

Species abundance distributions as a proxy for the niche–neutrality continuum

Xianzhi Wang¹, M. D. Farnon Ellwood², Dexiecuo Ai^{3,*},
Renyi Zhang³ and Gang Wang³

¹ State Key Laboratory of Grassland Agro-Ecosystems, College of Pastoral Agriculture Science and Technology, Lanzhou University, 768 Jiayuguan Road, Chengguan District, Lanzhou, 730020, China

² Centre for Research in Biosciences, University of the West of England, Coldharbour Lane, Bristol BS16 1QY, UK

³ State Key Laboratory of Grassland Agro-Ecosystems, School of Life Sciences, Lanzhou University, 222 Tianshui Road, Chengguan District, Lanzhou, 730000, China

*Correspondence address. State Key Laboratory of Grassland and Agro-Ecosystems, School of Life Sciences, Lanzhou University, Lanzhou 730000, China. Tel: +86-931-8912562; Fax: +86-931-8912562; E-mail: aidxc@lzu.edu.cn

Abstract

Aims

Species abundance distributions (SADs) are often used to verify mechanistic theories underlying community assembly. However, it is now accepted that SADs alone are not sufficient to reveal biological mechanisms. Recent attention focuses on the relative importance of stochastic dispersal processes versus deterministic processes such as interspecific competition and environmental filtering. Here, we combine a study of the commonness and rarity of species (i.e. the SAD) with mechanistic processes underlying community composition. By comparing the occurrence frequencies of each and every species with its abundance, we quantify the relative contributions of common and rare species to the maintenance of community structure. Essentially, we relate the continuum between commonness and rarity with that of niches and neutrality.

Methods

An individual-based, spatially explicit model was used to simulate local communities in niche spaces with the same parameters. We generated sets of assemblages from which species were eliminated in opposing sequences: from common to rare and from rare to common, and investigated the relationship between the abundance and frequency of species. We tested the predictions of our model with empirical data from a field experiment in the environmentally homogeneous alpine meadows of the Qinghai–Tibetan plateau.

Important Findings

Our simulations support the widespread notion that common species maintain community structure, while rare species maintain species diversity, in both local and regional communities. Our results, both from theoretical simulations and from empirical observations, revealed positive correlations between the abundance of a particular species and its occurrence frequency. SAD curves describe a continuum between commonness and rarity. Removing species from the ‘rare’ end of this continuum has little effect on the similarity of communities, but removing species from the ‘common’ end of the continuum causes significant increases in beta diversity, or species turnover, between communities. In local communities distributed in a homogenous habitat, species located at the ‘common’ end of the continuum should be selected by environmental filtering, with niche space partitioning governed by interspecific competition. Conversely, species located at the ‘rare’ end of the continuum are most likely subject to stochastic dispersal processes. Species situated at intermediate locations on this continuum are therefore determined by niche and neutral processes acting together. Our results suggest that, in homogeneous habitats, SAD curves describing the common–rare continuum may also be used to describe the continuum between niches and neutrality.

Keywords: rarity, commonness, continuum, occurrence frequency, community similarities

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INTRODUCTION

The species abundance distribution (SAD) characterizes the proportional abundance of species in an ecological community.

As one of the most basic descriptors of an ecological community, the SAD is a useful way of quantifying community structure (Connolly *et al.* 2005; Hubbell 2001; Magurran 2007; McGill *et al.* 2006, 2007; Pachevsky *et al.* 2001; Volkov *et al.*

2003). In general, natural communities contain large numbers of rare species, with a few exceptionally abundant, or ‘common’ species (Gotelli and Graves 1996; Krebs 1985; McGill 2003a, 2007; Putman 1994; Williams 1964). This universal pattern is what gives the SAD a long tail, a hollow curve or a hyperbolic shape on a histogram (Hubbell 1979, 1997).

SADs are often used to verify mechanistic theories attempting to explain the structure of ecological communities, otherwise known as species assembly rules (Cohen 1968; Hengeveld *et al.* 1979; MacArthur 1957, 1960; Marquet *et al.* 2003; McGill 2003b, 2007). For instance, the broken stick model, developed by MacArthur (1957), provided the first SAD by assuming that a given niche space was broken up simultaneously into different fractions (MacArthur 1957, 1960). Studies of community assembly during the 1980s continued to focus on the notion that communities could be ‘carved up’ into multidimensional niche spaces (Austin *et al.* 1990; Chesson and Warner 1981; Comins and Noble 1985; Pontin 1982; Sugihara 1980; Tilman 1980, 1982; Turelli 1981). Resource-based models followed, assuming that commonness and rarity are determined by environmental ‘filters’ (Chesson 2000; Cornwell and Ackerly 2010; Tilman 1982; Tilman and Pacala 1993). If the resources required by a particular species are available, then the abundance of that species will increase. Alternatively, if there are few suitable resources in an environment to which a particular species is adapted, the abundance of that species will decrease (Lennon *et al.* 2011).

