



Short communication

Accounting for the capacity of common and rare species to contribute to diversity spatial patterns: Is it a sampling issue or a biological effect?

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ABSTRACT

The contribution of common species to overall species richness in many cases is greater than that of rare species. However, the explanation of this phenomenon remains vague. One hypothesis is that this is a sampling issue and not a biological one. Therefore standardization methods like the information index and empirical variance have been proposed. But, these standardizations do not explicitly compare the significance of the dataset size of the common and rare sub-assemblage. Here, we investigate the role of dataset size in accounting for the capacity of common and rare species to contribute to diversity spatial patterns. We used a dataset of 5148 vascular plant species recorded in 16,439 sample plots in the Greek Natura 2000 network. Species were ranked according to the number of sample plots they occupied in ascending (rare to common), descending (common to rare) and random order. We analyzed the correlation between the richness of each sub-assemblage and total species richness. When comparing among sub-assemblages with equal number of species, common species are clearly the better predictors of total species richness. But, when comparing among sub-assemblages with equal number of occurrence records, the patterns changed. Common and rare species contribution to the overall richness pattern was comparable, with rare species contributing slightly less than widespread species in some cases and the opposite in other cases. However in all cases, sub-assemblages of random species remarkably outperformed the equal sized sub-assemblages of common or rare species. Our results suggest that common and rare species are biased samples of the community and that equal sized random samples are more representative; thus the greater contribution of common species than rare species to biodiversity patterns might be more a sampling issue than a biological effect of commonness or rarity.

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1. Introduction

One of the most noticeable patterns in macroecology and biogeography is the uneven distribution of species richness. An approach to understand the determinants of spatial variation in species richness is to decompose the overall richness patterns into those for different species groups and to ask how the distributions of individual species combine to produce the overall variation. Such an approach has been applied in several studies, deconstructing the overall species richness into groups classified using phylogenetic

information (Kallimanis et al., 2012; Mazaris et al., 2008a), life history traits (Keil et al., 2008) or according to their commonness and rarity (Jetz and Rahbek, 2002; Lennon et al., 2004; Mandelik et al., 2012). Previous studies have consistently shown that the contribution of widespread species to the overall richness patterns is greater than that of rare species (Keizer-Vlek et al., 2012; Kreft et al., 2006; Mazaris et al., 2010; Sizing et al., 2009; Vazquez and Gaston, 2004). This seems counterintuitive, since the old standing notion is that overall species richness is mainly driven by the large number of species with restricted distribution and low abundance (Berg and Tjernberg, 1996; Gaston and Blackburn, 1996).

Various explanations have been proposed as to why the spatial distribution of common species contributes disproportionately more to the distribution of species richness. Different factors drive the distribution of wide-ranging and restricted-range species (Jetz and Rahbek, 2002; Kallimanis et al., 2010; Lennon et al., 2004; Magurran and Henderson, 2003); and the richness of common species is more strongly correlated with environmental predictors than the richness of rare species (Jetz and Rahbek, 2002; Lennon

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et al., 2011; Tello and Stevens, 2010). Also, La Sorte and Boecklen (2005) provide evidence that widespread species have a greater contribution to spatial variation in species richness due to their better temporal turnover properties, which determine biodiversity via colonization events. In addition, anthropogenic activities reinforce such patterns, as the establishment of common species leads to increasing species richness.

Aiming to provide a better understanding on the underlying properties of common species to contribute disproportionately larger amount of information, Lennon et al. (2004) applied a standardization approach based on an information index that measures the information content of species sub-assemblages by using the cumulative binomial variance. The application of this index has demonstrated that, in most cases, the common species contribute more than the rare species to overall species richness patterns. According to this index, one species with 10% coverage corresponds to one species with 90% coverage. However, when we start adding species of unequal coverage then the picture changes, one species with 10% coverage corresponds to 9 species with 99% coverage. Also, this measure of variance does not take into account the spatial autocorrelation of biodiversity patterns. Lennon et al. (2011) used the empirical variance as an alternative way to weigh species, and suggest that previously obtained patterns on the greater contribution of common species might be a statistical artefact or a weakness of literature to explain these patterns, based on the shape of the frequency distribution of species occupancies. The most obvious difference among common and rare species as a predictor of total species richness is the amount of information that each species carries. Typically, rare species appear in few or even just one area, and thus they are characterized by few occurrence records. In other words, they carry information for only few sites to predict overall species richness. On the other hand each common species appears in many areas and thus contributes information for many sites. This disparity becomes even greater as we accumulate species.

