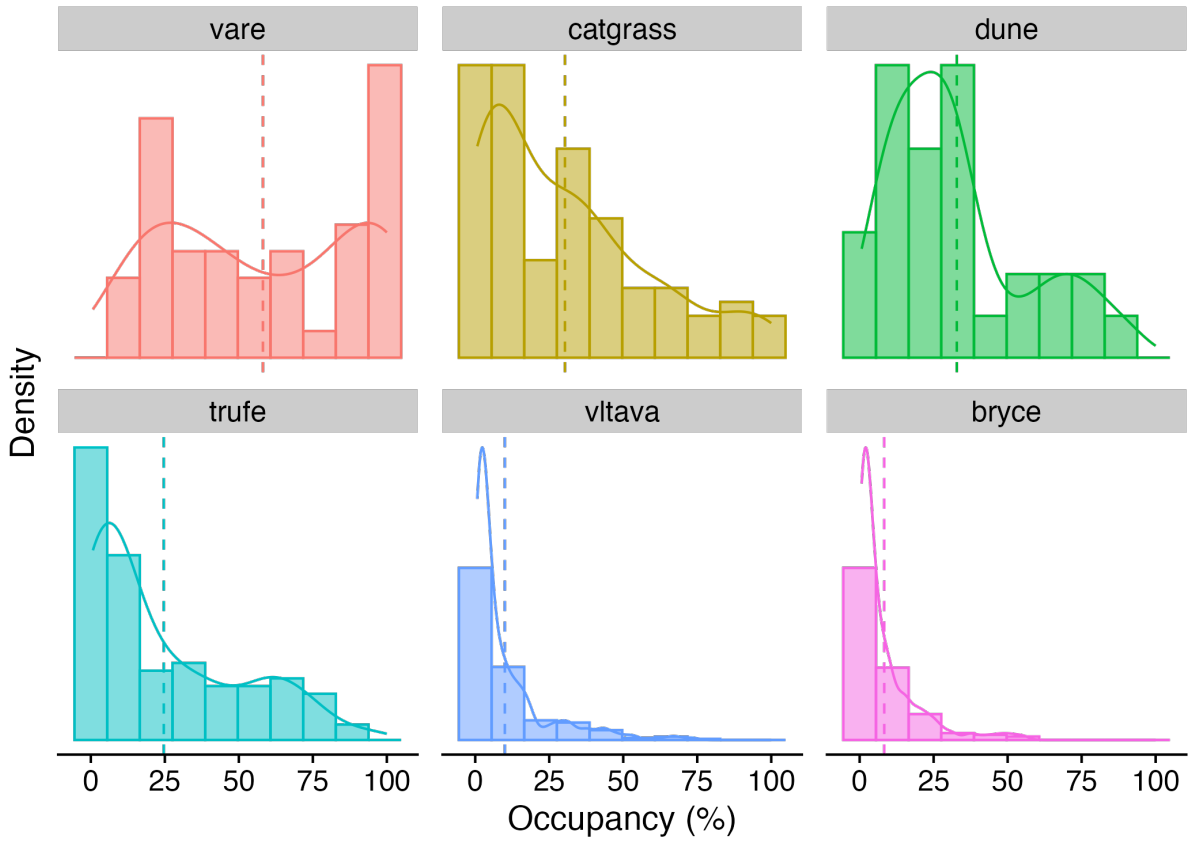

Figure 1. Species frequency distribution (occupancy percentage) in the six data sets. Histograms and smooth curves represent density. A vertical dashed line shows the mean species frequency of occurrence.

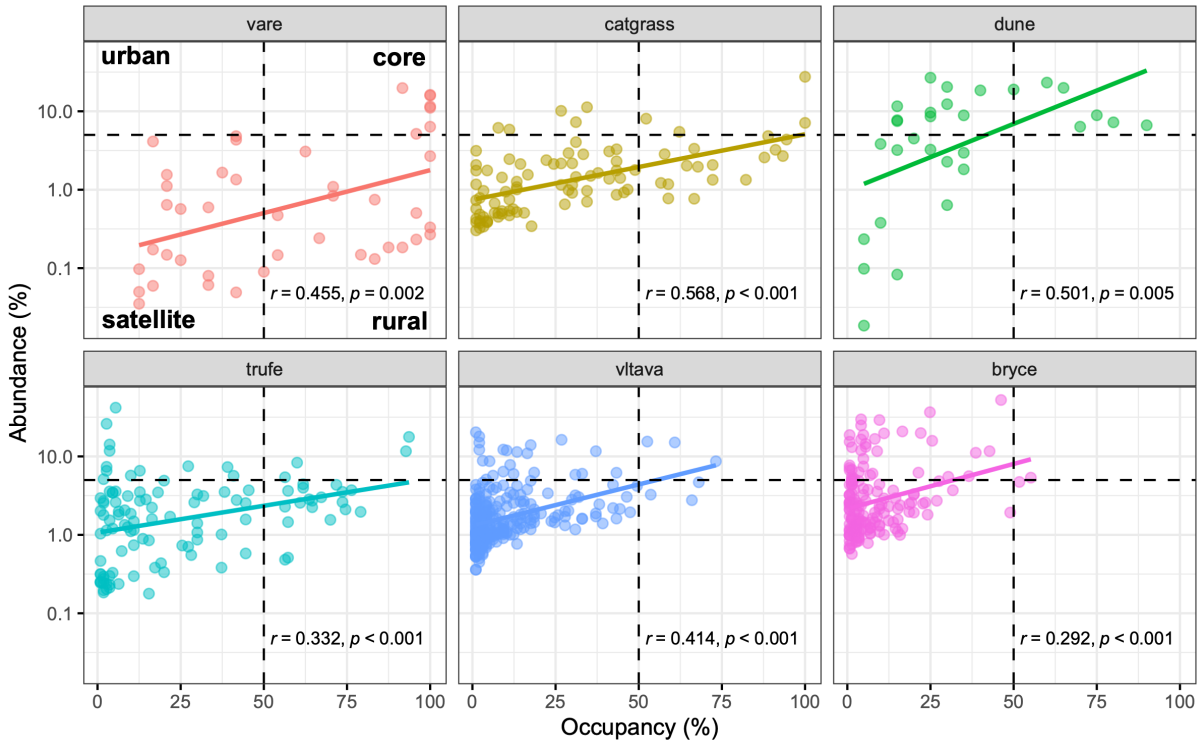

Figure 2. Abundance-occupancy scatterplots for the six data sets. Each point represents a species. The abscissa is occupancy, measured by the species frequency in the data set, i.e. the percentage of sites occupied by the species. The ordinate (on a log-scale) is the abundance-when-present, measured by the average relative cover of the species in occupied sites. Dashed lines represent boundaries between core (top-right quadrant), satellite (bottom-left quadrant), urban (top-left quadrant) and rural (bottom-right quadrant) species. The horizontal dashed line is positioned at 5% of relative cover and the vertical dashed line at 50% of frequency of occurrence. The solid straight line is the linear regression model of the logarithm of abundance-when-present by occupancy (with Pearson linear correlation coefficients *r* and *p*-values).

These six examples support the common report of significant positive correlations between the frequencies of the species and their average relative covers in occupied plots (Table 1, Fig. 2). However, the variation in local abundance may be very high among regionally rare species.

