Exogenous and endogenous determinants of spatial aggregation patterns in Tibetan Plateau meadow vegetation

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Abstract

Aims

We aim to quantify the relative importance of various endogenous and exogenous processes influencing the spatial distribution of the individuals of plant species at different temporal and spatial scales in a species-rich and high-cover meadow in the eastern Tibetan Plateau.

Methods

We calculated Green's index of dispersion to infer the spatial distribution patterns of 73 herbaceous species at two scales (0.25 and 1.0 m^2). We constructed a series of generalized linear models to test the hypotheses that different species traits such as mean plant stem density, per capita dry biomass, maximum plant height and mean seed mass contribute to their spatial distribution. We used the first principal component of soil C, N and P to explain abundance variation across quadrats and sub-plots.

Important Findings

The individuals of the species studied were highly spatially aggregated. At both spatial scales, biomass and stem density explained the most variation in aggregation, but there was no evidence for an effect of mean seed mass on aggregation intensity. The effects of soil carbon, nitrogen and phosphorus at different depths affected plant abundance mostly at the broader spatial scale. Our results demonstrate that self-thinning and habitat heterogeneity all contribute to determine the spatial aggregation patterns of plant individuals in alpine meadow vegetation in the eastern Tibetan Plateau.

Keywords: alpine meadow • community • dispersal limitation • habitat heterogeneity • self-thinning

INTRODUCTION

The spatial distribution of individual plants within a species and their relative abundance form the basis of richness patterns at different spatial scales (Green and Ostling 2003, He and Legendre 2002), and can in turn be influenced by different abiotic and biotic processes. Hence, quantifying the spatial distribution patterns of species has received much recent attention because determining the underlying processes can help identify the mechanisms of diversity maintenance at different temporal and spatial scales (Levin 1992). Individuals within a species can be either aggregated or distributed regularly or randomly in space and, these patterns often vary with the spatial scale of measurement (Levine and Murrell 2003).

The patterns of aggregation are well documented for many plant species (Armesto *et al.* 1986; Cardina *et al.* 1997;

Condit *et al.* 2000; He *et al.* 1997; Kikvidze *et al.* 2005), with growing evidence that such patterns influence the probability of maintaining observed diversity in plant communities (Purves and Law 2002; Rees *et al.* 1996; Stoll and Prati 2001). Many mechanisms have been proposed to explain the predominance of aggregation (Levine and Murrell 2003; Li *et al.* 2009; Molofsky *et al.* 2002; Toft and Fraizer 2003), such as dispersal limitation (Hubbell 2001), compensatory density feedback (He and Duncan 2000; Ratikainen *et al.* 2008) and environmental heterogeneity (Kikvidze *et al.* 2005; Sherman *et al.* 2008).

Despite the intensity of investigation in plants, many studies have focused on forest communities and fewer studies have examined the mechanisms driving the spatial patterns of grass species within high-diversity and high-cover herbaceous communities. Thus, a greater emphasis on investigating non-forest systems is required to validate the generalizations proposed previously for forest systems. Alpine meadow communities in the Tibetan Plateau are remarkably species-rich despite the harsh climatic and pedological environment (Chu *et al.* 2007). However, the spatial distribution patterns and the underlying mechanisms of structuring alpine meadow vegetation remain largely unknown.

We therefore investigated the spatial distribution patterns of individuals within 73 herbaceous species and the underlying mechanisms driving them in alpine meadows of the eastern Tibetan Plateau. Vegetation height, stand biomass and seed size are considered to be important plant traits influencing either the dispersion or the competition of herbaceous species in the Tibetan Plateau species (Guo *et al.* 2000), which might be key processes determining the spatial distribution of the species. Hence, we first hypothesized that the spatial aggregation patterns of dominant species are modified by endogenous processes such as plant stem density, vegetation height, stand biomass and seed size. Similar to species-rich rainforests (Wang *et al.* 2008), Tibetan Plateau meadow species are limited by low resource availability (exogenous conditions) necessary for growth and reproduction. We therefore also determined to what extent nutrient limitation modifies abundance by measuring soil carbon, nitrogen and phosphorus concentrations at various soil depths.

STUDY SITE

Our study site was on a southeast-facing slope of approximately regular topography (little slope) in the eastern Tibetan Plateau (101°53′E–35°58′N) at ~3500 m elevation. The climate is humid-alpine with a mean annual rainfall of 620 mm, most of which falls during summer. Mean annual temperature is 1.2°C, with averages of −10.7°C in January and 11.7°C in July. The average annual number of frost days is >270 and there is a mean of <150 growing degree-days per year. The soil is typical for alpine meadows and about 80 cm deep on average (Gong 1999).