Here, we investigate the relative importance of the amount of information that common and rare species contribute towards establishing patterns in species richness. We analyze the correlation patterns between the species richness of each sub-assemblage against the total number of species. To evaluate the role of amount of information we compare the contribution of rare and common species in two different ways. First, we compare sub-assemblages with the same number of species. Second, we use an alternative way for weighting species based on the number of occurrence records they contain and compare sub-assemblages with the same cumulative number of occurrence records. We test: (a) if there is a consistent correlation between species richness and the number of rare or common species, (b) if there are any differences in the patterns produced by different approaches, (c) if these results dependent upon the size of the sampling unit, (d) if these patterns hold for all habitat types.

2. Materials and methods

2.1. Database

We examined a dataset of the distribution of 5148 vascular plant species in the Greek Natura 2000 network of protected areas. This dataset included a total of 343,689 occurrence records sampled across 16,439 sample plots located in 254 sites throughout Greece.

We performed the analysis for 12 size categories of standardized sample plots (1140 plots <5 m², 732 plots 20–24 m², 1257 plots 25 m², 887 plots 30 m², 1620 plots 50 m², 955 plots 60–64 m², 3162 plots 100 m², 435 plots 150 m², 1935 plots 200 m², 829 plots 300 m², 458 plots 400 m² and 396 plots >400 m²). There are also

2633 plots with surface areas outside these ranges that were analyzed only in the entire dataset. We repeated the analysis on data collected for various habitat types (5670 plots in forests, 3151 plots in shrublands, 3457 plots in coastal sites and sand-dunes, and 2948 in grasslands and open landscapes). However, it was not possible to analyze the effect of size of the sampling unit across all habitats, as the size of sampling units depends on the habitat type surveyed.

2.2. Statistical analysis

Establishing a definition of rarity or commonness poses a major difficulty in biodiversity research (Poos and Jackson, 2012; Siqueira et al., 2012). Thus, to analyze the relative contribution of commonness and rarity to patterns of overall species richness across a large number of sample plots, we ranked the species according to the number of sample plots they occupied generating ascending (starting with the species occurring in the lowest number of sample plots and followed by the second more restricted species, rare-to-common sequence) and descending orders (starting with the species occurring in the highest number of sample plots and followed by the second more widely distributed species and so on, common-to-rare sequence) (see details in Lennon et al., 2004; Mazaris et al., 2008b; Vazquez and Gaston, 2004). For comparisons, we also generated 100 random sequences of species. The species order in the ranking list was not determined following certain criteria (e.g. like in Cucherousset et al., 2008), but it was rather based on species' distributions across the sample plots (common – geographically widespread species observed in a large number of sample plots while rare – geographically restricted species were found in disproportionately lower number of sample plots).

At each stage along the three sequences of richness patterns (ascending, descending and random), we measured the number of occurrences in each sub-assemblage and we correlated the richness pattern for the cumulative sub-assemblage (e.g. the first sub-assemblage in the common to rare sequence included only the most widespread species with the next sub-assemblage adding the second more widespread species, and so on) with that of the full assemblage (overall species richness). We then plotted the sequential correlation patterns between each sub-assemblage and species richness against the cumulative numbers of species, and against the cumulative numbers of occurrence records. To account for the possible effect of sample plot area or habitat type, we repeated the analysis for different sampling sizes and habitat types separately.

Spatial autocorrelation of biological data may lead to biased results. However, this is not the case here, since our sample plots were dispersed throughout Greece, with an average distance of km separating them. This was verified with the use of semivariogram for the values of species richness per sample plot, that showed little to none spatial autocorrelation (results not shown).

3. Results

3.1. Contribution of commonness and rarity to overall species richness

The frequency distribution of species was rightly skewed, with most plant species occurring in a limited number of sites. The 610 rarest species were recorded in only one sample plot, 408 and 289 rare species were recorded in two and three sample plots respectively. On the other hand, the most common species (*Dactylis glomerata*) was observed in 4041 sample plots (approximately 25% of all sample plots). Thus, the 1307 rarest species cumulatively accounted for 2293 occurrence records (less than 1% of the entire dataset), while the single commonest species has almost twice as

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