

# Community assembly along a successional gradient in sub-alpine meadows of the Qinghai-Tibetan Plateau, China

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Community assembly is a dynamic progression that reflects the interaction of several processes functioning at multiple scales. Understanding how these processes work in communities at different successional stages is important for identifying when regional or local processes are more important for community assembly, and for developing effective preservation and restoration strategies. We examined community assembly using a chronosequence of sub-alpine meadows in Qinghai-Tibetan Plateau that range from ‘natural’ (never farmed), to those that have been protected from agricultural exploitation for 1 to 10 years. We tested for shifts in species and traits among meadows and also for changes in environmental and spatial correlates of species distributions within meadows. We found that species richness increased and species composition returned to natural conditions within ten years of protection. These changes coincided with shifts in species traits; abundant species had high seed mass and specific leaf area in late-successional meadows, whereas the opposite occurred in early-successional meadows. Despite these shifts among meadows of different ages, spatial distributions of species within meadows did not change – when associated with abiotic variables, these spatial patterns reflected changes in soil pH and nitrogen. There was also no consistent change in the relative importance of environmental and spatial correlates of species distributions within meadows. These trends indicate that local processes of community assembly are similar within meadows even when species in those meadows differ. We conclude that successional change is a large-scale process that alters the species pool and resulting suite of traits that are present within meadows. As a result, regional planning that incorporates successional age should be the focus for the conservation of diversity in this area. In contrast, local processes work within the constraints of the species pool set by successional age, producing consistent patterns within meadows of different ages.

A central goal in ecology is to understand the processes that structure community assembly. Community assembly is recognized as a dynamic progression (Inouye et al. 1987) that is driven by processes as diverse as dispersal, the responses of species to environmental conditions, and biotic interactions such as competition and predation (Srivastava et al. 2008, Gilbert et al. 2009). Research on these processes traditionally ranged from studies on successional dynamics (Gleason 1917) to studies focusing on environmental controls of species distributions (Whittaker 1960). More recently, global environmental changes have generated countless natural experiments and ecologists are now revisiting these processes in order to understand and predict the effects of environmental changes, such as disturbance, on communities. A special emphasis of this work has been on areas that are facing pervasive anthropogenic changes to understand how to protect or restore such areas (Young et al. 2005). A key goal for such studies is in evaluating the relative importance of different processes on biological communities and identifying the scales at which these processes function.

There have been two broad approaches taken to understand the processes that drive community assembly in natural communities. One approach, which we term the species-specific method, attempts to model the abundances of species in communities and attribute these abundances to specific causal factors. For example, variation partitioning approaches pioneered by Borcard and Legendre (Borcard et al. 1992, Borcard and Legendre 2002, Dray et al. 2006), have been used in a wide variety of ecosystems to infer the role of environmental factors and spatial processes in structuring communities (Cottenie 2005, Gilbert et al. 2008, Legendre et al. 2009). The second approach, the trait-specific method, has focused on specific functional traits (McGill et al. 2006, Shipley et al. 2006) to model the relationship between these traits and environmental gradients (Kraft et al. 2008). Although both of these approaches have proven useful, they have rarely been integrated to understand if and how these two methods of analyzing communities might complement each other (Dray and Legendre 2008).

These two broad approaches to studying community assembly can be used to test different structuring forces

within communities. Species-specific methods are appropriate for testing whether there are consistent differences among species that cause predictable patterns of beta diversity on the landscape (Legendre and Legendre 1998), and if these patterns are consistent across spatial scales (Cottenie 2005, Karst et al. 2005, Gilbert and Bennett 2010). The spatial patterns of beta diversity can further be attributed to environmental conditions that structure species assemblages through species–habitat associations (Whittaker 1956, Bray and Curtis 1957) or through autogenic processes. For instance, dispersal limitation can produce aggregated patterns of conspecifics independent of, or in conjunction with, environmental heterogeneity (Chesson 2000, Chave and Leigh 2002, Bolker 2003), while intra-specific competition, herbivory or soil pathogens may cause overdispersion of conspecifics (Harms et al. 1999, Comita et al. 2010, Mangan et al. 2010). Partitioning the variation in species composition between environmental and spatial components provides a useful framework for inferring the underlying determinants of beta diversity (Legendre and Legendre 1998, Cottenie 2005).

Although patterns of beta diversity may be consistent with specific trait–environment relationships (Kraft et al. 2008), theoretical and empirical work suggests that they need not be (Reich et al. 2003, Marks and Lechowicz 2006, Messier et al. 2010). Recent research has indicated that species may show considerable intra-specific trait variation, potentially complicating species–environment relationships, but that trait–environment relationships may be more conserved (Messier et al. 2010). Trait-specific methods may therefore be used to test the role of local conditions on specific traits, regardless of species identity (Messier et al. 2010). For example, studies have shown that traits such as seed mass and specific leaf area (SLA, the ratio of leaf area to leaf dry mass) are highly correlated with local abundance and environmental conditions (Poorter and de Jong 1999, Leishman and Murray 2001, Zheng et al. 2010), and shifts in these traits with the successional age of grasslands have been shown in several North American grasslands (Mellinger and McNaughton 1975, Knops and Tilman 2000). Hence, exploring the relationship between these functional traits and local conditions provide an alternate method for inferring how local conditions may influence a community without necessarily altering species composition.

