On the Balance between Niche and Neutral Processes as Drivers of Community Structure along a Successional Gradient: Insights from Alpine and Sub-alpine Meadow Communities

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• *Background and Aims* Neutral theory predicts that the diversity and relative abundance of species in ecological communities do not depend on their specific traits. This prediction remains controversial, as many studies suggest that variations in the niches of species determine the structure of communities. The aim of this study was to test empirically the relative importance of niche and neutral processes as drivers of species abundance within plant communities along a successional gradient.

• *Methods* Information on the abundance (density and frequency) and traits (aboveground individual biomass and seed mass) of >90 species was collected in alpine and sub-alpine meadows of the Tibet Plateau (China). A successional gradient (1, 3, 15 and 30 years after abandonment) was established in a sub-alpine meadow. The relationships between species traits and their abundance were evaluated by regression models.

• *Key Results* Seed mass was negatively related to both species density ($r = -0.6270$, $P < 0.001$) and frequency ($r = -0.5335$, $P = 0.005$) in the 1-year meadow. Such relationships disappeared along the successional gradient evaluated ($P > 0.07$ in the 3-, 15- and 30-year meadows). Data gathered in all sites showed a significant negative relationship between the average individual biomass of a given species and its density within the community ($r < -0.30$, $P < 0.025$ in all cases).

• *Conclusions* The results show that seed mass was a key driver of species abundance in early successional communities, and that niche forces may become more important as succession progresses. They also indicate that predictions from neutral theory, in its current form, do not hold for the meadow communities studied.

Key words: Average individual biomass, niche, neutral theory, seed mass, successional gradient, meadow.

INTRODUCTION

The neutral theory of biodiversity proposed by Hubbell (2001) has invigorated research on the mechanisms driving the distribution and abundance of species within communities. This theory assumes that all individuals of all species are functionally equivalent, i.e. individuals do not have species-specific traits influencing their fitness, longevity, movements or likelihood of speciation (Bell, 2001; Hubbell, 2001). Accordingly, it predicts that any given species trait should be uncorrelated with its abundance in a community (Hubbell, 2001; McGill *et al.*, 2006*a*). Neutral theory strongly emphasizes the role of stochastic events such as dispersal, local extinction and speciation as drivers of community structure and diversity. Predictions from neutral theory are contrary to basic assumptions of niche theory, which asserts that the species must differ in their traits, and often show trade-offs, in order to co-exist within a community for long periods of time (Chesson, 2000; Chase and Leibold, 2003; Condit *et al.*, 2006; McGill *et al.*, 2006*b*; Westoby and Wright, 2006).

Empirical support for the neutral theory remains equivocal, with studies both supporting (Hubbell, 2001; Condit *et al.*, 2002; Volkov *et al.*, 2003; Hubbell, 2005, 2006) and rejecting (McGill, 2003; Gilbert and Lechowicz, 2004; Volkov *et al.*, 2005; Wootton, 2005; Gilbert *et al.*, 2006; Harpole and Tilman, 2006; Thompson and Townsend, 2006) its predictions. The fact that random forces alone cannot explain many patterns observed in nature suggests that factors such as variations in the niches of species are important determinants of the structure of ecological communities. Indeed, recent studies are incorporating elements of both niche and neutral theory to develop a more general framework for explaining such structure (Uriarte and Reeve, 2003; Tilman, 2004; Gravel *et al.*, 2006; Zhou and Zhang, 2006; Adler *et al.*, 2007). In this regard, the continuum hypothesis proposed by Gravel *et al.* (2006) assumes that communities are located in a continuum determined by stochastic and deterministic forces depending on three factors: species niche overlap, species richness and dispersal capabilities. According to their model, diversity and abundance patterns along environmental gradients will be the consequence of the balance between stochastic processes and competitive exclusion. Additionally, Gravel *et al.*

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(2006) show that there is a positive relationship between neutrality and the dispersal capabilities of species, suggesting that the latter may be a key process to link niche and neutral approaches.