According to resource-based models, environmental filtering generates local communities, and niche partitioning maintains community structure by determining which species are able to coexist (Gotzenberger *et al.* 2012). However, some studies have refuted the idea that local communities (especially plant communities) are structured by classical niche partitioning (Bell 2000; Hubbell 1997, 2001). Empirical evidence now suggests that stochastic dispersal processes play a more important role in determining community composition than previously assumed (Gotzenberger *et al.* 2012; Myer and Harms 2009; Zobel and Kalamees 2005). Consequently, community ecologists are now focusing on the combined effects of environmental filtering and stochastic dispersal to explain variation in SADs (Ellwood *et al.* 2009; Mouquet and Loreau 2003; Mouquet *et al.* 2006). More specifically, some studies have suggested that, while common species are affected mainly by environmental factors, rare species are affected mainly by stochastic dispersal processes (Ai *et al.* 2013b; Chase *et al.* 2005; Wang *et al.* 2012).

However, SADs show only the proportional abundance of species, they do not reveal the composition of communities (McGill *et al.* 2007). The SAD cannot identify which species are abundant and which are rare, and it can only show the relative proportions of abundant versus rare species in a community (Magurran and Henderson 2003; McGill *et al.* 2007). The compositions of communities under the same SAD are rarely the same, and in fact are often completely different. The universality of the SAD curve allows the comparison of

communities with few or no species in common, even communities in different guilds and at different trophic levels (McGill *et al.* 2007). However, this universality is also a major weakness of the SAD curve because it is impossible to ascertain the abundance of any particular species (McGill *et al.* 2007). The SAD is essentially useless for studies in which species must be identified, such as those exploring the turnover of species in either time or space (Wang *et al.* 2013) or defining the functions of different species in ecological communities (Sun *et al.* 2016). To add to this confusion, both niche and neutral models, each based entirely on different community assembly mechanisms, are capable of producing the same SAD (Du *et al.* 2011).

If we want to understand the biological mechanisms structuring communities, or at the very least to confirm the predictions of biologically realistic theory, we need to be able to record specific changes in community composition, while at the same time comparing the proportional abundance of each species. Community composition can be measured using any one of a number of similarity indices, such as the Bray–Curtis index (Ai *et al.* 2012; Faith *et al.* 1987; Yang *et al.* 2015).

Previously, ‘common’ and ‘rare’ species have been defined artificially. For example, species representing <1% of the total number of individuals have been defined as ‘rare’, whereas those species representing >1% were defined as ‘common’ (Clark and Tilman 2008). What is novel about our study is that we are able to locate the exact position of each species on the continuum between commonness and rarity, thus quantifying the relative contributions of common and rare species to the composition of each local community. We reasoned that if we could show that common species are affected mainly by deterministic environmental factors and that rare species are affected mainly by stochastic dispersal processes, it would follow that SADs could be used as a proxy for the relative importance of niches and neutrality in structuring ecological communities.

MATERIALS AND METHODS

Model analysis

As in our previous studies (Ai *et al.* 2012, 2013a, 2013b), the model presented here is individual-based, spatially explicit and integrates niche partitioning and dispersal limitation. The current model is a mainland-island model, the islands being local communities and the mainland representing the regional species pool. We assumed the regional species pool to be constant during simulations because we wanted to focus entirely on the dynamics of local communities.

The difference between the current model and the model by Ai *et al.* (2012) is that previously we focused on two separate models (neutral model and niche model), treating immigration and dispersal limitation separately. Here, we combine niche partitioning and stochastic dispersal across a homogeneous environment within the same model. One feature that the current model shares with our previous models is that immigration is from the regional species pool. However, an

important difference between the current model and the models of [Ai *et al.* \(2013a, 2013b\)](#) is that in [Ai *et al.* \(2013a, 2013b\)](#) dispersal occurred across a network of local communities, whereas in the current model, stochastic dispersal occurred from the regional species pool to the local communities. What all our models have in common is that all three combine niche partitioning and stochastic dispersal. The model description follows the Overview, Design concept, Details (ODD) protocol ([Grimm *et al.* 2006, 2010](#)) (see online supplementary Appendix 1). A list of model parameters and their values can be found in supplementary Table S1.