Most of the species belong to the satellite category in each data set. Core species never reach 25% of the species pool. Several data sets, such as ‘dune’ and ‘bryce’, contain a large proportion of urban species (Fig. 3).

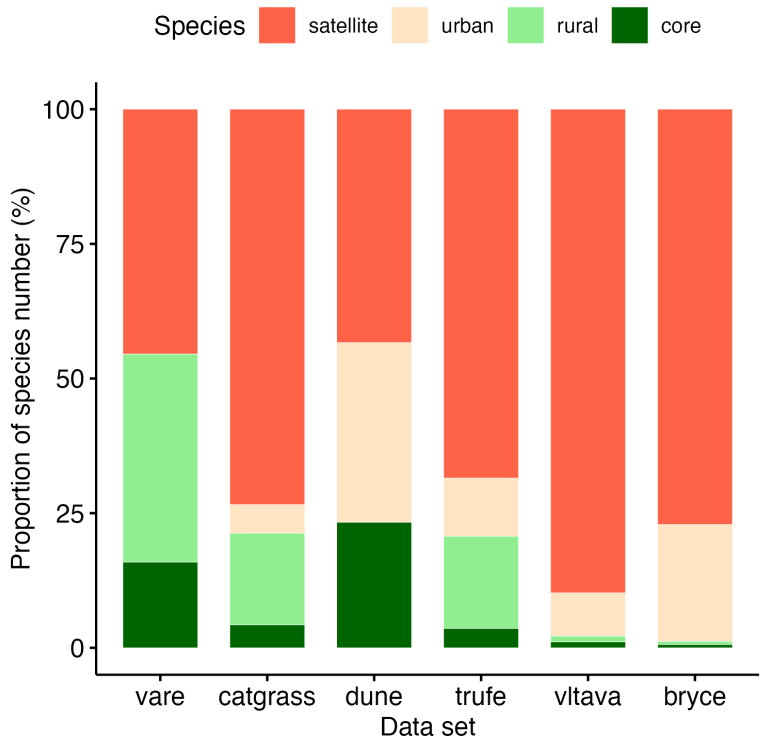

Figure 3. Proportion of core, rural, urban and satellite species in each data set.

Progressive removal of species records

In each of the selected data sets, species records were progressively removed according to either their increasing frequency of occurrence in the whole community data set (*rare species removal*) or their increasing relative cover in each site (*sparse species removal*). As for sparse species removal, we fixed a constant interval between two successive minimum abundance values, that is 2% relative cover, and at each step all species records with an abundance lower than the minimum value were assigned the value zero. The phasing out was stopped before a site became empty and continued until the remaining dataset contained only five species.

We assessed impacts of species removal on abundance-occupancy patterns, on β-diversity estimates and on the model performance of redundancy analysis, without or after pre-transformation of absolute cover data (Fig. 4).

For each data set, the number of core, urban, rural and satellite species was plotted in a stacked area plot against the minimum species occupancy or abundance applied during the progressive removal of rare or sparse species, respectively.

α, β and γ taxonomic diversity indices were computed using the d() function available in the R package vegetarian (Charney & Record, 2012), with equal community weights. Such diversity indices are referred to as species numbers equivalents or Hill diversity numbers (Hill, 1973; Jost, 2007; De Bello et al., 2010). Three orders were considered (q = 0, 1 and 2), corresponding to an increasing sensitivity to differences in species abundances (Jost, 2006). More specifically, we compared three multiplicative β taxonomic diversities: βN_0, or Whittaker β-diversity, is the inter-site diversity of all species ignoring their abundance; βN_1 or Hill-Shannon β-diversity is the inter-site diversity of abundant species; βN_2 or Hill-Simpson β-diversity is the inter-site diversity of dominant species. Multiplicative β-diversity was calculated as the ratio between γ-diversity and mean α-diversity for q = 0, q = 1 and q = 2, respectively. Finally, additive β-diversity was calculated as the difference between γ-diversity and mean α-diversity for q = 0, 1 and 2.

At each step of the progressive species removal, we compared the performance of redundancy analysis (RDA) after five optional pre-transformations of the species abundance data: raw absolute percentage cover (no data transformation), presence-absence transformation (binary data), chord transformation of the presence-absence data (normalization of binary site vectors), Hellinger transformation (square root of relative cover by site), and χ^2 (chi-square) double transformation (by site and by species). Site profiles (chord or Hellinger transformation) or double profiles (χ^2 transformation) make double

absences invisible in the computation of distances between sites; this transformation is recommended before the RDA of species data sets with many zeros (Legendre & Gallagher, 2001). The Euclidean distance computed after a chord transformation of the presence-absence data is proportional to the Ochiai dissimilarity, which allows double zeros in the presence-absence data to be ignored (Borcard et al., 2018, p. 42); therefore and for simplicity, this transformation will be named Ochiai transformation hereafter. Double profiles based on χ^2 distance make RDA similar (but not equivalent because eigenvalues and eigenvectors are computed in different ways) to canonical correspondence analysis (CCA), another popular constrained ordination method in community ecology (Borcard et al., 2018). Since we wanted to compare transformations and not constrained ordination methods, we have chosen to only apply RDA on our test data and not CCA.

Every vegetation data set was associated with an environmental data set used to constrain the ordinations with the same explanatory variables at each step of the rare or sparse species removal. Performance of RDA was assessed by (i) the unbiased percentage of variation explained by the environmental variables (adjusted R^2, Peres-Neto et al. (2006)) and (ii) the contribution of the first canonical axis to the explained variation (expressing the efficiency of the ordination space reduction).

All analyses were performed in the R environment (RCoreTeam, 2024), using packages vegan, labdsv, vegetarian, tidyverse (Wickham et al., 2019) and ggpubr (Kassambara, 2023). The data and the R code used to perform these analyses are provided as electronic Supplementary Material (Appendix S2).