The vegetation is typical of alpine meadows; the plant community is dominated by a few graminoids of the genera *Poa, Kobresia, Elymus* and *Stipa* and by various dicots such as *Trollius, Anemone, Aconitum, Ligularia, Saussurea, Pedicularis, Potentilla* and *Gentiana* (Zhang *et al.* 2004). The dominant animals observed in the area include livestock (e.g. yaks, horses), marmots, meadow mice and ants. We established a 100 × 100 m permanent plot in July 2009. The plots are fenced and grazing is only permitted in winter.

DATA

We established permanent quadrats by sinking aluminium pipes into the ground in July 2009. We regularly distributed within the plot forty-five 1 × 1 m sub-plots, divided into four 0.5 × 0.5 m quadrats. We recorded species composition and abundance in each quadrat at the peak of the growing season in August 2009 by determining the species of all stems. For many plants, it was difficult to distinguish individuals, so in those cases we attempted to distinguish individuals of the same species by separating their roots.

We also recorded in each quadrat the height of five randomly selected individuals of each species. After identifying the species of each individual, we cut all the stems in the quadrat at ground level, dried and weighed them to 0.1 mg. We also took four soil cores near each 1 × 1 m sub-plot and measured the concentration of carbon (C), nitrogen (N) and phosphorus (P) at 5-, 10-, 15- and 20-cm depths (Li *et al.* 2011) to examine the effects of soil C, N and P concentrations on plant abundance.

ANALYSIS

Dispersion

We calculated Green's index of dispersion (Green 1966), which is appropriate for measuring positive spatial contagion regardless of variation in sample number, sample size and average density among areas to be compared, to infer the spatial distribution patterns of the herbaceous species sampled. We calculated the index (G) using sampling data of the species at two scales, i.e. 1.0 × 1.0 m sub-plots and 0.5 × 0.5 m quadrats located at the southwest corner of each 1.0 × 1.0 m sub-plot:

$$G = \frac{\frac{s^2}{\bar{x}} - 1}{\sum_{i=1}^{n} x_i - 1}$$

where $\bar{x}$ = mean species stem count (abundance) over all n sampling units, s^2 = count variance over all units (Green 1966).

Traits analysis

To test the hypotheses that different species traits contribute to their spatial distribution as measured by Green's dispersion index, we constructed a series of generalized linear models

relating the index at both spatial scales (0.5 × 0.5 m quadrats and 1.0 × 1.0 m sub-plots) to mean plant stem density, per capita dry biomass, maximum plant height and mean seed mass. We constructed models with a gamma distribution and a log-link function to account for non-Gaussian error distributions. To rank models, we calculated Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 2002), the difference between the model's AIC_c and that of the top-ranked model i (ΔAIC_c), and the relative model weights ($wAIC_c$). Thus, the strength of evidence ($wAIC_c$) for any particular model varied from 0 (no support) to 1 (complete support) relative to the entire set of M candidate models. We did all analyses using the open-source R statistical program, version 2.12.1 (R Development Core Team 2012).

Because species are phylogenetic units with shared evolutionary histories and are not statistically independent (Felsenstein 1985), we also attempted to minimize any potential bias arising from non-independence of statistical units via resampling. Here, we randomly chose one species from each family represented in the full dataset and reapplied the generalized linear model set described above to each random iteration. Over 10 000 iterations, we calculated the median $wAIC_c$ and %DE for each model (standardizing $wAIC_c$ to sum to 1) and used these to rank all models in the absence of potentially correlated species within taxonomic families.

Soil C, N and P analysis

To test the hypothesis that soil nutrient composition affected plant abundance, we combined the C, N and P measurements at each depth (5, 10, 15 and 20 cm) for each sub-plot using a principal components analysis (PCA). We then used the first principal component from each PCA as an explanatory variable in a Poisson-distributed (log-link) generalized linear model relative to total abundance of each species at both the 0.5 × 0.5 and 1.0 × 1.0 m spatial scales. For each depth and species, we calculated the information-theoretic evidence ratio (ER) as the $wAIC_c$ of the model incorporating abundance divided by the $wAIC_c$ of the intercept-only model (Burnham and Anderson 2002) and used this a measure of the relative weight of evidence for the contribution of the first principal component to explain variation in abundance across quadrats and sub-plots (i.e. at both spatial scales).