Field data

To test the predictions of the model, we collected field data in an alpine meadow located in the eastern part of the Qinghai-Tibetan plateau, at the Alpine Meadow and Wetland Ecosystems Research Station (Hezuo, 34°55'N, 102°53'E; 2900 m.a.s.l.) of Lanzhou University. The average annual temperature and precipitation are 2.4°C and 530 mm, respectively. In the first plot, located on a west-facing slope, the vegetation is dominated by grasses such as *Kobresia humilis* (C.A. Mey) Serg. and *Festuca sinensis* Keng, so we named these plots the grass communities (abbreviated to GC). In the second plot, located on a north-facing slope, the vegetation is dominated by *Potentilla fruticosa* L., so we named these plots the *Potentilla fruticosa* community (abbreviated to PC). The soils are classical alpine meadow soil ([Gong 1999](#)).

In July 2013, we sampled forty 1 m × 1 m quadrats within each plot ([Fig. 1](#)). We sampled two columns 1 m apart, with identical orientation, aspect and slope position. Twenty samples, each 1 m apart, were arranged along each column. We avoided sampling in gaps and on zokor mounds, so the distance between each sample was not always strictly equal to 1 m. We regarded each sample as a local community. The abundance of each species was measured in each of these local communities.

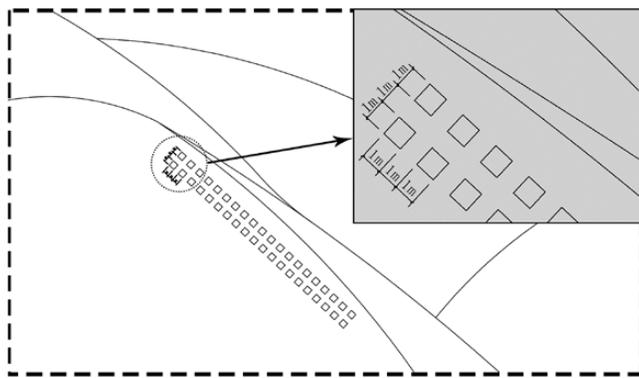


Figure 1: sampling design for both GC and PC plots. Different plots have different but constant orientation, aspect and slope position to ensure environmental homogeneity. We arranged two columns in each plot, with 20 samples set in each column. Hence, the total number of samples in each plot is 40. The distance between two adjacent samples is almost 1 m, but not strictly 1 m due to zokor mounds and gaps.

The measurement of community composition similarity

We used the Bray–Curtis index to measure the similarity of community composition, as this index accounts for both relative abundance and species richness ([Ai *et al.* 2012](#); [Bray and Curtis 1957](#); [Davies *et al.* 2001](#); [Faith *et al.* 1987](#)). To quantify the relative contributions of common and rare species to overall similarities in community composition under the same habitat, we generated sets of assemblages in each local community. These sets were generated by ranking species based on their abundance. In each local community, we ranked all species based on the common–rare continuum (CR_c) and generated two sequences: (i) common to rare species and (ii) rare to common species. All species were divided into several sets, with each set containing five species. The number of species in the final set depended on total species richness, with those left over usually numbering fewer than five species. For the common to rare sequence, the set with the highest species abundance was eliminated first from the local community, followed by the next most abundant set, and so on. For the rare to common sequence, the set to be eliminated first would be that with the lowest abundance, followed by the set with the next lowest abundance, and so on.

Both sequences started with complete community assemblages (LC1-0, LC2-0 in [Fig. 2](#)). After each iteration, we compared the community composition of the two resulting local communities, before removing a set from the next simulation. For the common to rare sequence ([Fig. 2A](#)), the set with the highest species abundance was eliminated first from both LC1 (red panels) and LC2 (green panels), which then became LC1-1 and LC2-1. The second most abundant set was then eliminated from both local communities LC1-1 and LC2-1, which became LC1-2 and LC2-2. This process continued until only those communities with the lowest species abundance (LC1-N-1 and LC2-N-1) remained ([Fig. 2A](#)). The rare to common sequences eliminated species in the opposite direction ([Fig. 2B](#)). Once the eliminations and iterations had taken place, we measured the similarity between all 40 local communities within the same assemblage set. Essentially, we measured the mean similarity of the full assemblage (such as LC-0) by averaging the similarity of $\{(n-1)+1\}(n-1)/2$ without elimination. Here, n is the number of local communities, $n = 40$ for all simulated landscapes in this study. Finally, to investigate the relative contributions of common and rare species to community composition, we correlated the relative abundance with the relative frequencies of each species in every quadrat. We measured Bray–Curtis similarity indices using the fossil package ([Vavrek 2011](#)) implemented in the program R, version 2.13.1 ([R Development Core Team 2009](#)).