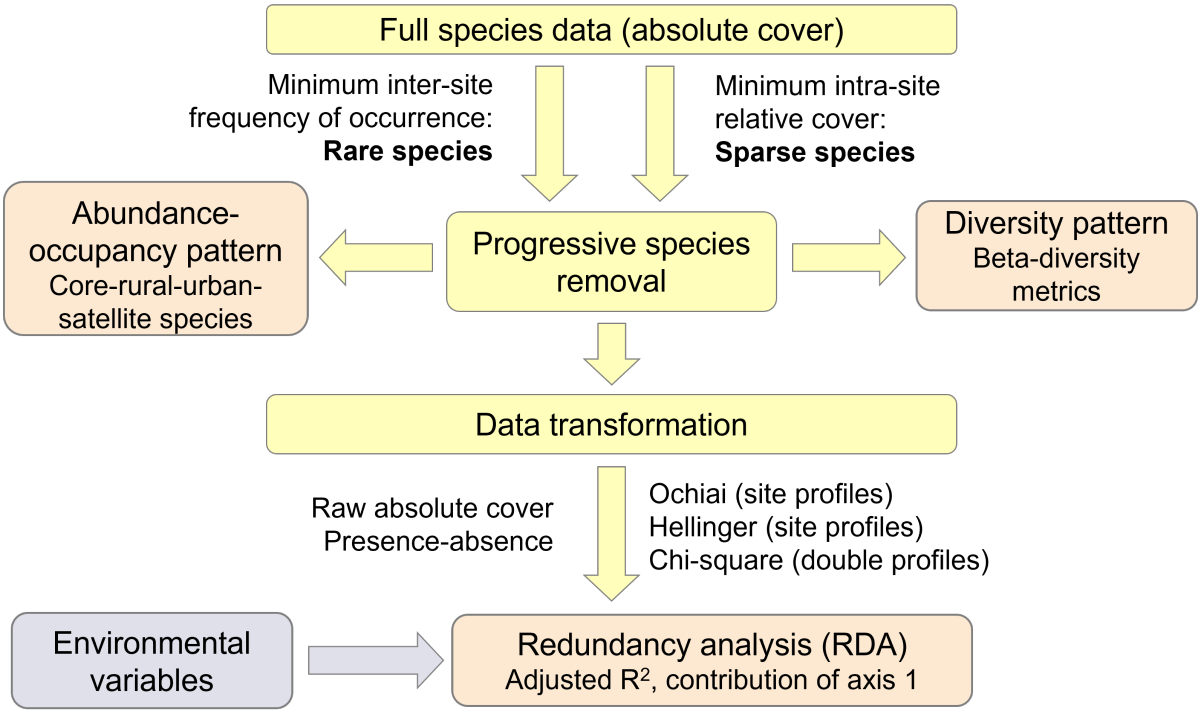

Figure 4. Summary of the methodology applied to assess the impact of progressive species removal on abundance-occupancy pattern, diversity pattern and constrained ordination.

Results

Impact of progressive species removal on abundance-occupancy patterns

The impact of excluding the least frequent (rare) species or the least abundant (sparse) species from the original data set is consistent among the data sets (Fig. 5). When removing rare species, satellite and urban species disappear first, and the proportion of core species tends to increase. Rural species, when present, disappear more slowly. By contrast, the elimination of locally sparse species leads to a dramatic increase of the proportion of urban species. Rural species first disappear, followed by satellite and core species. Note that the exclusion of rare or sparse species in large and heterogeneous data sets (‘vltava’ and ‘bryce’) quickly leads to empty sites, and therefore short series.

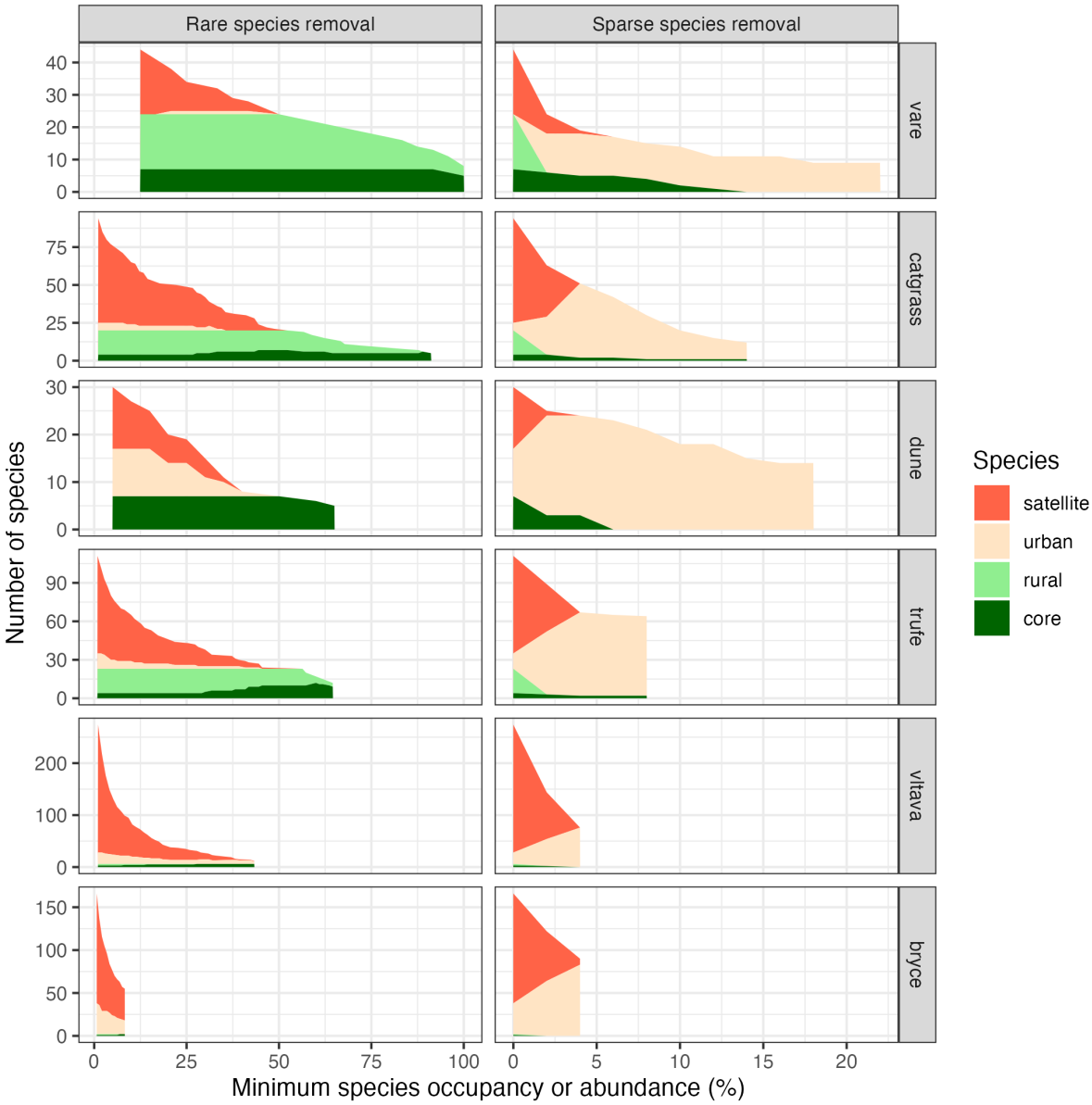

Figure 5. Impact of rare (left) or sparse (right) species exclusion from each data set on the number of core, rural, urban and satellite species. For rare species removal, percentages on the x axis represent minimum frequency of occurrence (occupancy) and for sparse species removal they represent minimum relative cover (abundance-when-present).