Our study system, the sub-alpine plant community in the Qinghai-Tibetan Plateau, is a particularly important system for addressing questions of community assembly. Despite its high diversity, relatively little is known about this ecosystem (Chu et al. 2007, 2008). Meadow degeneration is a serious threat to the biodiversity of the area, mainly due to agricultural exploitation and over-grazing in recent years (Fan et al. 2010, Li et al. 2011, Lü et al. 2011). Consequently, research on the restoration and preservation of the Qinghai-Tibetan Plateau ecosystem is a priority (Li et al. 2011). More generally, the extensive degradation of meadows globally (Millennium Ecosystem Assessment 2005) makes these areas particularly important for understanding community assembly following protection from exploitation in order to plan appropriate restoration activities.

A better understanding of the changes in meadows with successional age, and how communities within these meadows are structured, is needed if conservation and restoration efforts are to be successful.

We use a multi-scale sampling approach to test for species-specific patterns of beta diversity and trait-specific responses to environmental conditions in a series of sub-alpine meadows that were formerly plowed and farmed. The meadows studied were either never farmed ('natural'), or had farming stopped 1, 3, 7, 9 or 10 years prior to sampling. We test whether changes in species and functional traits over this relatively short time indicate that meadows can recover to pre-agricultural, undisturbed states. We also test whether the environmental and spatial determinants of species distributions change within meadows or, alternately, whether within-meadow patterns are consistent regardless of successional age, thereby testing the importance of local (within-meadow) and regional (among-meadow) processes in determining community assembly.

The specific questions that we test are, first, do meadows show directional shifts in species composition and/or functional traits when they are released from exploitation? Second, do patterns of diversity within meadows change as these areas recover from agricultural exploitation? The answers to these questions indicate the importance of regional (among-meadow) and local (within-meadow) processes, and how they might differ in their influences on traits and species. In addition to informing us about the processes of community assembly, we use the answers to these questions to determine if shifts in diversity following protection will cause meadows to return to undisturbed conditions.

## Material and methods

### Study sites

Sampling was conducted in the sub-alpine plant community located in the eastern part of the Qinghai-Tibetan Plateau, Hezuo, China (34°55'N, 102°53'E; 2900 m a.s.l.) in 2010. Mean annual precipitation of 530 mm is mainly distributed in summer, and the mean annual temperature is 2.4°C. The vegetation at the study site is typical species-rich sub-alpine meadows, which is dominated by perennial herbaceous species such as *Elymus nutans*, *Kobresia humilis* and *Thermopsis lanceolate*. Soils are classified as alpine meadow soils (Chu et al. 2007). All sampled sites except one (our control) had been used agriculturally for highland barley. Farming was stopped 1 to 10 years ago in different meadows. Fences were constructed in 2000 to prevent grazing in the whole sampling area. These fences were repaired in 2008, after recognizing that some were damaged and failed to prevent occasional grazing, and have been well-maintained since 2008. The gradient measured therefore represents a difference among meadows in time since abandoned from planting, but also represents a two-year period of no grazing for all meadows. Time since planting was determined by interviews with farmers.

## Field sampling

Sampling was performed in 2010 in one control meadow and five previously cropped meadows within an area of 4000 ha that had been abandoned 1, 3, 7, 9 or 10 years ago. We use the term 'successional age' to refer to the time since each meadow was protected from cropping. Meadows were selected so that meadows with similar successional ages were not closer to each other than to meadows with dissimilar ages. The area of each meadow was at least 120 ha, and had similar orientation, aspect and slope position. An area of 100 × 100 m was randomly selected in each meadow. We placed two transects within each area, one originating at the northwest corner (angled toward the southeast corner) and the other at the northeast corner (angled at 30° off the eastern side of the 100 × 100 m plot). Thirty 50 × 50 cm quadrats were regularly arranged along the two transects, with 5-m intervals between adjacent quadrats. Thus the two transects were placed in different orientations, but the number of plots restricted the length of each transect so that they did not overlap. Plants were sampled within quadrats in August during the peak of the growing season. In each quadrat, we recorded the number of ramets of each species and species richness. In each quadrat, we also recorded the slope and sampled soil (soil cores taken from 0–20 cm). We analyzed these cores for total nitrogen, ammonium and nitrate with an auto analyzer. In addition, soil carbon and phosphorus were analyzed by atomic absorption spectrophotometer, and soil pH was determined by pH acidometer.

