

# Convergence of community composition during secondary succession on Zokor rodent mounds on the Tibetan Plateau

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## Abstract

### Aims

The community succession theory is much debated in ecology. We studied succession on Zokor rodent mounds on the Tibetan Plateau to address several fundamental questions, among them: (i) During secondary succession, does the community composition converge towards one community state or multiple states depending on the initial colonization? (ii) Do mound communities located in different background communities exhibit different assembly trajectories?

### Methods

In a sub-alpine meadow, we investigated a total of 80 mound communities at several successional stages in three different background communities resulting from different management histories and compared their changes in species composition. The distribution of plant communities over time was analyzed with quantitative classification and ordination methods. The co-occurrence patterns of species were evaluated at each successional stage, and the degree of convergence/divergence among communities was obtained by calculating two beta-diversity indices.

### Important Findings

During secondary succession, species richness of mound communities changed over time, and this change was dependent

on the background community. Five life-form groups exhibited different dynamic patterns in species richness and plant cover. Community composition and the degree of species co-occurrence between communities increased over time since disturbance. There was much variation in species composition at earlier stages of succession, but communities on older mounds became more similar to each other and to their surrounding vegetation over the course of secondary succession. Post-disturbance succession of Zokor mound communities transitioned from ‘multiple alternative states’ to ‘background-based deterministic community assembly’ over time. Tradeoffs between competition and colonization, as well as the characteristics of different life-forms and mass effects within a limited species pool are the mechanisms responsible for convergence of mound communities.

**Keywords:** multiple alternative states, background-based deterministic community assembly, sub-alpine meadow, disturbance, plant communities

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## INTRODUCTION

Climatic determinism and historical contingency are alternative theories that have been proposed to explain patterns of succession: plant community change over time (Lepš and Rejmánek 1991; Samuels and Drake 1997; Suding *et al.* 2004; Suding and Hobbs 2009; Young *et al.* 2001). Deterministic climax refers to

successional convergence of plant communities within a region on one state determined by environmental factors (Clements 1916), primarily climatic conditions and soil parent material (Lanta and Lepš 2009; Lepš and Rejmánek 1991). Historical contingency, on the other hand, suggests that plant communities can diverge towards multiple states due to stochastic factors (Egler 1954), such as the order and timing of species arriving at different localities,

even if environmental conditions and species pool are similar (Chase 2010; Fukami 2010; Fukami *et al.* 2005). When an ecosystem is severely degraded, the original community can move to an alternative state after disturbance that causes niche release (Erfanzadeh *et al.* 2010; Fukami and Lee 2006; Saccone *et al.* 2014), after which priority effects affect community assembly process through niche preemption and modification. In some productive ecosystems, regional diverse species pool and local rapid revegetation dynamics together can also provide the conditions for divergent community development (Chase 2003a, 2003b).

In contrast to alternative equilibrium states, increasing similarity during the course of community development has been reported in long-term primary succession on lava flows (Cutler 2010) and in secondary succession of tropical forests (Lebrija-Trejos *et al.* 2010). To date, most experiments testing deterministic versus alternative trajectories in succession have focused on restoration of abandoned lands (Fukami *et al.* 2005; Lebrija-Trejos *et al.* 2010), damaged or degraded ecosystems (Beals *et al.* 2014; Erfanzadeh *et al.* 2010; Larios *et al.* 2013) or other specific situations (Fridley 2013; do Nascimento *et al.* 2014; Yang *et al.* 2013), but few studies have investigated small-scale disturbance in a degraded system (Lanta and Lepš 2009). In the present study, we investigated the patterns of small-scale secondary succession under different land-use backgrounds using quantitative methods.

On the Tibetan Plateau, one quarter of the natural grasslands are seriously damaged by rodents, which consume much vegetation and alter the soil physically (Wang *et al.* 2008). Plateau zokor (*Eospalax baileyi* syn. *Myospalax baileyi*), is one of the two burrowing mammals in the high-elevation interior of Qinghai-Tibetan Plateau. It feeds primarily on plant roots at a depth of 3–20 cm below the soil surface (Kang *et al.* 2007) and builds soil mounds on which succession is initiated. It has been estimated that one plateau zokor can produce ~240 mounds each year with a total mound surface area of around 22.5 m<sup>2</sup> of grassland (Kang *et al.* 2007). These mounds are ideal systems to investigate changes of species composition during early succession.

Sub-alpine meadow ecosystems on the Tibetan Plateau have been experiencing serious degradation due to overgrazing and planting of grasses or crops. Several attempts at ecological restoration are changing the community structure. For example, enclosure fencing has been established to prevent intensive grazing. These local interventions mean that secondary succession of zokor mounds is not occurring within a single type of climax or sub-climax 'background' or 'matrix community' vegetation (Zhang and Liu 2003). We sampled the local communities within the fenced area to investigate the influence of the local community on succession on mounds.