Impact on beta diversity assessment

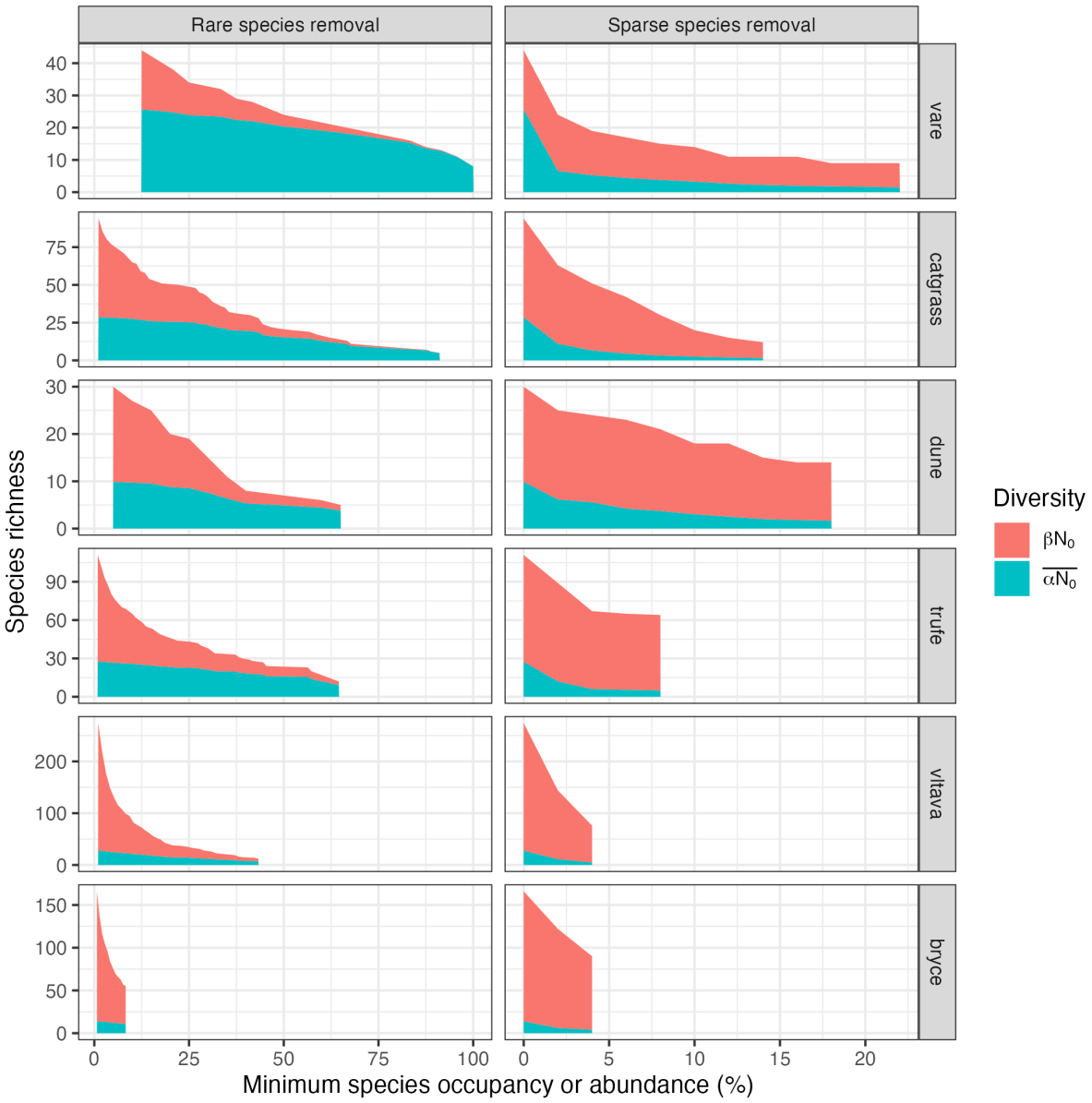

Figure 6. Impact of rare (left) and sparse (right) species exclusion from each data set on the additive partitioning of gamma species richness ($q = 0$). Blue area: mean alpha species richness (average number of species present at each site of the data set); red area: additive beta species richness (average number of species absent from each site but present in other sites of the data set); total area: gamma species richness (total number of species in the data set).

When excluding rare species based on minimum frequency, additive beta species richness ($q = 0$) decreases more than mean alpha species richness, contrary to exclusion of sparse species based on minimum relative cover, for which alpha diversity declines more rapidly (Fig. 6). Similar patterns are obtained for Hill-Shannon ($q = 1$) and Hill-Simpson ($q = 2$) diversity (Supplementary Material, Appendix S1).

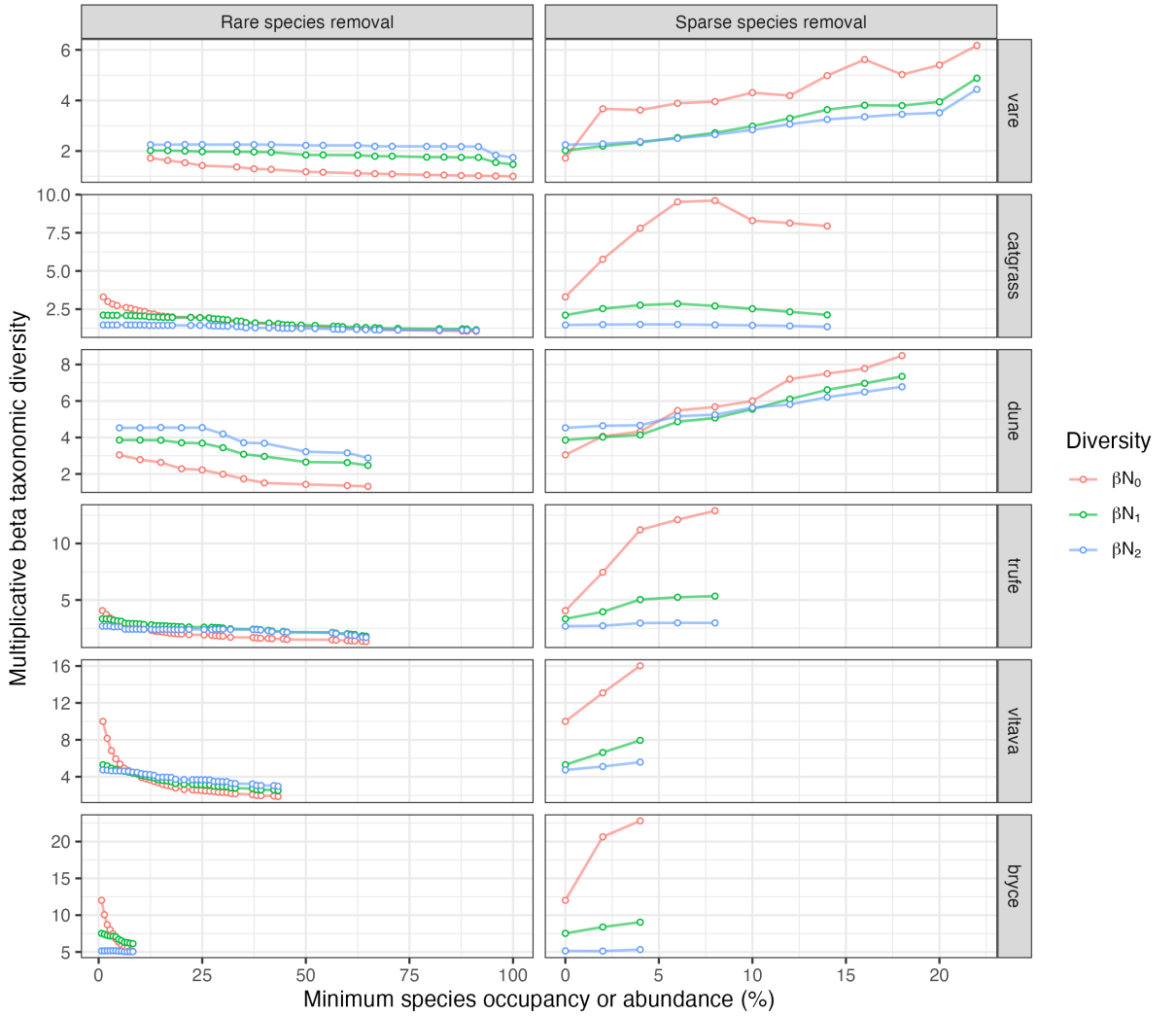

Figure 7. Impact of rare (left) or sparse (right) species exclusion on the multiplicative beta taxonomic diversity. βN_0: multiplicative beta diversity of all species (Whittaker); βN_1: multiplicative beta diversity of abundant species (Hill-Shannon); βN_2: multiplicative beta diversity of dominant species (Hill-Simpson).