RESULTS

Our simulations produced typical SADs, with rank abundance distributions showing few common species and many

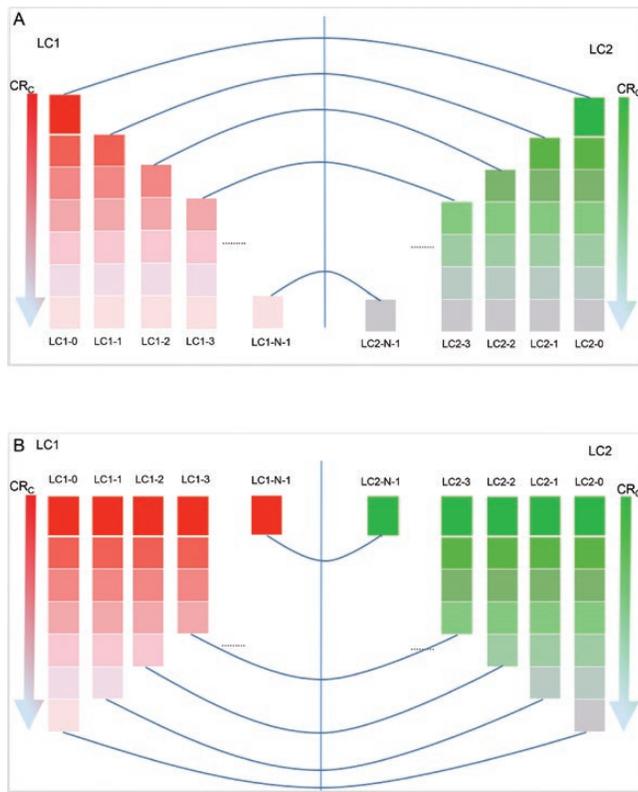


Figure 2: the measurement of similarity for two local communities, LC1 and LC2.

rare species in each of the local communities and across the whole plot (Fig. 3A). SADs based on empirical data from field observations showed the same pattern (Fig. 3B and C). The total species richness of each plot was higher (black lines in Fig. 3) than that of each local community (colored lines in Fig. 3), meaning that the species in the local community were not the same.

We quantified the relative contributions of common and rare species to community compositional similarity by removing common species before rare species (lines with solid circles in Fig. 4) and by removing rare species before common species (lines with hollow circle in Fig. 4). Both sequences (common to rare and rare to common) were modeled under identical environmental conditions. It was therefore rather striking that we observed such close agreement between the results of the simulations (Fig. 4A) and the results from the field data (Fig. 4B and C). Those data points appearing at zero on the x -axis represent the similarity between the full assemblages (i.e. with no species removed). Both sequences started from the full assemblage. Bray–Curtis similarities decreased in the common–rare sequence; but we observed little change in Bray–Curtis similarities in the rare–common sequence.

Essentially, we have analyzed the relationship between the mean abundance and the occurrence frequency of each species in all local communities across a range of homogeneous habitats. As the relative abundance of a species declined