Many studies have shown that the dispersal ability of a species is closely correlated with traits such as its seed mass (Leishman and Murray, 2001; Coomes *et al.*, 2002; Mabry, 2004) which, indeed, is strongly correlated with plant abundance in many communities (Leishman and Murray, 2001; Muller-Landau, 2003; Murray and Leishman, 2003; Murray *et al.*, 2004, 2005). Leishman and Murray (2001) proposed a successional model to explain the relationship between seed mass and the abundance of species within communities. In their model, communities in early successional stages are dominated by small-seeded species with good dispersal capacities (Leishman and Murray, 2001; Schippers *et al.*, 2001; Coomes *et al.*, 2002; Mabry, 2004; Mouquet *et al.*, 2004). As succession progresses, communities become dominated by large-seeded species with competitive superiority (Leishman and Murray, 2001; Murray and Leishman, 2003; Murray *et al.*, 2005). These predictions have been theoretically evaluated in a series of studies (Leishman and Murray, 2001; Guo, 2003; Eriksson, 2005), but very few empirical tests have been conducted so far to test them (but see Leishman and Murray, 2001; Coomes *et al.*, 2002). Leishman and Murray (2001) found similar results in open woodland communities along a successional gradient determined by fire. These authors found a negative and non-significant relationship between seed size and abundance in areas burned <10 years ago, but this relationship became significant and positive in sites burned >15 years ago. Coomes *et al.* (2002) found that at least some large-seeded species are restricted to late-successional, nutrient-rich sites in dune communities.

To our knowledge, no previous study has empirically evaluated the relative importance of niche and neutral processes as determinants of community structure along a successional gradient. The aim of this study was to do this using the relationship between species abundance and both seed mass and average individual biomass (hereafter AIB) in species-rich alpine and sub-alpine meadow communities. The working hypothesis was that both stochastic and niche processes dominate in the early stage of succession, while the niche process dominates in later successional stages (Coomes *et al.*, 2002; Gravel *et al.*, 2006). The main objectives of the study were to: (*a*) determine empirically the relative importance of niche and neutral processes along a successional gradient; (*b*) explore whether successional time affects the neutrality of a community; and (*c*) evaluate whether AIB determines species abundance in sub-alpine and alpine meadows.

MATERIALS AND METHODS

Study sites

A series of experiments were carried out in alpine (Maqu and Azi) and sub-alpine (Hezuo) meadows of the eastern part of the Qing-Hai Tibet Plateau, China (Table 1).

TABLE 1. *Characteristics of the study sites evaluated*

	Sites		
Parameters	Hezuo	Maqu	Azi
Latitude	34°55′N	35°58′N	33°58′N
Longitude	102°53′E	101°53′E	101°53′E
Altitude (m)	2900	3500	3500
Annual mean temperature (°C)	2·4	1·2	1·2
Annual mean precipitation (mm)	532	620	620
Vegetation type	SM	AM	AM

SM, sub-alpine meadow; AM, alpine meadow.

The vegetation at the alpine sites is typical of species-rich alpine meadows, and is dominated by species such as *Scirpus pumilus* Vahl, *Kobresia capillifolia* (Decne.) C. B. Clarke, *Festuca ovina* Linn, *Poa poophagorum* Bor, *Roegneria nutans* (Keng) Keng, *Anemone rivularis* Buch.-Ham. and *Kobresia macrantha* Boeck. In the sub-alpine meadow, the vegetation is dominated by *Agrostis hugoniana* Rendle, *Stipa aliena* Keng and *Kobresia humilis* (C. A. Mey.) Serg.

Field sampling

To evaluate the relationships between seed mass and species abundance along a successional gradient, experimental plots were established in Hezuo in 2003. These were laid out in fields abandoned 1, 3, 15 and 30 years ago. The fields, located within an area of 10 km^2, had the same orientation, facing aspect and position within the slope. At each plot, thirty 50 × 50 cm sampling quadrats were randomly arranged in August, during the peak of the growing season, and the number of ramets of every species in each quadrat (i.e. density) was counted. After these measurements, the aboveground biomass of each species was cut, dried at 80 °C to constant weight and weighed. A total of 91 species were found in the surveys. Seeds of each species were collected in nearby sites when mature between the years 2000 and 2003. Seeds were air-dried and kept in the laboratory. To estimate seed mass, seeds from the collections, were pooled, 100 seeds for each species were weighed three times, and then the average weight was taken.