The difference is even more evident when considering multiplicative beta diversity of orders 0, 1 and 2 (Fig. 7). All beta diversity indices decline when removing rare species, whereas they tend to increase when removing sparse species. Apart from these general trends, we observe strong differences in the relative impact of species removal on these indices among data sets, depending on their initial structure. However, the multiplicative beta diversity of dominant or abundant species (βN_2 and βN_1, respectively) is generally less affected by species removal than beta diversity computed on presence-absence data (βN_0). Irrespective of the initial values of beta diversity indices, beta species richness βN_0 becomes always the lowest at the end of rare species exclusion and the highest at the end of sparse

371 species exclusion. This confirms that the exclusion of rare species leads to an increasingly
372 apparently homogeneous community composition, whereas the exclusion of sparse species
373 leads to greater apparent heterogeneity among the sites.

374 *Impact on RDA and community-environment relationship assessment*

375 The impact of species removal on RDA results was assessed by the variation of the
376 percentage of explained variation (model performance expressed by adjusted R^2, Fig. 8) and
377 of the contribution of the first axis to this explained variation (Fig. 9) following a progressive
378 exclusion of rare species (left) or of sparse species (right) records.
379 In the case of 'catgrass', the data set for which the percentage of explained variation was
380 initially the highest, both model performance and contribution of the first axis are slightly
381 improved by rare species removal until the suppression of most satellite and urban species (at
382 about 30% frequency), whatever the pre-transformation of relative cover data. By contrast,
383 the elimination of sparse species tends to decrease model performance in all simulations.

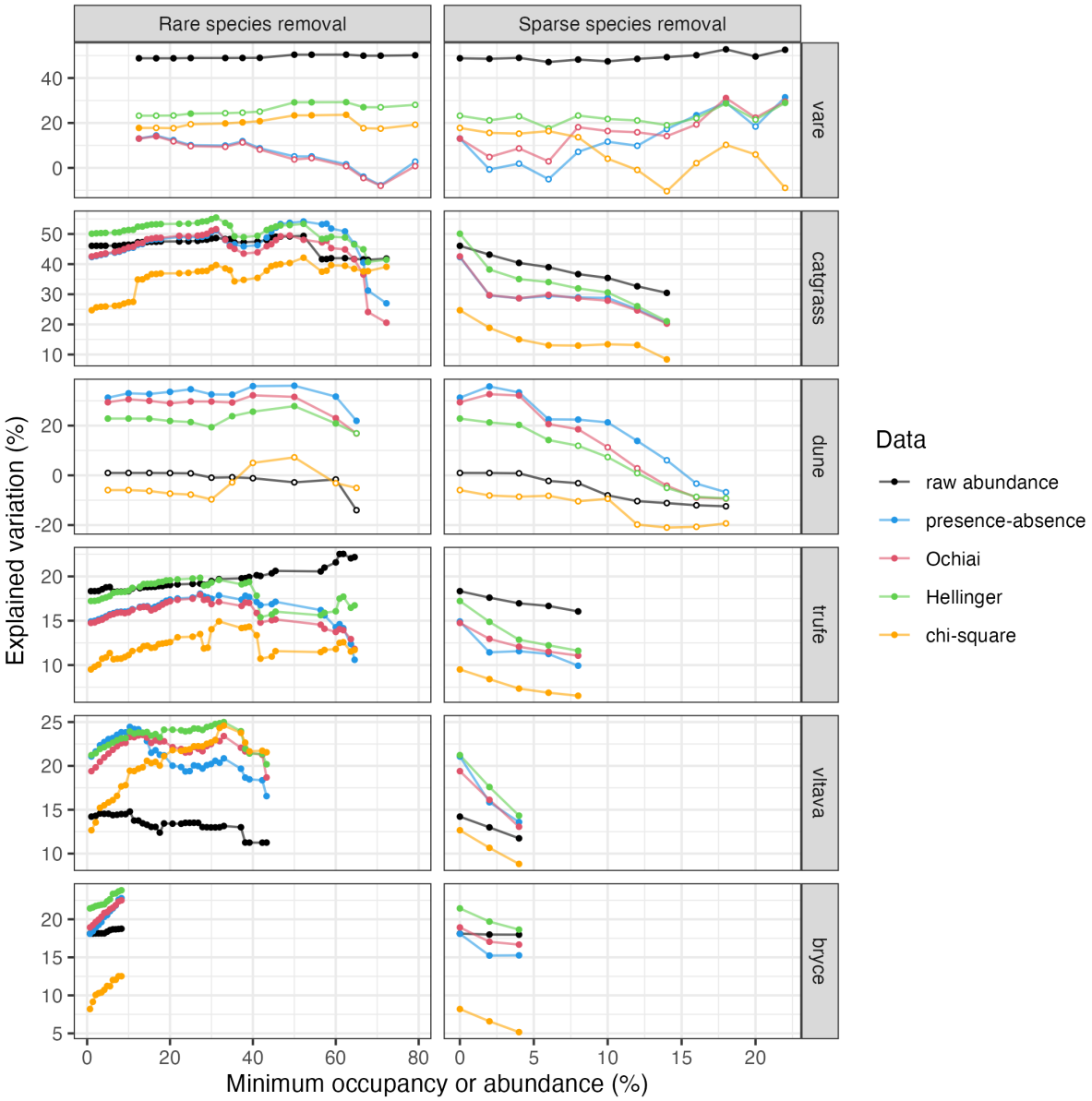

Figure 8. Impact of rare (left) and sparse (right) species exclusion on the percentage of explained variation of RDA (adjusted R^2) without or after several pre-transformations of each species matrix. Solid circles indicate significant results of permutation tests ($p < 0.05$, 999 permutations).