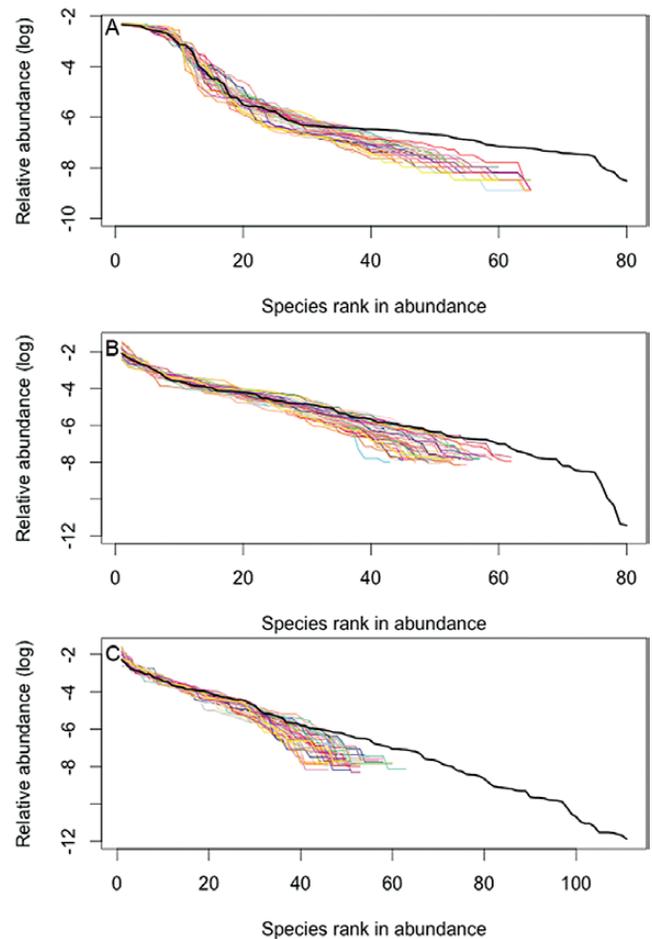


Figure 3: species relative abundance distributions (SAD) of simulation (A), GC plot (B) and PC plot (C). Each short line represents the SAD of a local community, and 40 local communities were sampled in both simulations and two kinds of plots. The bold black line of each panel represents the SAD of the total species in each plot.

within its local community, the occurrence frequencies of that particular species also decreased monotonically (Fig. 5). This observation was true for both simulated (Fig. 5A) and field (Fig. 5B and C) conditions.

DISCUSSION

We set out to investigate the relative importance of common and rare species to the maintenance of community composition. To do this, we correlated the abundance of each species with its occurrence frequency for all species in local communities across a plot, first with species data from simulations and then with field data. Our field data consisted of 40 repeated quadrats within a similar habitat (each plot with identical orientation, aspect and slope position). The results from our field investigations were consistent with our simulations (comparing Fig. 3B, C with A; Fig. 4B, C with A; Fig. 5B, C with A). Species located at the common end of the continuum had occurrence frequencies of 100% (Fig. 5) and