Mature seeds of each species were collected in nearby sites. The seeds were air-dried, and 100 seeds of each species from the collections were weighed to determine average seed mass. To explore differences in leaf traits among meadows, the second and the third leaf of every plant in three randomly selected quadrats per meadow were selected to measure leaf traits. Leaf area was measured to 0.001 cm<sup>2</sup> by a scanner and leaf area software, Image J. In measuring the SLA, we rejected species with leaf areas less than 10 cm<sup>2</sup> in any of the meadows (Garnier et al. 2004). This cut-off left us with 12–30 species per meadow that were included in the analysis (approximately 40–50% of species). After that, all collected leaves were used to measure leaf mass, nitrogen, and phosphorus content.

## Statistical methods

### *Species distributions among and within fields of different successional ages*

We first tested for a correlation between the species richness of meadows and their successional ages. For all tests such as this one, successional age was rank transformed in order to include our control (no disturbance meadow). Other options, such as setting the control meadow to other, higher values (> 10 years) yielded similar significance results ( $\alpha = 0.05$ ), but altered the variation explained in tests as very high values caused it to have a large influence.

To determine if the time since cropping was a significant predictor of species composition, we first used redundancy analysis (RDA). This and all other analyses were done using R ver. 2.12 (R Development Core Team). Because of

the nesting of the quadrats within meadows, with 30 quadrats per meadow but only one meadow per successional age, we averaged all quadrats within a meadow and tested whether successional age was a significant predictor of species distributions. This provides a conservative test, as we reduced our observations to one replicate in each of the six meadows in order to eliminate pseudoreplication.

Because our first tests of species-richness and species composition were significant, we performed an additional test of beta diversity (Chase et al. 2011). In this test we used the Raup–Crick dissimilarity metric to determine if differences in beta diversity are different than would be expected by chance, given the observed differences in alpha diversity. In other words, it tests whether the differences observed in beta diversity arise solely because there are more species in some meadows, or alternately if older meadows favor different species. We used the R code provided in Chase et al. (2011) to generate the Raup–Crick dissimilarity values, and then tested whether these values changed predictably with the difference in successional age among meadows using a Mantel test. Raup–Crick dissimilarity values can range from –1 (very similar communities) to 1 (very dissimilar communities).

To test the determinants of beta diversity within each of the meadows, we used a multivariate variation-partitioning approach that tested the contribution of environmental and spatial variables (Borcard et al. 1992, Peres-Neto et al. 2006) within each of the meadows. Our spatial matrix within each meadow was constructed using Moran's eigenvector mapping (MEM) (Dray et al. 2006), based on PCNM axes (Borcard and Legendre 2002, Borcard et al. 2004). This method has been shown to be more conservative and statistically sound than PCNM (Gilbert and Bennett 2010). The environmental matrix consisted of polynomial terms of each of the variables measured. Based on an initial investigation of species–environment relationships, we used the first and second order terms for pH, and the first through third order terms for soil N, P, NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup> and C. Linear and higher-order polynomials of each variable were transformed to ensure that they were orthogonal using the R function *poly*. The MEM matrix was constructed for each field sampled, and all partitioning was done within meadows (i.e. using 30 quadrats). Forward selection of variables was performed using method developed by Blanchet et al. (2008) ('packfor' library, R), and partitioning was done using the 'varpart' function in R. By partitioning variation within meadows, and comparing the partitioning results among meadows of different ages, we are able to determine if local (within meadow) processes change with successional age.

### *Changes in species traits along the successional gradient*

In addition to determining if there were trends in species distributions along the successional gradient, we tested if there were systematic shifts in species traits. In particular, we used an ANCOVA on trait data to determine if there was a significant relationship between a species' trait value and its relative abundance, and also whether this relationship changed with the number of years since agricultural exploitation. We did this analysis for all measured traits. We log-transformed species' abundances and specific leaf

area to normalize the data, and used the rank of the meadow age as in the multivariate analyses.

## Results

Species richness and composition changed rapidly following meadow protection from agriculture. Species richness increased with successional age (Fig. 1,  $r = 0.84$ ,  $p = 0.039$ ), with the one-year old meadow containing 43 species and the older meadows containing up to 63 species. Species composition also showed a marked change (Fig. 2A), with approximately 38% of species distributions explained by the successional age of the meadow (RDA;  $p = 0.02$ ,  $n = 6$  meadows). The change in species composition was not due solely to older fields containing more species, however. We calculated the Raup–Crick (RC) distance among meadows to determine if the shift in species composition was greater than expected given differences in meadow species richness. We found that species composition changed more than expected by chance (Mantel  $r = 0.88$ ,  $p = 0.008$ , Fig. 2A–B), with similarly-aged meadows more similar than expected by chance and those of different successional ages being more dissimilar ( $RC < -0.99$  and  $RC > 0.75$  respectively). Moreover, the extremely high similarity between the control meadow (never disturbed) and the 9 and 10-year old meadows indicate that relatively little time is required to reach a late-successional species composition (Fig. 2A–B). These changes in species richness and composition occurred without significant changes to the abiotic environment of the meadows ( $p > 0.05$  for all Spearman correlations of mean environmental characteristics vs successional age), although the soil phosphorus data were suggestive of a negative trend with age ( $p = 0.06$ , Table 1).