RESULTS

Distribution and composition

We counted a total of 76 717 individuals from 74 species in the forty-five 1 × 1 m sub-plots. There was only one woody species *Hippophae rhamnoides*, but it was rare, with only 21 individuals identified in total. Herbaceous perennials accounted for 63.9% of all recorded species. *Euphrasia regelii* was the most abundant species with 6728 individuals. Among the 73 herbaceous species, 11 had fewer than 10 individuals (*very rare*), of which 8 were represented by only one individual; 24 had fewer than 500 individuals (*rare* mean density <11.11), 29 had 500–2500 (*intermediate*; 11.11 < mean density < 55.56) and 9 had >2500 individuals (*common*; mean density >55.56). Sixty-three of the species appeared in ≥1 of the 0.5 × 0.5 m quadrats.

To investigate the effect of sampling area on the spatial distribution patterns, we included the 58 species that appeared in both sub-plots and quadrats in a spatial pattern analysis (Table 1). At the 0.5 × 0.5 m scale, 50 species were aggregated (within their 95% confidence interval produced by random bootstrap), whereas this value was 54 at the scale of 1 × 1 m (Table 1). All intermediate to common species were aggregated at both scales while the percentages of aggregated rare species increased from 63.6 to 82.6% with increasing scales. Of the aggregated species shared at both scales, 17 of 50 species differed in aggregation intensity between two scales, with Green's index of only one species increasing and the others decreasing as the spatial scale increased.

Aggregation as measured by Green's index generally decreased with increasing mean stem density (Figs 2 and 3). Rare species were more aggregated than intermediate and common species and rare species also had a greater range of aggregation. At both spatial scales, biomass and stem density explained the most variation in aggregation (Tables 2 and 3), with Green's index decreasing with increasing stem density and biomass (Figs 2 and 3). There was little evidence for an effect of seed mass on aggregation (Tables 2 and 3). The minor effect of vegetation height effectively disappeared once we accounted for phylogenetic non-independence in the resampled generalized linear models (Table 3, Fig. 3), most likely because taxonomic family was a reasonable proxy for plant height.

Soil C, N and P

The first principal component axis varied mainly from extremes of C to N/P at all depths (i.e. sub-plots rich in carbon were relatively poor in N/P and vice versa, Fig. 3), but the variation among quadrats decreased with depth (Fig. 3). The proportion of variance described by the first principal component ranged from 0.71 (15 cm) to 0.84 (5 cm). According to the Poisson-distributed generalized linear models, the ER for an effect of the first principal component from the nutrient PCA was >2 (i.e. twice as much bias-corrected support as the intercept-only model) for 0.45 to 0.58 of the species tested at the 0.5 × 0.5 m scale; this increased to 0.68 and to 0.79 at the 1.0 × 1.0 scale (Table 4). In other words, the effect of soil C, N and P was much greater at the broader spatial scale of the entire sub-plot for most species.

DISCUSSION

Aggregation is well documented in many different types of plant communities (Condit *et al.* 2000) and we have shown that aggregation dominates in species-rich alpine meadows in the eastern Tibetan Plateau. Rare species are, in general, more aggregated

Table 1: plant longevity, mean stem density and Green's dispersion index (G) for 58 species appeared in both 1×1 m sub-plots (G_1) and 0.5×0.5 m quadrats ($G_{0.5}$)