To evaluate the relationship between species abundance and AIB in natural communities, additional data were collected at the Hezuo, Maqu and Azi sites during 2001 and 2006, respectively. A total of 30 (Hezuo), 45 (Maqu) and 20 (Azi) 50 × 50 cm sampling quadrats were randomly arranged in August, during the peak of the growing season. The density and aboveground biomass of each species were obtained as described above. A total of 55, 87 and 50 species were found at the Hezuo, Maqu and Azi sites, respectively. The AIB of each species in a given quadrat was calculated as its biomass divided by its density in the quadrat.

Statistical analyses

To avoid confusion, density (number of individuals per sampling quadrat) and frequency (number of quadrats a

species appeared in) were used as surrogates of species abundance (Guo, 2003; Murray and Leishman, 2003). The relationship between species abundance and both seed mass and AIB was evaluated using linear regressions. Seed mass, AIB and abundance data were in all cases $\log_{10}$-transformed prior to these analyses.

In the regressions involving AIB, density is both the response variable and the denominator of the predictor variable (AIB, see above). Statistically, this causes non-independence between predictor and response variables, and may lead to spurious analyses because of violations in the assumptions of regression (Berges, 1997; Brett, 2004). To overcome this issue, and following Brett (2004), the relationship between AIB and species abundance was evaluated using bootstrapping (Roff, 2006). Regression and boot-strapping analyses were conducted with the SigmaPlot 2006 (SPSS Inc., Chinago, IL, USA) and LSS (http://biol-chem. uwb.edu.pl/IP/ENG/biologia/statystyka/stats.php) software, respectively. A total of 10 000 bootstrap replications were used in the bootstrapping analyses.

RESULTS

At the Hezuo site, seed mass showed a significant negative relationship with both frequency and density in the field abandoned 1 year ago (Table 2). For the fields abandoned 3, 15 and 30 years ago, the relationships were not significant. However, it is interesting to note a change in the sign of the relationship from negative in the fields abandoned 1, 3 and 15 years ago to positive in the field abandoned 30 years ago (Fig. 1, Table 2). In both alpine and sub-alpine natural meadow communities, species density showed a significant negative relationship with AIB (Table 3). However, species frequency only showed a significant relationship with AIB in one of the study sites (Table 3).

DISCUSSION

Is the relationship between species abundance and seed mass consistent along a successional gradient in sub-alpine meadow communities?

The results showed that the magnitude and direction of the relationship between seed mass and species abundance varied along succession, with a negative relationship during early successional stages and a trend towards a positive relationship as succession progresses (Fig. 1, Table 2). This pattern is consistent with the successional model proposed by Leishman and Murray (2001). The model predicts that in the early stages of succession, superior colonists (including those with strong dispersal abilities) are the most abundant species, resulting in a negative correlation between seed mass and abundance. Over time, larger-seeded species arrive, and they progressively outcompete the smaller-seeded species. Thus, in intermediate stages of succession, no clear relationship between seed mass and abundance should occur. As time progresses and with no disturbance, there will be a positive correlation between seed mass and abundance. As illustrated in classical studies of MacArthur (1962) and MacArthur and Wilson (1967), high disturbance levels select for species that produce many and well-dispersed offspring, while low disturbance levels would favour competitive species.

It is important to point out that the model of Leishman and Murray (2001) is based on the trade-off between seed mass and seed number within species throughout succession, and that such trade-offs are always considered as evidence of niche processes (Chase and Leibold, 2003; Kneitel and Chase, 2004; Kearney and Porter, 2006). The strong dispersal ability of small-seeded species in early stages of succession, and the strong competition ability of large-seeded species in later successional stages, are key functional traits implying that niche forces are at work. The present results showed that small-seeded species were much more abundant than large-seeded species in the early phase of succession, indicating that dispersal processes were an important determinant of the structure of the studied meadows (Gravel *et al.*, 2006). Dispersal itself is not only a key trait of species but also an important process shaping the structure of plant communities. Therefore, and according to the initial hypothesis, it could be concluded that both random and niche processes have an impact on the structure of community in early successional stages, while deterministic forces such as competitive ability of large-seeded species are dominant in later successional stages. According to the present results, successional stage may also be an important factor to determine where on a continuum from niche to neutrality a particular community will fall (Gravel *et al.*, 2006).