Two functional traits also changed significantly with successional age, mirroring the change in species composition. In early-successional meadows, specific leaf area

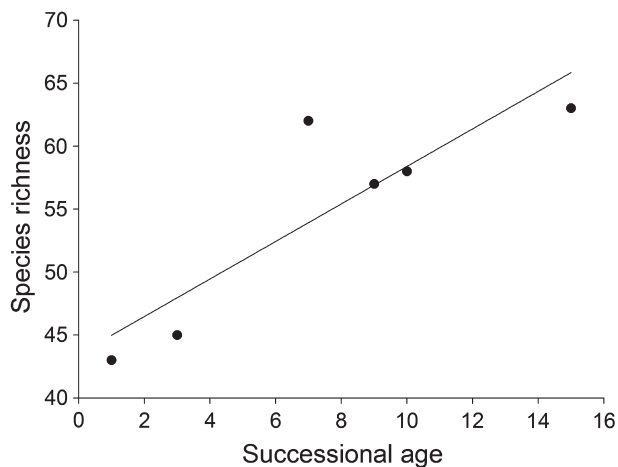


Figure 1. The relationship between successional age and species richness among meadows. Species richness per meadow was measured as the total number of species in thirty 0.25-m<sup>2</sup> quadrats. Note that the control site (furthest to the right) is given an age of 15 years for illustration purposes only. The relationship was tested by rank-transforming successional age ( $r = 0.84$ ,  $p < 0.05$ ).

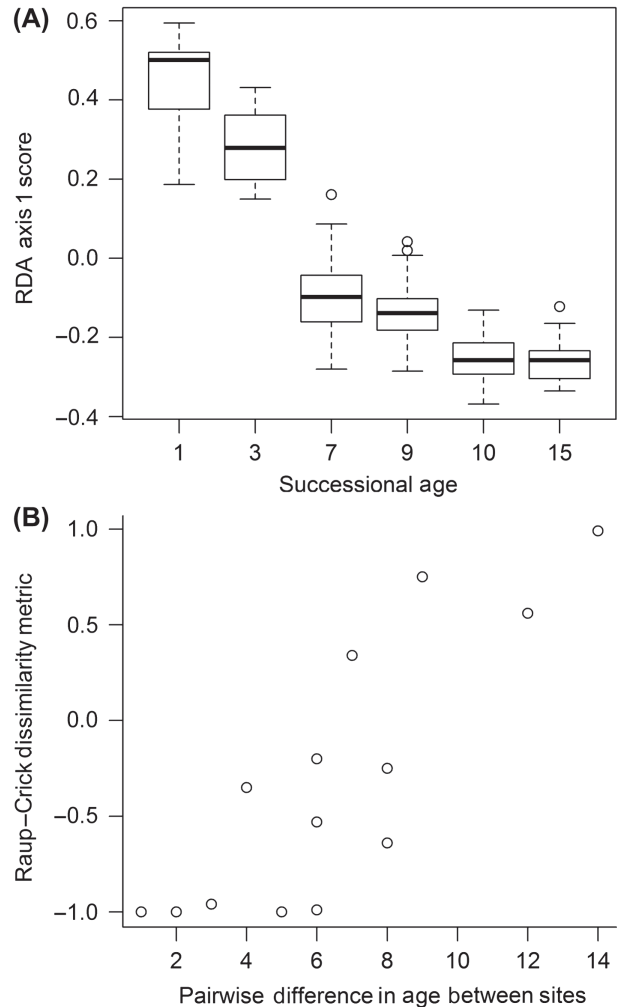


Figure 2. The relationship between species composition and successional age. (A) Species composition, taken as the only RDA axis, shows a trend with successional age ( $R^2 = 0.38$ ,  $p < 0.05$ ). Each boxplot represents the data from 30 plots within a single meadow to show within-meadow variation, but the analysis was performed by combining all plots within a meadow. (B) Raup–Crick dissimilarity among meadows shows that the change in beta diversity is greater than would be expected by the change in alpha diversity (Mantel  $r = 0.88$ ,  $p < 0.05$ ). Note that the control site is given an age of 15 years for illustration purposes only, but that all relationships were tested by rank-transforming successional age. Each point represents the pairwise distance between two meadows, with a total of six meadows included in the analysis.