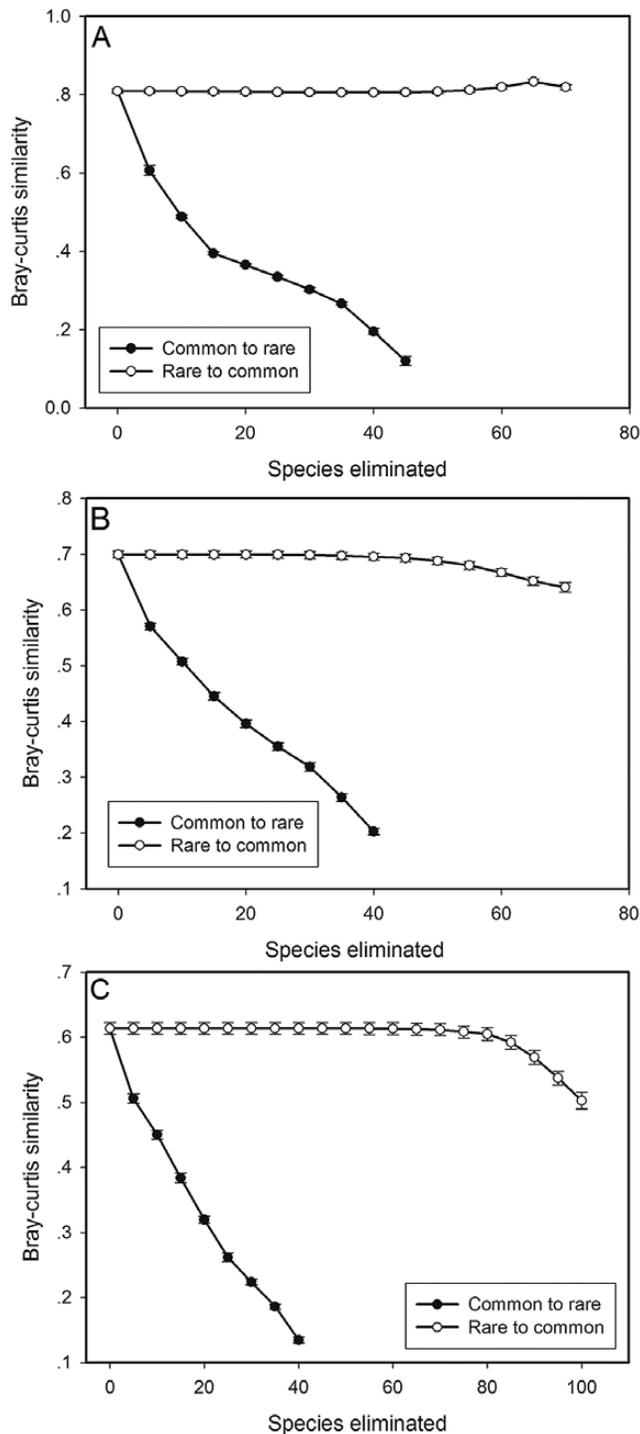


Figure 4: relative contributions of common and rare species to the compositional similarity of communities under the same habitat conditions for (A) simulations, (B) GC plot and (C) PC plot. Each point is the similarity of communities after eliminating a given number of species on the common to rare continuum, starting with either the most common (common to rare sequences) or the rarest species (rare to common sequences). Each point represents the mean of 780 similarities, and the standard error of each point is also shown.

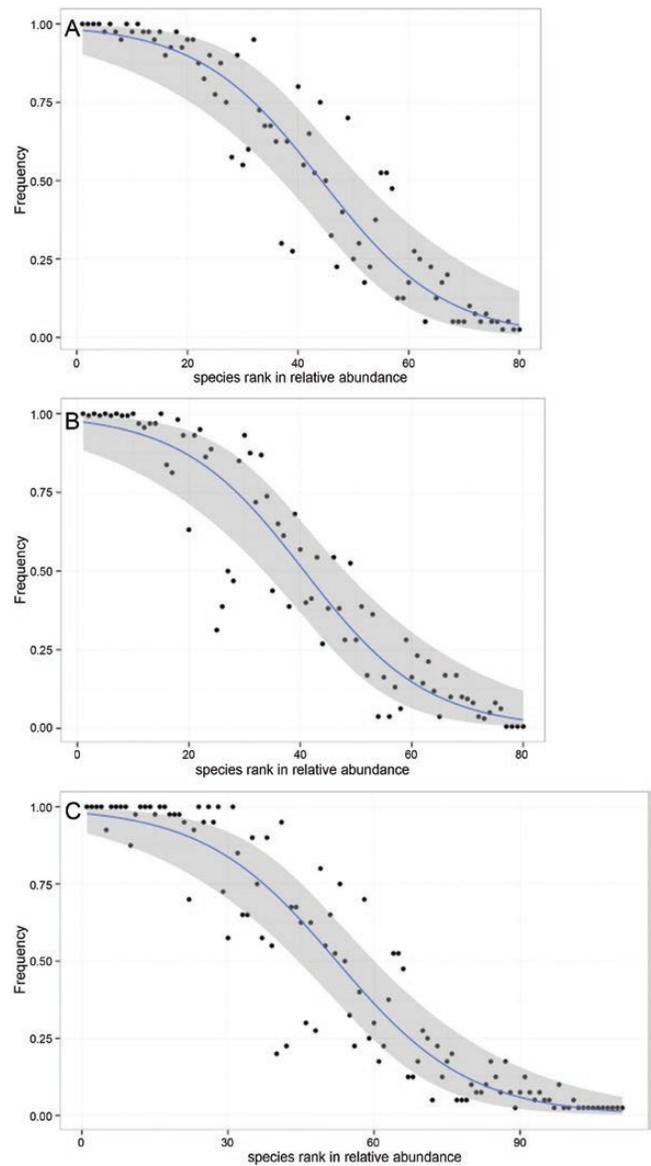


Figure 5: the relationship between frequency and species relative abundance for (A) simulations, (B) GC plot and (C) PC plot. Each point represents a species that occurred in a plot. The line is a regression and the shadow represents the 95% confidence interval.

dominated every local community (e.g. *K. humilis*, *Thalictrum alpinum*, *Polygonum viviparum* etc. in the GC plot and *Geranium pylzowianum*, *Potentilla anserine*, *K. humilis* etc. in the PC plot). These species are probably selected by environmental filtering, coexisting largely due to niche partitioning within the local community. In contrast, species located at the least common end had occurrence frequencies of almost 0 and made little contribution to community similarity (e.g. *Anaphalis hancockii*, *Ligularia sagitta*, *Androsace gmelinii* etc. in the GC plot and *Sibbaldia procumbens*, *Hypocymum leptocarpum*, *Agrimonia pilosa* etc. in the PC plot). These species probably enter the local communities by stochastic dispersal processes.