Genus	Species	Longevity	Mean stem density (stems m^{-2})	$G_{0.5}$	G_1
Agrostis	gigantea	P	20.38	0.1063	0.0601
Ajania	tenuifolia	P	4.77	0.5473	0.0984
Ajuga	lupulina	P	3.37	0.8444	0.1868
Allium	sikkimense	A	0.88	0.0682	0.0245
Anaphalis	lactea	A	12.86	0.0809	0.0257
Anemone	obtusiloba	P	115.71	0.0151	0.0044
Anemone	rivularis	P	46.19	0.0057	0.0011
Anemone	trullifolia	P	85.14	0.031	0.0069
Arenaria	serpyllifoliaL	A	16.89	0.0893	0.016
Aster	alpinus	P	26.13	0.0293	0.0067
Aster	diplostephioides	P	6.76	0.1446	0.0315
Astragalus	polycladus	P	15.90	0.0642	0.0121
Carex	kansuensis	P	2.04	0.0905	0.092
Cerastium	arvense	P	4.8	0.0652	0.0232
Delphinium	kamaonense	P	4.76	0.0936	0.0534
Elymus	nutans	P	19.52	0.0114	0.0047
Euphorbia	esula	P	76.95	0.0082	0.0016
Euphrasia	regelii	A	140.98	0.0139	0.0036
Festuca	sinensis	P	4.09	0.0504	0.015
Foeniculum	vulgare	P	24.71	0.1666	0.0525
Gentiana	sino-ornata	P	26.29	0.0623	0.0139
Gentiana	spathulifolia	A	10.86	0.1743	0.035
Gentianopsis	paludosa	A	3.71	0.0214	0.0132
Geranium	pylzowianum	P	35.81	0.0759	0.0282
Halenia	elliptica	A	10.76	0.0857	0.0243
Herminium	monorchis	P	3.91	0.1124	0.0467
Kobresia	capillifolia	P	41.33	0.0255	0.0058
Kobresia	humilis	P	12.10	0.0101	0.0028
Koeleria	cristata	P	17.43	0.0296	0.0154
Lancea	tibetica	P	50.29	0.0555	0.0147
Leontopodium	nanum	P	26.00	0.0614	0.0283
Leymus	secalinus	P	6.31	0.069	0.0259
Ligularia	virgaurea	P	51.90	0.0255	0.0065
Medicago	hispida	P	112.10	0.0416	0.0214
Melandrium	himalayense	A	2.22	0.0284	0.0187
Oxytropis	ochrocephala	P	16.86	0.0301	0.0103
Parnassia	trinervis	P	11.90	0.0178	0.0076
Pedicularis	spp	P	15.52	0.0616	0.0153
Poa	crymophila	P	69.33	0.0208	0.0068
Polygonum	sphaerocephalum	P	17.69	0.2301	0.0646
Potentilla	anserina	P	3.64	0.4724	0.1291
Potentilla	bifurca	P	1.69	0.2105	0.0662
Potentilla	fragarioides	P	89.05	0.0154	0.0038
Ranunculus	tanguticus	P	34.10	0.0345	0.0073
Rumex	patientia	P	30.48	0.6296	0.2246
Saussurea	hieracioides	P	4.10	0.0922	0.0255
Saussurea	nigrescens	P	45.62	0.0506	0.0124
Saussurea	stella	P	50.10	0.0371	0.0096
Scirpus	pumilus	P	9.78	0.0329	0.0133

Table 1:
Continued

Genus	Species	Longevity	Mean stem density (stems m^{-2})	$G_{0.5}$	G_1
Scutellaria	*baicalensis*	P	81.87	0.0473	0.0129
Sphallerocarpus	*gracilis*	P	9.43	0.0651	0.0203
Stipa	*aliena*	P	19.71	0.025	0.0053
Thalictrum	*alpinum*	P	100.38	0.0419	0.0088
Thermopsis	*lanceolata*	A	14.00	0.0231	0.0057
Tibetia	*himalaica*	P	11.14	0.0431	0.0231
Veronica	*eriogyne*	P	14.57	0.0146	0.0033
Viola	*verecumda*	P	43.29	0.032	0.0114