(SLA) was negatively correlated with species abundances. This trend gradually shifted to a positive correlation with abundance at later successional ages (Fig. 3; interaction term  $F_{1,106} = 4.5$ ,  $p = 0.04$ ). Similarly, seed mass was negatively correlated with abundance in early-successional meadows, but positively correlated in late-successional meadows (Fig. 4; interaction term  $F_{1,66} = 5.8$ ,  $p = 0.02$ ). Although significant, these relationships were weaker than those observed for species-level shifts ( $R^2 = 0.07$  and  $0.08$  respectively). Other species traits (leaf N, leaf P) showed no relationship with abundance or successional age (all  $p > 0.1$ ). Although species did show some intraspecific variation in traits among meadows, the trait responses that we report here are largely driven by differences among species – the



Table 1. The average content of soil variables and standard deviations (in brackets) in 30 quadrats for each of six meadows along the successional gradient.

Content	Successional age (years)					
	1	3	7	9	10	undisturbed
N (mg kg <sup>-1</sup> )	1365 (416.85)	1069 (403.74)	577 (102.62)	680 (180.60)	1158 (222.29)	1101 (367.08)
P (mg kg <sup>-1</sup> )	46 (4.50)	40 (3.12)	35 (3.24)	36 (4.61)	36 (2.19)	34 (4.42)
C (mg kg <sup>-1</sup> )	399 (160.1)	244 (140.91)	263 (113.88)	226 (99.89)	320 (105.82)	357 (151.39)
pH	8.22 (0.09)	8.34 (0.05)	8.17 (0.12)	8.23 (0.11)	8.06 (0.13)	7.99 (0.18)
NO <sub>3</sub> <sup>-</sup> (mg kg <sup>-1</sup> )	333 (52.24)	188 (94.03)	114 (95.32)	140 (69.99)	242 (80.14)	255 (48.81)
NH <sub>3</sub> (mg kg <sup>-1</sup> )	404 (73.35)	602 (100.76)	172 (107.13)	485 (86.08)	342 (69.55)	541 (103.50)

large shifts in species composition with successional age minimized the importance of intraspecific trait variation.

The determinants of beta diversity within communities varied amongst meadows but did not show any consistent trends with age (Fig. 5), suggesting that similar environmental and spatial processes can structure different species assemblages. Patterns of beta diversity were spatially structured in all meadows, with 2–5 of the MEM axes found to be significant depending on the meadow. In part, this spatial structuring reflects endogenous processes, as some portion of species' distributions was only explained by the MEM spatial predictors (4% in control to 28% in age 10 meadow; Fig. 5). In some meadows, the abiotic variables measured were also significant predictors (ages 1, 7 and control), with some correlation to MEM spatial predictors. The significant abiotic variables that predicted species distributions were always a combination of soil pH and total nitrogen or ammonium. The level of variation explained by this local partitioning appeared to be low, which may be due in part to unmeasured variables, such as soil moisture and herbivores. In addition, multivariate partitioning often appears to generate low estimates of explained variation, as has been shown in other studies (Gilbert and Bennett 2010).

## Discussion

In this study, we examined species distribution patterns and their underlying determinants in sub-alpine meadows along a successional gradient. We found that species change rapidly following protection from farming and grazing, with species richness increasing and species composition following a directional shift from disturbed to late-successional composition within ten years of protection. These changes coincide with shifts in functional traits, indicating that species with specific traits are favored in late-successional meadows. In particular, species with larger seed masses and greater specific leaf areas were more abundant in late successional meadows than early-successional meadows. Despite these consistent shifts in species composition and traits among meadows, determinants of beta diversity within meadows showed no directional change. In other words, we found strong support for the hypothesis that large-scale (i.e. among-meadow) changes in successional age are important for structuring biodiversity in this region, but little support for the hypothesis that local (within-meadow) processes influence these successional effects.

Our results are important for understanding how to restore meadows in the Qinghai-Tibetan Plateau and offer insights into grassland conservation globally. Over-grazing and agricultural exploitation are widespread in grasslands; these activities are degrading the biological and economic viability of meadows in the Qinghai-Tibetan Plateau and pose a serious threat to their biodiversity (Li et al. 2011). Hence, the rate of restoration and viable restoration methods are predominant concerns in the region. We found that the rate of sub-alpine meadow restoration following protection from farming and grazing is rapid, occurring within a short period of about ten years. This rapid recovery is consistent with other research on meadows in the area, but is much faster than recovery in other areas. For example, previous research indicates that dormant seed banks may help in the recovery of meadows; Li (2008) showed that seedbanks in meadows abandoned for 10 years earlier resembled that of undisturbed ones, suggesting that many 'old-growth' species may remain dormant in the seedbank for long periods of time. Similarly, Gao and colleagues demonstrated that soils in over-grazed meadows recovered quickly following the removal of grazers (Gao et al. 2011), suggesting that the soil conditions required for natural vegetation are also responsive to restoration efforts. However, research in other grasslands has shown that successional processes can be much slower than reported here. In the Indian Himalayans, for example, Rikhari et al. (1993) reported that meadows require 20–30 years for late-successional species to establish. Similarly, at the Cedar Creek LTER, USA, grasslands require over 30 years for late-successional species to become abundant (Tilman 1994, Foster and Tilman 2000). These differences suggest that comparative studies among grasslands could provide important insights into rates of succession.