There were striking similarities between our theoretical and empirical observations. Using the same parameters as earlier simulations (Ai *et al.* 2012), we derived SADs with similar numbers of species as the alpine meadows (Fig. 3A). For example, we found ~60 species/m² both in the GC plot and in the PC plot, and the SADs are shown in Fig. 3B and C. Meanwhile, the shape of the SADs from our current simulations is also consistent with the field plots (comparing SADs in Fig. 3). As is often the case with SADs, our results reveal far more rare species than common species, both in our simulations (Fig. 3A) and in two different kinds of field plots (Fig. 3B and C). Around 60 species (75% of the total species richness) had relative abundances of <10% in the GC plot. While it is clear that rare species are responsible for increasing species richness, the total abundance of common species account for the majority of individuals. It is, therefore, also clear that in natural communities, common species should play key roles in maintaining community structure and function (primary productivity, biogeochemical cycles etc.). Species with higher abundance contribute more to community similarity, whereas species with low abundance make minimal contributions (Fig. 4). Our results confirm that common species determine the structure of communities, whereas rare species increase the species richness of both local communities and the regional species pool.

In the current model, as in previous studies (Ai *et al.* 2013a), we set the niche breadth of species at $w = 0.1$ and migration rate at $m = 0.01$, and repeated 40 times. The simulation of local communities with the same parameters means that they share the same niche space under identical environmental conditions. Species whose optimal niche values were most compatible with the niche space were the best competitors and were highly abundant. These species were located at the common end of the CR_c and occurred in all local communities. The occurrence frequencies of these highly abundant species were close to 1 (Fig. 5), and they contributed more strongly to community similarity (Fig. 4). Environmental conditions were homogeneous throughout the simulations, exerting a constant selection pressure, and thus ensuring that these species would be heavily selected by environmental filtering. Coexistence between those that could survive was governed by interspecific competition (May and McLean 2007). However, species located at the other end of the CR_c were weak competitors, with optimal niche values beyond the niche space, therefore having the lowest (almost 0) competitive ability. These species could not appear in local communities once there was no immigration from the regional species pool. Moreover, the rare species that did appear in different local communities were all different, entering the local communities through stochastic dispersal processes. This is why rare species occur infrequently (Fig. 5) and thus make smaller contributions to community similarity (Fig. 4). Species located at intermediate positions along the CR_c were those whose preferred niches were intermediate between those species winnowed by environmental

conditions, and those species able to survive the environment, but unable to overcome competitors. However, we have shown that such species could not exist while the immigration rate was zero, but having arrived by stochastic dispersal, were able to outcompete rare species at the edge of their environmental tolerance. The appearance of these species was therefore determined not just by environmental filtering, and not just by stochastic dispersal, but by a combination of both mechanisms.

If niche processes determined community composition, communities in the same habitat would be identical. However, if community composition were determined by neutral process (Hubbell 2001), communities, even those in the same environment with similar SADs, could be completely different (Ai *et al.* 2012). It follows that natural communities could also be different under neutral processes. However, our results suggest that SADs could be used to identify which biological mechanisms are most likely to be responsible for structuring the communities. Environmental filtering and niche partitioning govern species located at the most common end of the common to rare continuum, whereas stochastic dispersal processes triggered by a range of disturbances (e.g. zokor mounds, feces patches of yak and sheep etc.) govern species located at the rarest end of the continuum. Species located between these two extremes are probably determined by niche partitioning and stochastic dispersal processes.

CONCLUSION

Our results support the notion that rare species increase the species richness of local communities and the regional species pool and shape the SAD, while abundant and therefore common species play key roles in maintaining the structure of local communities. It is now widely accepted that niche and neutral processes jointly determine community composition and that natural communities exist at some point on the niche–neutrality continuum. SAD curves also represent a continuum, from commonness to rarity. We conclude that the role of a particular species on the CR_c changes gradually from a typical ‘niche’ species to a typical ‘neutral’ species. Intermediate types of species will coexist in communities, determined by both niche and neutral processes.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Journal of Plant Ecology* online.

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