A = annual, P = perennial.
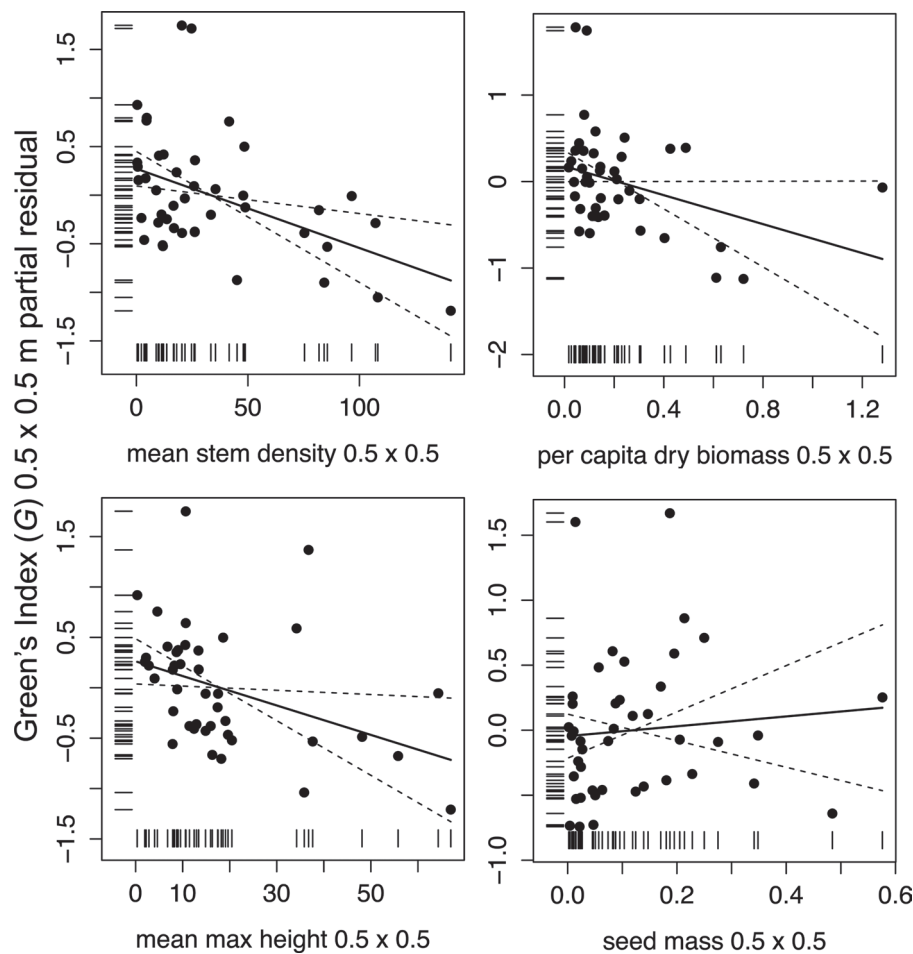
Figure 1: partial residual plots of mean stem density (stem m^{-2}), per capita dry biomass (g), mean maximum plant height (cm) and seed mass (g) and Green's index of aggregation at the quadrat scale (0.5 × 0.5 m). Each point represents a different species.

and have a greater range of aggregation patterns than common species. Furthermore, spatial patterns of the plant species tended to become more regular or random with increasing spatial scale. We found that a species' stem density (abundance), biomass and spatial heterogeneity in soil C, N and P concentrations are all important components determining the distribution patterns of

alpine meadow vegetation in the eastern Tibetan Plateau. Thus, the realized spatial distribution pattern of a given species is the result of interactions between these exogenous and endogenous processes. Although the underlying mechanisms of the spatial aggregation in the meadow we examined are complicated, several important generalizations can be made.
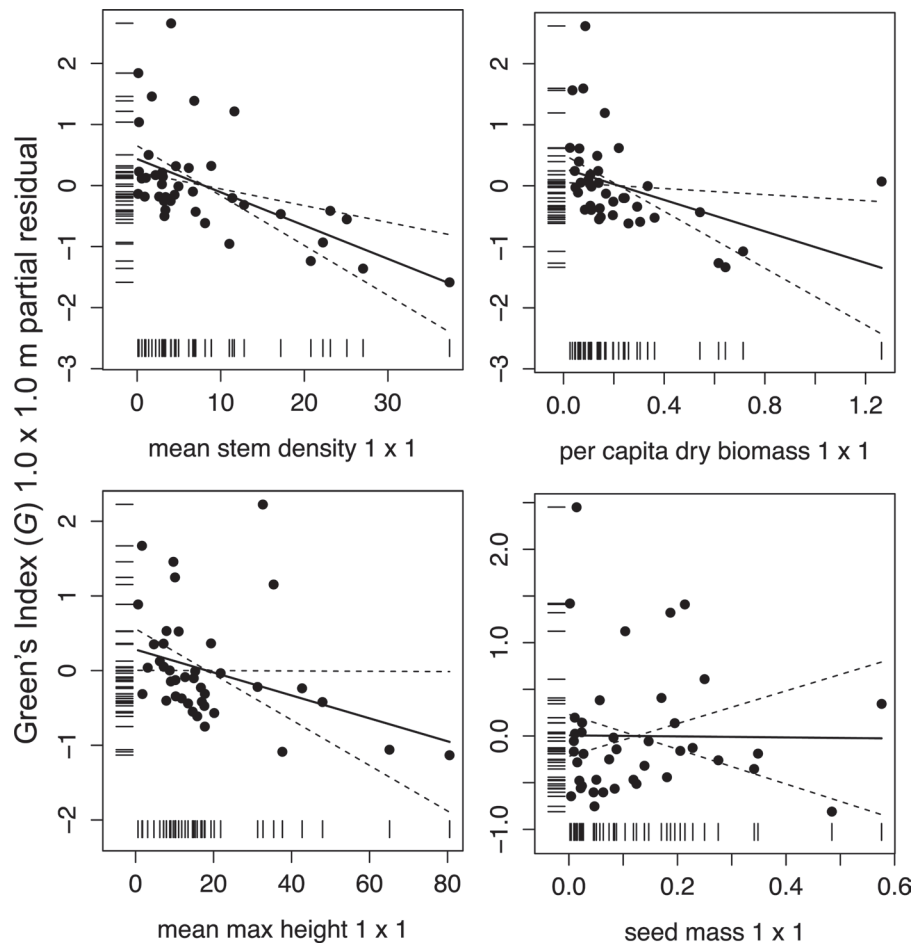
Figure 2: partial residual plots of mean stem density (stem m^{-2}), per capita dry biomass (g), mean maximum plant height (cm) and seed mass (g) and Green's index of aggregation at the sub-plot scale (1 × 1 m). Each point represents a different species.