TABLE 2. *Linear regression models fitted to the relationship between species abundance (Y) and seed mass (X) along the successional gradient evaluated*

Years after abandonment	*n*	Abundance measure	Regression equation	*r*	*P*
1	26	D	$Y = 0.10 - 0.64X$	−0.6270	**<0.001**
		F	$Y = 0.15 - 0.31X$	−0.5335	**0.005**
3	39	D	$Y = 0.67 - 0.35X$	−0.2851	0.079
		F	$Y = 0.28 - 0.12X$	−0.2236	0.171
15	49	D	$Y = 1.40 - 0.04X$	−0.0275	0.851
		F	$Y = 0.55 - 0.0004X$	−0.0006	0.997
30	43	D	$Y = 1.54 + 0.14X$	0.1204	0.442
		F	$Y = 0.70 + 0.08X$	0.1264	0.419

n refers to the total number of species used in the analysis. D, density, F, frequency. *P*-values <0.05 are in bold.
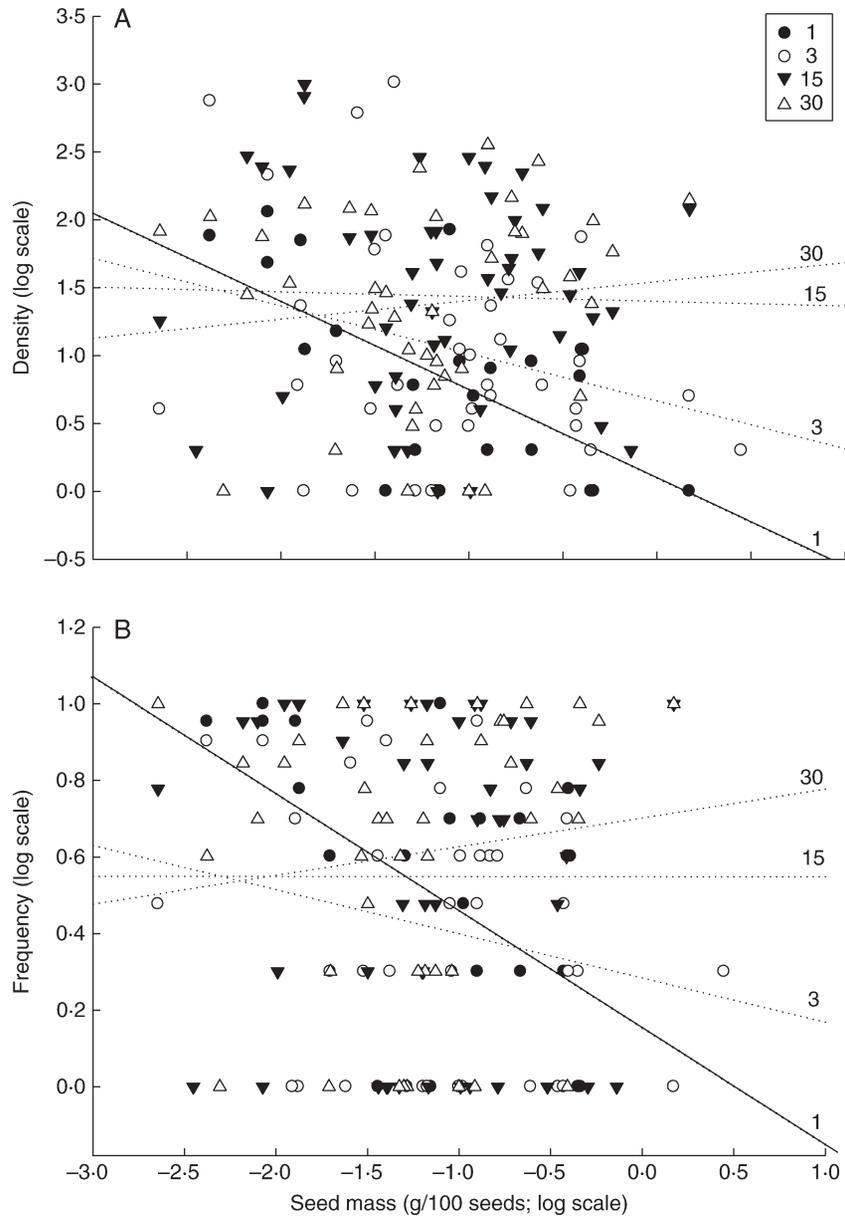
FIG. 1. The relationship between abundance, i.e. (A) density and (B) frequency, and seed mass along a successional gradient (1-, 3-, 15- and 30-year meadows). Significant relationships ($P < 0.05$) are denoted with solid lines.