The observed shift in species traits along a successional gradient supports previous accounts of directional change following succession. At the early stages of succession, species with small seeds, rapid growth rate and short life-span are likely to invade and dominate communities (Mellinger and McNaughton 1975, Berendse 1990, Gleeson and Tilman 1990, Knops and Tilman 2000). As succession proceeds, the amount of light reaching the ground, available soil nutrients, and decomposition of branches and leaves all decline (Odum 1969, Inouye et al. 1987, Garnier et al. 2004). Abundant species in late successional communities are predicted to be superior competitors for those limiting resources (Tilman 1994). Our results are consistent with this hypothesis. Abundant species in meadows of late successional stages are those with high SLA,

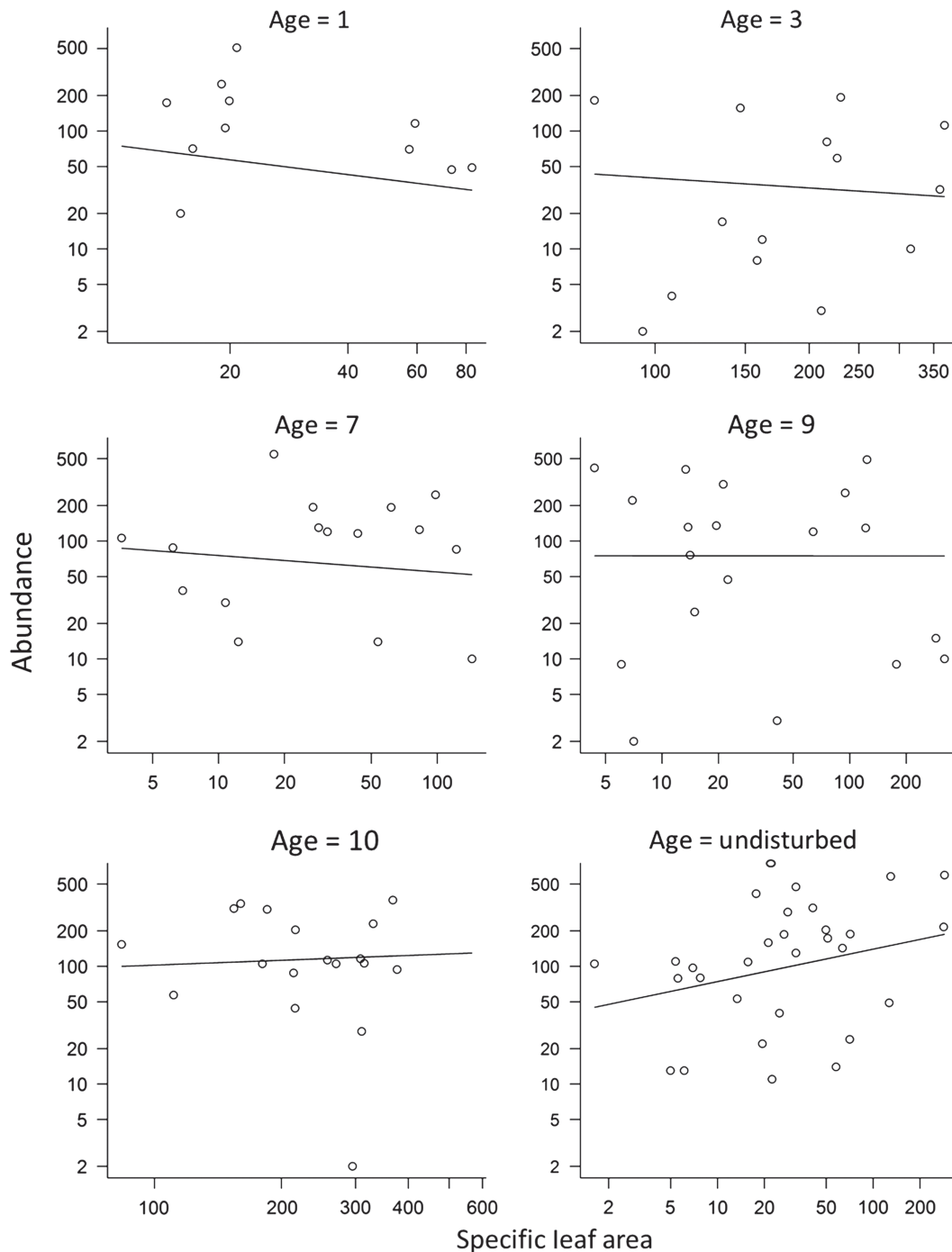


Figure 3. The relationship between the abundance of a species (no. of plants/7.5 m<sup>2</sup> sample in each meadow) and its specific leaf area (SLA, g cm<sup>-2</sup>) with successional age. Panels illustrate the distribution of species' abundances and SLA over successional time (points), with the best-fit lines (lines, generated from ANCOVA) changing from a negative slope in early-successional meadows to a positive slope in late-successional meadows. Sample size varied from 12 to 30 species for each successional age.