It has long been recognized that the abundance and spatial distribution of plants are intimately interrelated. That rare species are more aggregated than common species is reported in many studies (Condit *et al*. 2000; Hubbell 1979; Li *et al*. 2009; Rees *et al*. 1996) and we confirm this pattern that rare herbaceous species are, in general, more aggregated and have a greater range of aggregation patterns than common species. The mean intensity of aggregation of rare species in alpine meadows was 2.56 times larger than that of intermediate and common species based on Green's index, and the range of variation in patterns in the distribution of stems in rare species also encompassed that of intermediate and common species. Rare species were more aggregated than common species because the distribution of rare species should be more affected by localized seeding and mortality patterns. When a species' stem density is low, the mean seed dispersal distance could be far shorter relative to the distance among conspecific neighbourhoods (patches), thereby resulting in the clumped pattern we observed. Total average stem density was 80.9–94.7% lower in rare species in our samples, so differences in spatial distribution would be expected anyway by random

patterns of density alone. However, we found that both mean stem density and per capita dry biomass together can predict the spatial pattern of aggregation much better than mean stem density alone at both spatial scales considered (Tables 2 and 3). Feedback underpins the processes believed to contribute to the creation of spatial aggregation—competition, facilitation, nutrient cycling and predation. Miriti *et al*. (1998) found that variation in conspecific density leads to spatially variable mortality, leading either to higher recruitment at greater distances from conspecifics or to higher juvenile survival beyond some critical distance from adults. This can result in rare species becoming more aggregated after long periods of natural succession. Density feedback and the uneven distribution of soil C, N and P might additionally interact to create variation in plant survival. This could allow space for the related self-thinning and environmental heterogeneity believed to create aggregation in natural vegetation (Harms *et al*. 2001). For example, large individuals, regardless of species, rarely co-occur (Li *et al*. 2009). The phenomenon is largely explained by self-thinning, partially because an aggregated stand of large plants is more prone to herbivore and pathogen attacks
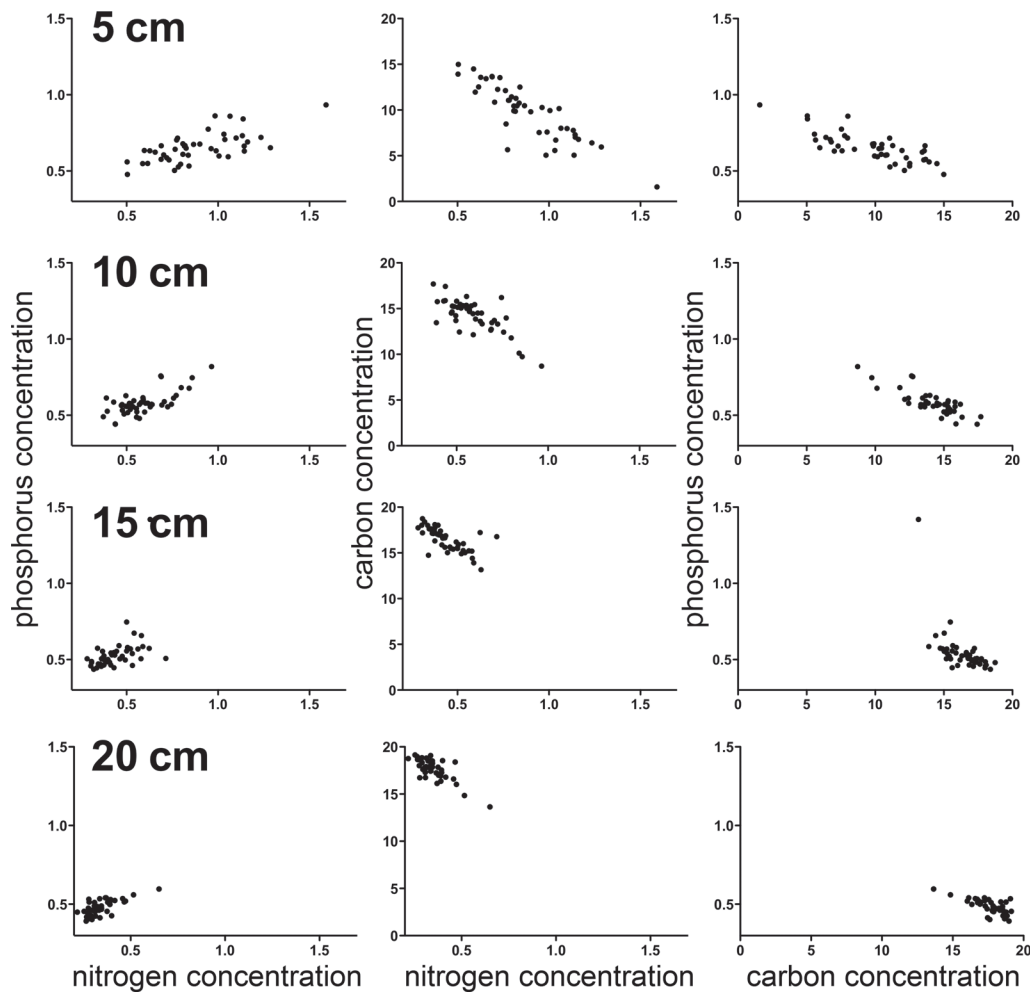
Figure 3: relationships between concentrations (mg kg^{-1}) of soil C, N and P at four different depths (5, 10, 15, 20 cm) for measured sub-plots. Each point represents a different sample.