TABLE 3. *Linear regression models fitted to the relationship between species abundance (Y) and average individual biomass (X) in the alpine and sub-alpine meadows evaluated*

Sites	n	Abundance measure	Regression equation	r	P
Azi	50	D	$Y = -0.20 - 0.76X$	-0.3579	**0.0105**
		F	$Y = 0.71 - 0.19X$	-0.1782	0.2110
Maqu	87	D	$Y = -0.52 - 1.01X$	-0.3767	**0.0001**
		F	$Y = 0.73 - 0.55X$	-0.3243	**0.0021**
Hezuo	55	D	$Y = 1.29 - 0.50X$	-0.3003	**0.0243**
		F	$Y = 0.60 - 0.07X$	-0.0930	0.4955

n refers to the total number of species used in the analyses. P and r values shown for density were obtained after bootstrapping with 10 000 simulations. D, density; F, frequency. P-values <0.05 are in bold.

What is the relationship between abundance and AIB in both alpine and sub-alpine meadow communities?

The clear negative relationship between species density and AIB found in all the sites evaluated was in clear contradiction to the neutral theory prediction that any given species trait should be uncorrelated with their abundance in the local community. The results agree with predictions from the metabolic theory of ecology, which seeks to explain the consistent relationship between a species' body size and metabolic rate (Brown, 2004), and match those of studies conducted with different organisms showing that the individual body mass of a species is correlated significantly and negatively with its abundance (Damuth, 1981, 1991; Brown and Nicoletto, 1991; Enquist *et al.*, 1998;

White *et al.*, 2007). Body mass is perhaps the most fundamental property of an organism, and is related to many biological traits, such as abundance, lifespan and metabolism (White *et al.*, 2007). The importance of body mass–abundance relationships has been widely recognized in both terrestrial and aquatic ecology (Brown, 1995; Gaston and Blackburn, 2000; Kerr and Dickie, 2001). Such relationships are also essential to link species- and population-specific traits to the structure and dynamics of ecological communities (Kerr and Dickie, 2001; Woodward *et al.*, 2005). The present results clearly suggest that AIB plays an important role in shaping the abundance of species in the studied meadows. In addition to the merging of neutral and niche theories, recent theoretical developments are also attempting to combine neutral theory with the theory of metabolic scaling (Gewin, 2006). Such a combination will provide better predictions on the relationship between AIB and species abundance.

Concluding remarks

A set of experiments was conducted to test the relative importance of niche and neutral processes as drivers of community structure along succession, and to evaluate if the AIB of a species is related to its abundance within communities. The results indicate that, in the early stages of succession, both stochastic processes, such as dispersal, and deterministic processes, such as the trade-off between seed mass and number, were important determinants of the structure of the studied communities. In the meadow communities studied, AIB was negatively related to species abundance. Advances in the development of a unified theoretical body incorporating elements of neutral theory, niche theory and metabolic scaling theory will give rise to refined theory and models, improving our ability to understand the relative importance of those factors driving the composition and structure of plant communities.

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