maximizing light catchment (Wilson et al. 1999). Based on the prevalent tradeoff between seed mass and the number of seeds produced per plant, species producing a great number of small seeds are more likely to invade vacant sites (Tilman 1994, Chu et al. 2007). However, as succession progresses, larger-seeded species slowly establish and become abundant, presumably due to greater seed investments causing higher survival and competitive ability (Tilman 1994, Moles and Westoby 2004). It is important to note

that leaf N and P content did not shift systematically with successional age. Indeed, plants within meadows of varying ages differentiated along a gradient of nitrogen availability (Fig. 5, abiotic signal), suggesting that both early- and late-successional species can have nitrogen-specific niches.

Despite changes in alpha diversity, beta diversity, and species traits along the successional gradient, we found no directional change in the processes that drive beta diversity within meadows. It appears that successional processes

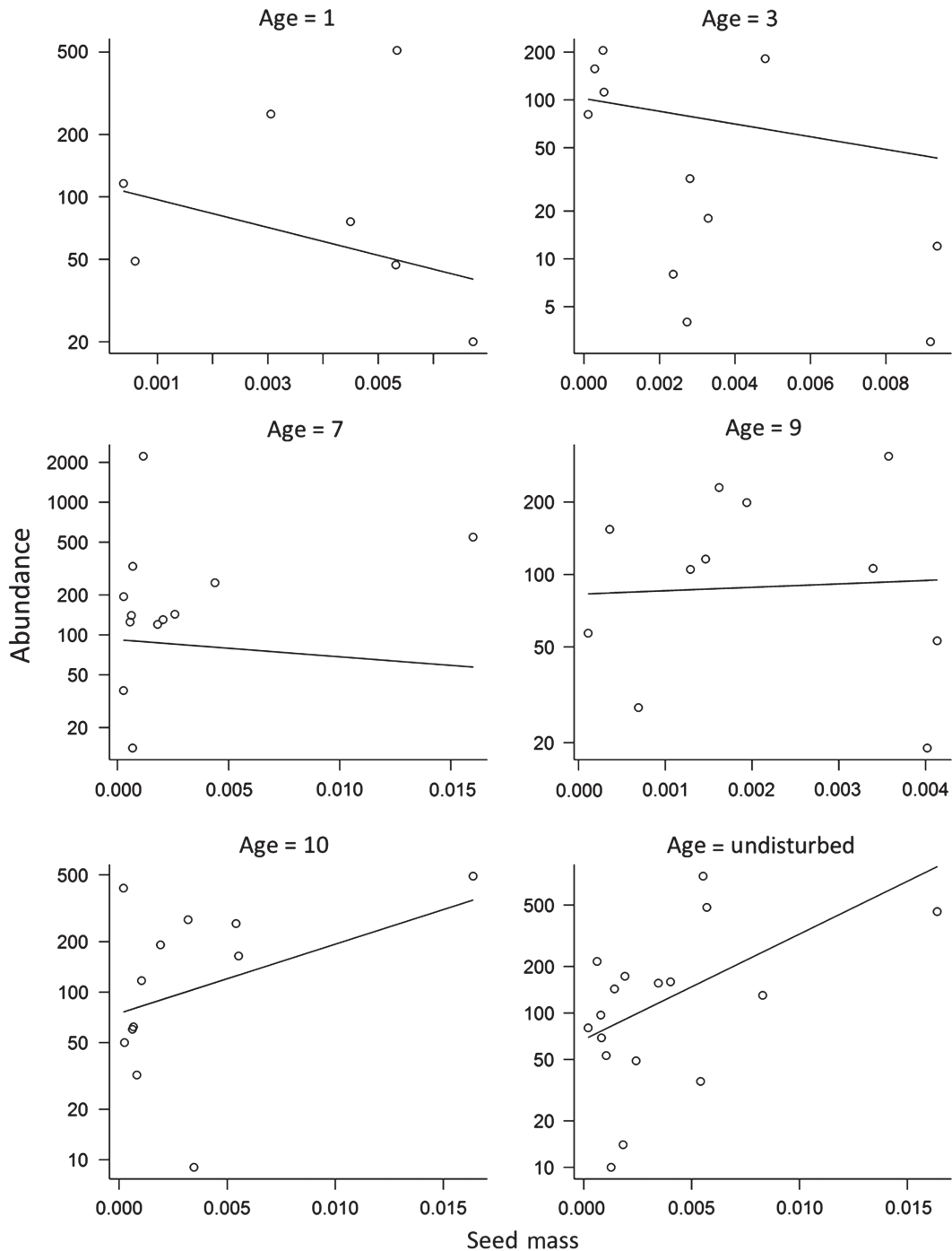


Figure 4. The relationship between the abundance of a species (no. of plants/7.5 m<sup>2</sup> sample in each meadow) and its seed mass (g) with successional age. Panels illustrate the distribution of species' abundances and seed mass over successional time (points), with the best-fit lines (lines, generated from ANCOVA) changing from a negative slope in early-successional meadows to a positive slope in late-successional meadows. Sample size varied from 7 to 17 species for each successional age.