than more dispersed individuals. The negative relationship between aggregation intensity and tree species' diameter at breast height, an approximate measure of biomass and life history stage, suggests similar mechanisms for maintaining the spatial aggregation patterns of tree species (Li *et al.* 2009).

Maximum individual height is an important trait determining seed dispersal potential, which in turn can influence the degree of aggregation of plant species (Soons *et al.* 2004). However, we found only a minor influence of vegetation height relative to per capita biomass, with the effect disappearing once we accounted for phylogenetic non-independence (Table 3, Figs 1 and 2). In grasslands, seed transport is restricted to the neighbourhood of the parent plant; therefore, we expect *a priori* that height would be less influential on the distribution patterns of alpine meadow vegetation than for trees. Compensatory density feedback can also further reduce the degree of, or even eliminate, the aggregation of seedlings through severe local competition (Levine and Murrell 2003).

We also found no evidence for a correlation between seed mass and mean stem density and small-seeded species had a greater stem density range than large-seeded species (results not shown), which is consistent with the results of Guo *et al.* (2000). As expected, small-seeded species were less aggregated on average than larger seeded species, but the differences failed to demonstrate any statistical effect on aggregation. This could reflect the relatively low predictability of seed size as a measure of dispersal and perhaps that small seed size confers only a maximum, rather than a mean, dispersal advantage. Furthermore, large-seeded species are rarer and tend to produce fewer seeds, although large seeds have been hypothesized to confer survival advantages in harsh conditions (Paz and Martinez-Ramos 2003). Tibetan Plateau meadows are dominated by perennial plant species (Table 1), so severe intra- and interspecific competition probably diminishes the effect of seed mass on plant distribution. At the same time, many plant species adopt clonal rather than sexual reproduction in harsh conditions, which would reduce the importance of height and

Table 2: contribution of stem density (den), per capita dry biomass (bio) and maximum plant height (ht) to explaining variance in Green's dispersion index at the 0.5 × 0.5 m quadrat scale

Model	k	LL	ΔAIC_c	$wAIC_c$	%DE
a) Full data set					
den + bio	3	113.726	0.000	0.5944	36.2
den + bio+ht	4	114.524	0.902	0.3786	45.5
den + ht	3	109.874	7.704	0.0126	34.2
bio + ht	3	109.495	8.8462	0.0086	33.2
den	2	107.176	10.717	0.0028	17.4
ht	2	106.543	11.981	0.0015	24.8
bio	2	106.494	12.080	0.0014	15.2
b) Family bootstrap					
den + bio	3			0.6466	51.1
den	2			0.1634	26.9
bio	2			0.0619	18.7

a) Generalized linear models (gamma error distribution and log-link function) are ranked according to the weights of Akaike's information criterion corrected for small samples ($wAIC_c$). Full model set includes 16 models (with various combinations of mentioned covariates and seed size—full set not shown). Also shown are the number of parameters (k), maximum log-likelihood (LL), difference in AIC_c between the top-ranked and current model (ΔAIC_c), and the percent deviance explained as a measure of goodness of fit (%DE). b) To account for the potential confounding effects of taxonomy on the results (i.e. non-independence due to shared phylogenetic history), we resampled the data set to include one representative species from each family represented in the full data set and iterated 1000 times to produce a standardized median ranking ($wAIC_c$) and goodness of fit.