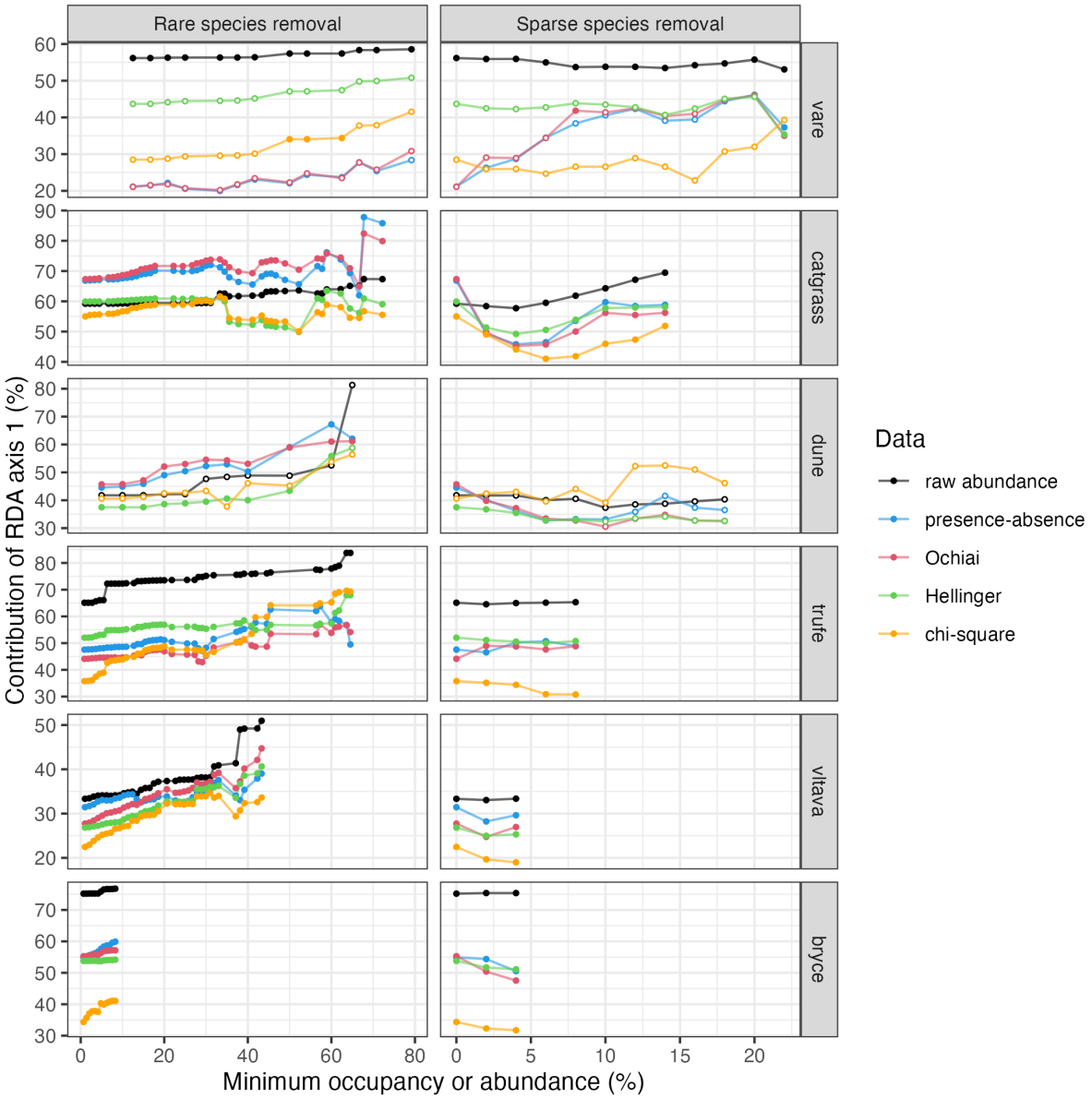

Figure 9. Impact of rare (left) and sparse (right) species exclusion on the contribution of axis 1 of RDA without or after several pre-transformations of each species matrix. Solid circles indicate significant results of permutation tests ($p < 0.05$, 999 permutations).

For 'vare', a homogeneous data set in which β-diversity is mainly due to dominant species, the best results are obtained with raw absolute cover data, which are not affected by rare or sparse species exclusion. Most prior transformations of the data lead to non-significant results. Nevertheless, the performance of the model can be slightly improved by eliminating rare species after Hellinger or chi-square transformation.

With 'dune', the best results are obtained after presence-absence or Ochiai transformation. They are improved by the elimination of rare species, but worsened by the exclusion of sparse species.

For ‘trufe’, conclusions are similar to those obtained from the ‘catgrass’ example, but with better results for raw abundance, even at the end of rare species removal.

For ‘vltava’, Ochiai and Hellinger site profiles, as well as presence-absence data produce the highest explained variation slightly improved by the removal of species below 10% occupancy, but strongly impaired by the loss of sparse species.

Finally, in the most heterogeneous data set (‘bryce’), the adjusted R^2 of the model and the contribution of axis 1 are positively affected by the removal of rare species whatever the transformation applied, whereas the removal of sparse species affects model performance negatively, except for raw abundance data.

Despite strong differences among data sets, some general conclusions may be drawn after comparing the results of these simulations:

(1) With raw data or site profiles of abundance data (i.e. Hellinger transformation), model performance is not or only slightly enhanced when removing the least frequent species.

(2) By contrast, model performance is generally negatively affected by the progressive exclusion of sparse species, which mimics a decreasing sampling effort in each community.

(3) The ranking of prior transformation of absolute cover data according to model performance varies strongly among the data sets, yet without affecting the general effect of rare or sparse species removal. Interestingly, the Ochiai transformation of presence-absence data does not improve model performance, as compared to the simple binary transformation, in any data set. However, canonical redundancy analysis on raw absolute cover data or on presence-absence data considers double zeros in the calculation of distances between sites and for this reason should only be applied to matrices with very few zeros (Borcard et al., 2018).

(4) In large and heterogenous datasets, the removal of rare species clearly improves the performance of RDA after double transformation (chi-square), contrary to the removal of sparse species.

Discussion

Minor species, β-diversity and ecological assessment

To assess the impact of reduced sampling effort and incomplete representation of local plant diversity on mean ecological indicator values of vegetation relevés, Ewald (2003)

simulated a reduction of an original compositional matrix by randomly deleting 1, 10, 20, 40 and 80% of species records with low abundance. The random omission of low-abundance species affected the correlation between log-abundance weighted average ecological indicator values and measured environmental variables only weakly. Incomplete recording of taxonomic information increased multiplicative β-diversity, due to the non-proportional relationship between α-diversity, which declined linearly with sparse species removal, and γ-diversity, which was little affected until ca. 40% of the records had been deleted (Ewald, 2003). These last findings are consistent with the results of our progressive exclusion of sparse plant species. In addition, the author applied Mantel correlation to test the overall multivariate association between distance matrices of species composition and environment; however, this method is now considered inappropriate for this kind of study and should be replaced by the computation of RV coefficients (Escoufier, 1973; Legendre & Legendre, 2012; Omelka & Hudecová, 2013; Legendre et al., 2015).

As for animal communities, Sgarbi et al. (2020) compared the effect of sequential removal of genera from the most to the least locally abundant, sequential removal from the least to the most abundant or random removal on the ordination patterns of stream benthic invertebrate communities. By comparing Procrustes correlations based on abundance data, they found that taxon-based reduction in sampling effort, consisting in the omission of up to 50% of the least abundant species (confusingly called “rarest” by these authors), affected only weakly the multivariate pattern observed in the complete assemblage data, contrary to the removal of the most abundant species (called “commonest”).

However, focusing on the effect on ecological assessment of excluding stream dwelling macroinvertebrate taxa with low abundances or with small distribution ranges, Nijboer & Schmidt-Kliber (2004) concluded that neither sparse nor rare taxa should be excluded, because of their essential ecological indicative power. In addition, our study shows that the omission of rare species had an opposite (i.e. negative) effect on multiplicative β-diversity. This finding supports the determinant role of these infrequent species in the differentiation of habitats. The removal of rare species may have similar or greater influence in biological assessment as other choices inherent in its computation, such as the choice of ordination method or measures of multivariate resemblance (Poos & Jackson, 2012).

Indeed, rare species may be indicators of rare environmental conditions or specific habitats, to which these species could be adapted better than common species. According to Rabinowitz et al. (1986), habitat specificity (ecological specialization) is the most important

dimension of ‘rarity’ (in a broad sense). It could explain why many rare species often co-occur in one or few sites, where they may be dominant. For example, the ‘vltava’ data set contains a plot with nine unique species including one dominant. Such sites and species appear as outliers in ordinations and can hide the main gradients, especially when applying chi-square-based methods such as CA and CCA.