play an important role in determining the species present in sub-alpine meadow communities: They determine the 'species pool' of local communities. Local processes, such as dispersal within meadows and species' responses to local soil conditions, do affect the distribution of species within these communities, but are restricted by the species pool. In addition, the spatial processes and environmental gradients that drive species distributions within meadows

appear to be fairly consistent regardless of the age of the meadows. For example, diversity in both the youngest and oldest meadow was structured by soil pH and nitrogen, indicating that these local determinants of diversity within meadows are not shifting with successional age. This result appears consistent with an investigation of beta diversity in forests along latitudinal and elevational gradients (Kraft et al. 2011). Kraft et al. (2011) concluded that

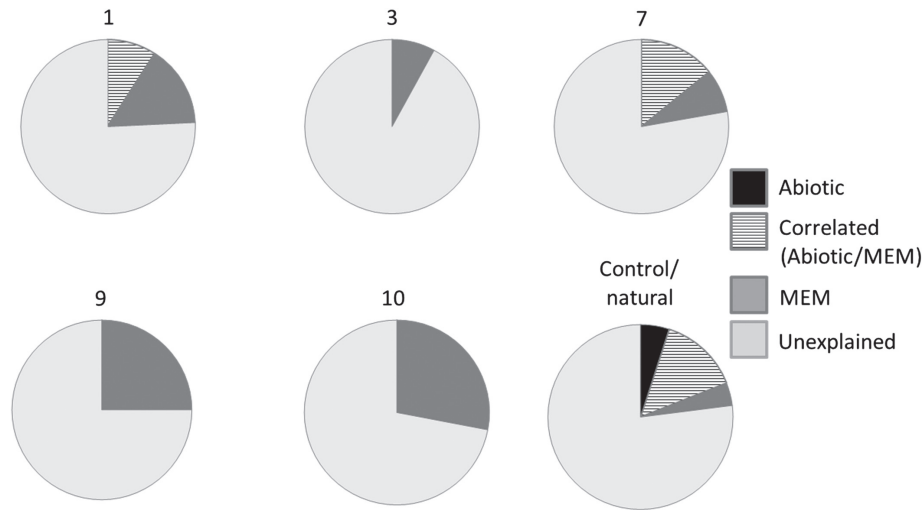


Figure 5. The distribution of beta diversity within meadows of different successional ages. Variation explained by the abiotic or MEM spatial predictors is shown if it is statistically significant ( $p < 0.05$ ). The striped portion (correlated response to spatial MEM and abiotic variables), cannot be tested but represents variation that can be explained either by abiotic or MEM spatial predictors. Each analysis was performed on 30 plots in a single meadow.

there may be no need to invoke different local assembly processes when trying to explain differences in beta diversity at different sites along a latitudinal or elevational gradient. Here we find a similar result for a successional gradient, suggesting that this pattern is likely common to large-scale processes. These large-scale processes, such as succession, set the size of the species pool – local processes act in a consistent way to regulate the patterns of species turnover within sites along these gradients.

It should be noted that the results from our study had to be especially strong to be detected because of the low power of the tests. All among-meadow trends were based on differences among only six meadows of different successional ages, yet the differences in meadow successional age drove clear differences in species and traits (Fig. 1–4). As with many ‘natural experiments’ in conservation ecology, our sample size was limited by a low number of protected areas in this region. The results should therefore be taken as the best evidence to date of the importance of successional processes in our study area. Nonetheless, future manipulative studies with higher statistical power may uncover additional processes that are important to species diversity in this ecosystem.

Taken together, our results indicate that restoration of grasslands after agricultural exploitation can be rapid and follow predictable trajectories. This conclusion is a best-case scenario for restoration but should be considered with two important caveats: first, successional rates in our study area appear to be faster than in some other grasslands, suggesting that bioregional differences in grasslands need to be explored more fully (Rikhari et al. 1993, Foster and Tilman 2000). Second, meadows in the Qinghai-Tibetan Plateau, as in much of the world, are quickly being degraded (Lü et al. 2011, Millennium Ecosystem Assessment 2005). Estimates of the increase in degradation range from 13–29% over the last 30 years (Lü et al. 2011). If this increased degradation continues, depletion and fragmentation of regional species pools are likely to slow or

stop recolonization of late-successional meadows (Hanski and Ovaskainen 2002). Restoration of meadows should be implemented while natural successional trajectories still occur – postponing restoration until after further degradation may require additional and expensive restoration measures such as seed addition or restoration of soil seed banks.

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