seed mass on the spatial patterns we observed. Considering the relatively short dispersal distance of the seeds produced by the alpine meadow vegetation, we hypothesize that the lack of effect of plant height and seed mass would most likely persist at broader spatial scales, although sampling at such scales is still required to test this hypothesis.

In addition to the aforementioned endogenous processes, the spatial distribution patterns of alpine meadow vegetation can be influenced by exogenous soil nutrient profiles. Seabloom *et al.* (2005) suggested via experimental manipulation that environmental heterogeneity leads to aggregation at scales of 1–2 m in successional grasslands and our results appear to confirm this in a natural setting. We found that environmental heterogeneity in the form of varying C, N and P concentrations across depths were all related to plant abundance at the sub-plot level. However, different plant species responded to different soil nutrient extremes at all depths. Indeed, the first principal component combining the correlated C, N and P concentrations at 5 cm depth accounted for the largest proportion of variance in abundance and the effect was strongest at the broader spatial scale for most species. This implies a neighbourhood effect that likely overwhelmed the influence of soil characteristics.

We found that herbaceous species in a species-rich, high-cover alpine meadow in the eastern Tibetan Plateau are predominantly

Table 3: contribution of stem density (den), per capita dry biomass (bio) and maximum plant height (ht) to explaining variance in Green's dispersion index at the 1.0 × 1.0 m plot scale

Model	k	LL	ΔAIC_c	$wAIC_c$	%DE
a) Full data set					
den + bio	3	162.009	0.000	0.9887	43.9
den	2	155.592	10.449	0.0112	28.1
den + bio + ht	4	154.366	17.783	0.0001	52.4
den + bio + ht + seed	5	140.922	47.293	<0.0001	54.6
b) Family bootstrap					
den + bio	3			0.7874	61.4
den	2			0.2004	38.6
bio	2			0.0061	15.9

a) Generalized linear models (gamma error distribution and log-link function) are ranked according to the weights of Akaike's information criterion corrected for small samples ($wAIC_c$). Full model set includes 16 models (with various combinations of mentioned covariates and seed size—full set not shown). Also shown are the number of parameters (k), maximum log-likelihood (LL), difference in AIC_c between the top-ranked and current model (ΔAIC_c) and the percent deviance explained as a measure of goodness of fit (%DE). b) To account for the potential confounding effects of taxonomy on the results (i.e., non-independence due to shared phylogenetic history), we resampled the dataset to include one representative species from each family represented in the full data set and iterated 1000 times to produce a standardized median ranking ($wAIC_c$) and goodness of fit.

Table 4: relationship between the first principal component of a three-way PCA combining soil C, N and P concentrations (mg/kg^{-1}) relative to plant abundance across quadrats at two spatial scales (0.5 × 0.5 and 1.0 × 1.0 m)

Depth	n	Median ER	ER >2	Proportion
a) 0.5 × 0.5 m				
5 cm	62	2.3	32	0.52
10 cm	62	1.3	28	0.45
15 cm	62	5.3	36	0.58
20 cm	62	3.8	36	0.58
b) 1.0 × 1.0 m				
5 cm	62	204.2	43	0.69
10 cm	62	29.2	42	0.68
15 cm	62	237.1	43	0.69
20 cm	62	9650.3	49	0.79

Relationships are assessed for four different depths (5–20 cm) over all 62 species assessed. Shown are the number of species (n), the median information-theoretic evidence ratio (ER) comparing the nutrient principal component to abundance, the number of species where ER >2 and that number expressed as a proportion of the total number of species assessed.

aggregated. Spatial structure of the herbaceous community arises from interactions between different exogenous and endogenous processes, with stem density, biomass and environmental heterogeneity playing a greater role than local dispersal in shaping aggregation patterns. These results add to our understanding of

the spatial distribution patterns and the processes influencing these patterns in species-rich meadow vegetation.

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