Minor species in canonical ordination

By removing rare species from fish and odonatan communities Brasil et al. (2020) found that rare species are of little importance for understanding the relationships with spatial and environmental gradients using variation partitioning based on partial RDA (Borcard et al., 1992; Peres-Neto et al., 2006). As shown in our study, the only improvement one can expect from rare species removal in canonical ordination is with double profiles (after chi-square transformation).

Of course, RDA model performance cannot be reduced to an adjusted R^2 and a contribution of axis 1 to the analysis. The purpose here was not to use these indicators to grade the different pre-transformation options, since their choice depends upon the questions and hypotheses of the modeling framework. Rather, the purpose was to figure out whether the effect of species removal on the RDA results was dependent on this choice. Indeed, whatever the various ranking of the four options for abundance transformation (presence-absence, Ochiai, Hellinger or chi-square) in terms of variation explained, a common general trend emerged from the six examples, i.e. a slight improvement after a moderate exclusion of rare species, and a clear degradation after any exclusion of sparse species. The only exception is the ‘vare’ data set after presence-absence or Ochiai transformation, for which sparse species removal has a positive effect on both variation explained and contribution of axis 1. In this homogeneous, species-poor data set, species-environment relationships are mainly expressed by variations in absolute cover among frequent species.

Conclusion

The positive correlation between inter-site occupancy (frequency of occurrence) and average intra-site dominance (relative abundance-when-present) should not hide the profound differences between rare (uncommon) and sparse (undominant) species. They must not be confounded because they play a completely different role in vegetation analysis and ecological studies of other groups of organisms. As for biodiversity assessment, removing

rare species decreases the proportion of satellite species, hence decreasing multiplicative beta diversity, whereas removing sparse species increases the proportion of urban species, hence dramatically increasing multiplicative beta diversity. As for ecological assessment, focusing only on dominant species during sampling or multivariate analyses by ignoring sparse species is likely to limit the performance of ecological empirical models. These conclusions are also applicable to animal and microbial communities, to which we applied the same methodology in a preliminary study (results not shown here).

One of the main findings of our simulation study was that the multiplicative beta diversity decreased when removing rare species, but increased when removing the sparse ones. A possible explanation is that when you ignore the most infrequent species, the whole dataset becomes more homogenous because rare species, which are often numerous, are the most responsible for differences in community composition, hence *decreasing* beta diversity. By contrast, when you ignore sparse species (based on their average relative cover, not based on their absolute cover in each separate site), you focus more on dominant and abundant species, irrespective to their occupancy, while increasing the contrast between communities dominated by different species, hence *increasing* beta diversity.

Provided that meaningful transformations are applied, there is no need to remove any species prior to RDA. For homogeneous data sets ("short gradients") in which total vegetation cover and differences in species cover among sites are of interest, absolute cover data should not be transformed. For heterogeneous data sets ("long gradients") and a focus on local dominance relationships, site profiles (e.g. Hellinger or other Box-Cox family transformation) should be used. Removing rare species is only useful for the ordination of double profiles, achieved by RDA after chi-square transformation or, more commonly, by canonical correspondence analysis (CCA). If CCA is preferred, down-weighting of rare species has proved to be more efficient than eliminating them (Jing et al., 2015).

If canonical ordination is used to extract the main ecological gradients while taking into account differences in species abundances among sites, then RDA should be applied without pre-transformation of abundance data, but only in case of "short gradients" (species-poor communities with a small proportion of absences in the data set). To preserve the differences in total abundance among sites, reflecting site productivity, in a data set containing a high proportion of zeros, distance-based redundancy analysis (db-RDA) should be preferred, based on a percentage difference or Ružička dissimilarity matrix (Legendre & Anderson, 1999). If the community data set is very heterogeneous ("long gradient" or multiple gradients) and researchers are most interested in relative proportions of species within a community rather

than absolute comparisons of species abundances across multiple sites, then site transformation (e.g. Hellinger) should be applied prior to RDA.

By encouraging researchers to recognize the contrasting roles of rare and sparse species in community assemblages, the results of the present study will motivate them to formulate more precise working hypotheses in their own studies.

Our study focused on plant communities, but the question is more general and may be investigated for any animal or microbial communities at a given trophic level. Recently, new tools have been developed to standardize Hill diversity indices based on sample completeness or coverage (Roswell et al., 2021, 2023; Chao et al., 2023). In ecology, the concept of sample coverage has been only described and applied to species assemblages for which we can count individuals (typically animal or tree communities), which is not the case for most plant communities, where species "abundance" is generally measured by the percentage of aboveground cover (or classes of absolute or relative cover). As a matter of fact, all current formulae and implementations of the coverage-based or size-based standardisation of Hill diversity indices (iNEXT.beta3D; Chao et al., 2023) apply to individual-based or incidence-based data (point-based or grid-based frequency) and cannot be applied to continuous abundance measures, such as cover or biomass. From a perspective of statistical inference, rare and sparse species carry the most essential information about sample coverage. However, we cannot presently apply such standardisation to our cover-based vegetation data.

Future work is needed to assess the role of rare and sparse species on other beta diversity indices, such as dissimilarities or variance-based methods (Legendre & De Cáceres, 2013) and, as soon as it is available for any type of abundance data, coverage-based standardisation of Hill diversity indices, including phylogenetic and functional facets of community diversity.

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723

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730

731 **Author contributions**

732 F.G. conceived the research idea; F.G. and A.R. performed statistical analyses; F.G., with
733 contributions from D.B. and P.L., wrote the paper; all authors discussed the results and
734 commented on the manuscript.

735

736 **Data availability statement**

737 The data supporting the article's results and the R scripts used to generate the analyses and the
738 figures are provided in the electronic Supplementary Information Appendix S2.

739

740 **Supporting information**

741 Appendix S1. Additional figures.

742 Appendix S2. Data and R code.

743

744

Appendix S1. Additional figures.

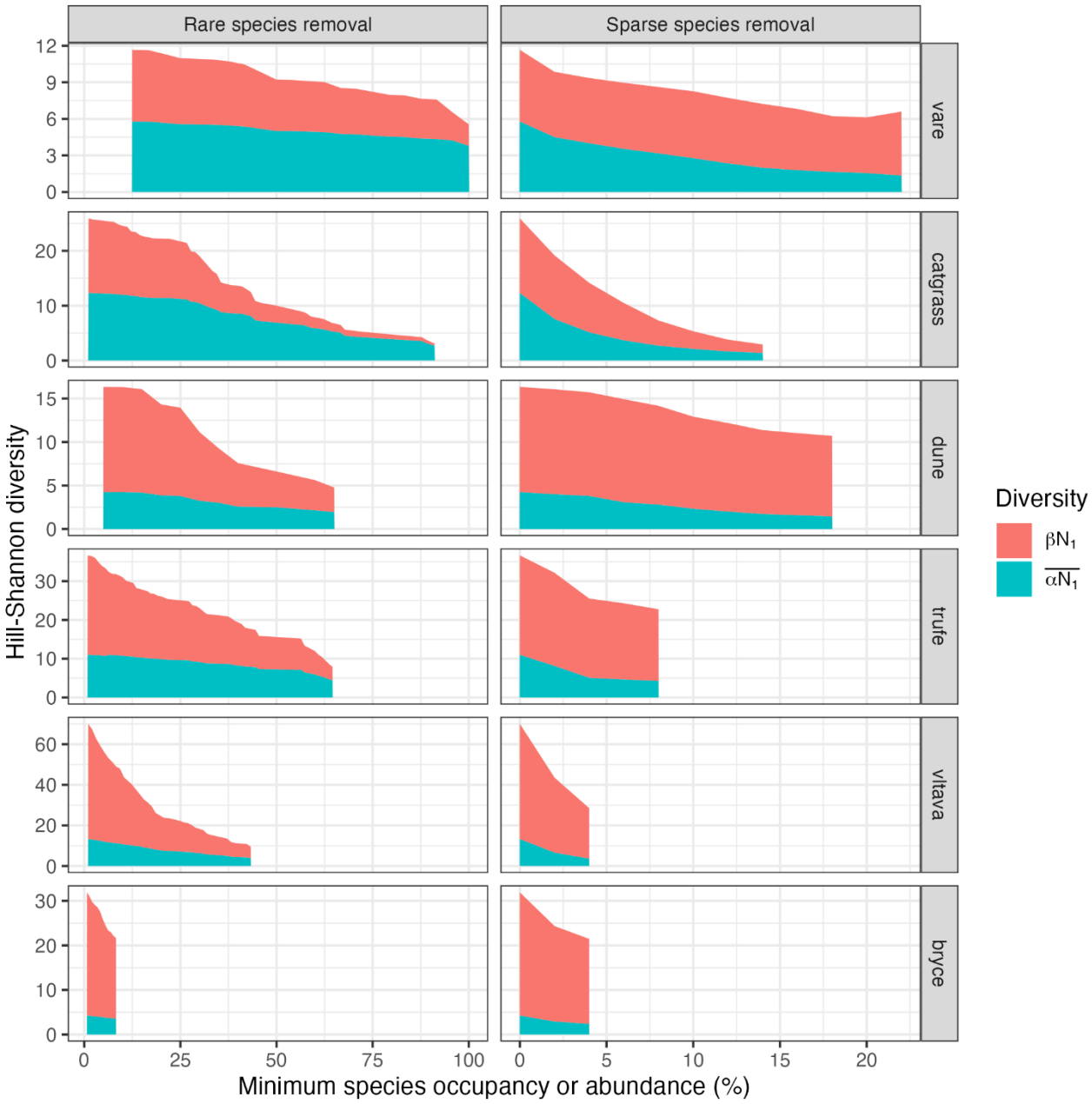
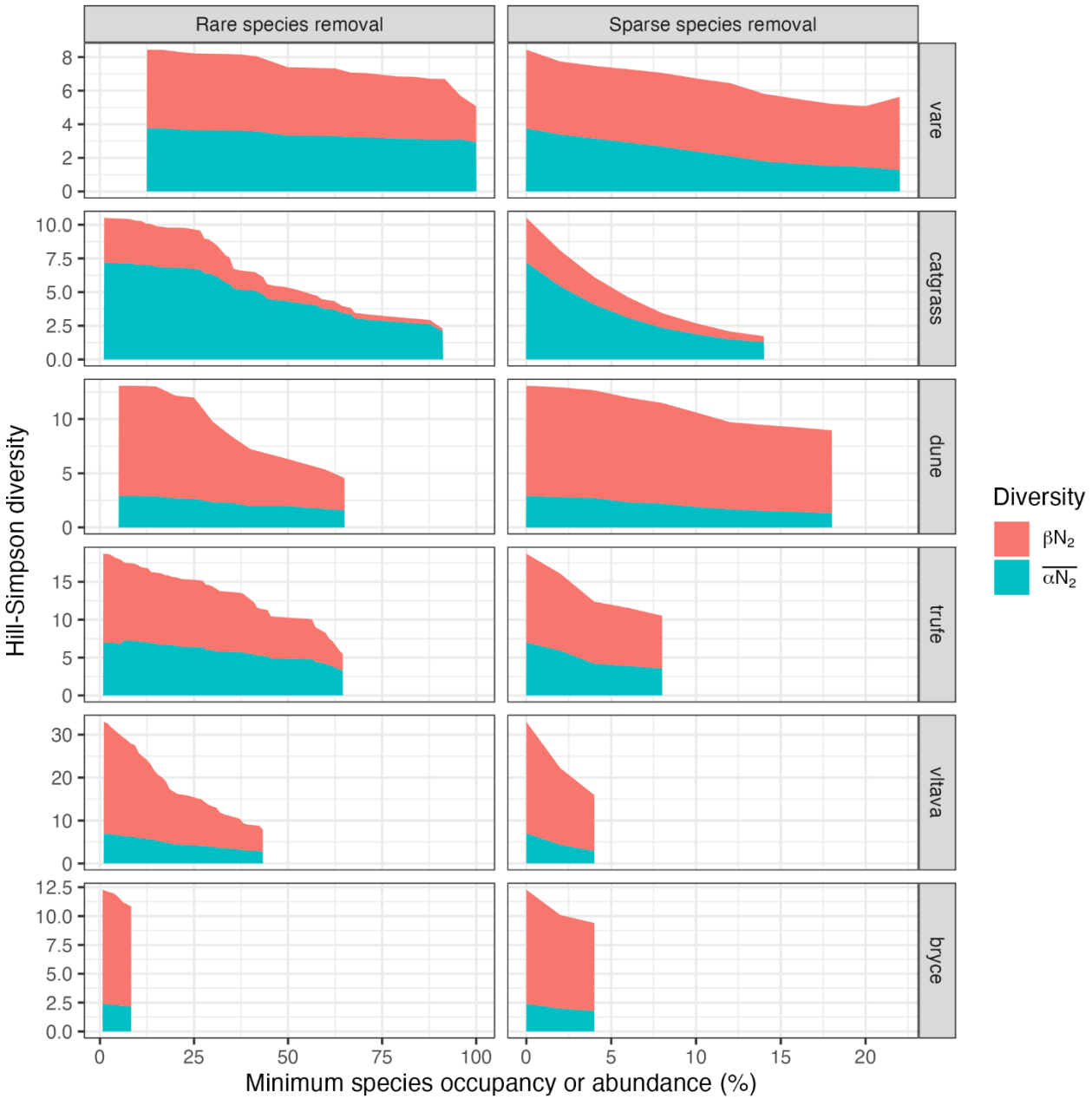


Figure S1. Impact of rare (left) and sparse (right) species exclusion from each data set on the additive partitioning of gamma Hill-Shannon diversity. Blue area: mean alpha Hill-Shannon diversity (average number of abundant species present at each site of the data set); red area: additive beta Hill-Shannon diversity (average number of abundant species absent from each site but present in other sites of the data set); total area: gamma Hill-Shannon diversity (total number of abundant species in the data set).



754
755 **Figure S2**. Impact of rare (left) and sparse (right) species exclusion from each data set on the additive
756 partitioning of gamma Hill-Simpson diversity. Blue area: mean alpha Hill-Simpson diversity (average
757 number of dominant species present at each site of the data set); red area: additive beta Hill-Simpson
758 diversity (average number of dominant species absent from each site but present in other sites of the
759 data set); total area: gamma Hill-Simpson diversity (total number of dominant species in the data set).
760