In the present study, our aims are to (i) describe the dynamics of species replacement, co-occurrence patterns and species diversity during succession on Zokor mounds, (ii) determine effects of different background communities on the development of local communities, (iii) test the alternative models of

succession and (iv) ask which potential mechanism are consistent with the patterns observed.

## MATERIALS AND METHODS

### Study area

Our study was conducted at the Research Station of Alpine Meadow and Wetland Ecosystems of Lanzhou University (34°55'N, 102°53'E; 2900 m.a.s.l.), located on the northeast part of the Tibetan Plateau, China. The region has a continental dry climate, with a mean annual temperature of ~2°C, mean annual precipitation of 550 mm, and a plant growth period of 120–140 days from May to September. The topography is flat, and the vegetation is classified as sub-alpine meadow, dominated by *Artemisia tangutica*, *Trigonella ruthenica* and *Potentilla anserina*. The soil is classified as a chestnut soil or a typical calcareous soil (Table 1). The vegetation has deteriorated due to digging by rodents and overgrazing by antelope and yaks.

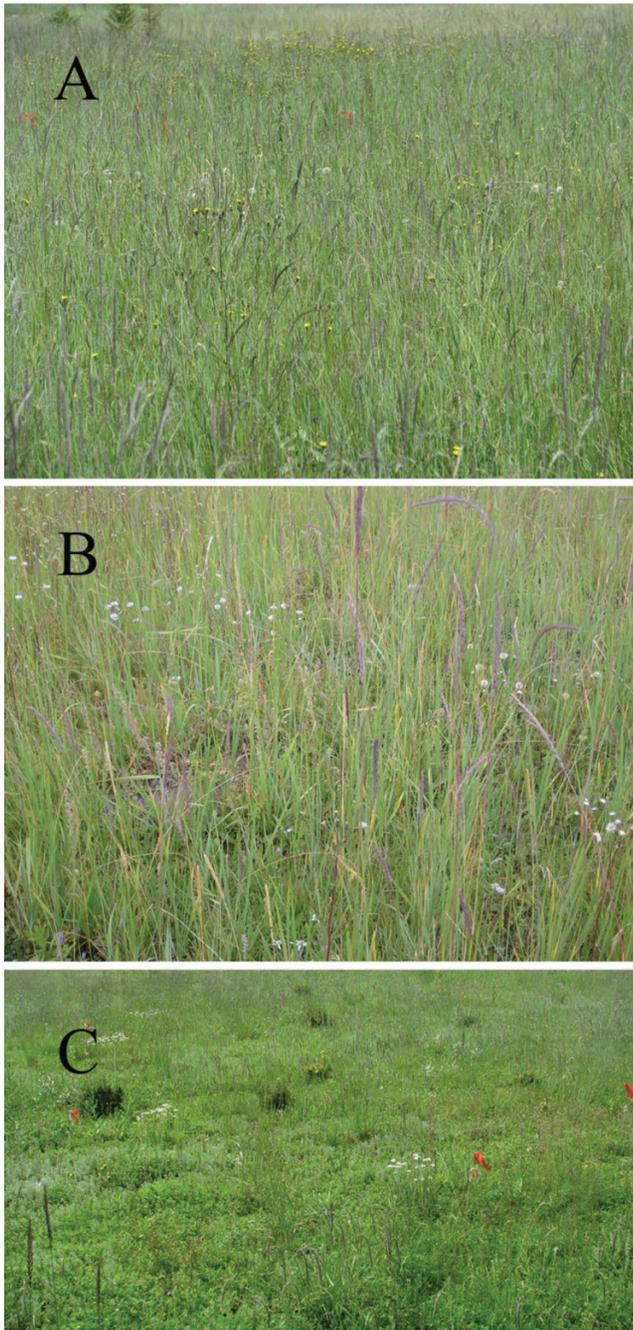
### Experimental design and data collection

A 300 × 300 m field has been fenced to control grazing since 2001, but 15 days of grazing by antelope and yaks each winter has been permitted. The field was equally divided into three 300 × 100 m areas (A, B and C) representing 3 different vegetation management histories (Fig. 1). Areas A and B were managed for domination by native perennial grasses until 2002 according to government guidelines, after which the natural succession was permitted. Before abandonment, *Festuca sinensis* was planted on area A and *Leymus secalinus* on area B. *F. sinensis* is common in later native primary succession, while *L. secalinus* is considered a mid-successional species. In contrast, area C has been allowed to undergo natural succession since the enclosures were established in 2001. Fifty-eight plant species were identified on area A, 71 on B and 80 on C.

Fieldwork was carried out in the summer of 2009. A 50 × 50 m plot was placed in the center of each area. To investigate the severity of zokor activity under different management regimes, we have followed mound-making activity in the three plots since 2003. Zokor mounds were labelled with the year they were created. In July 2009, 4–6 mounds of each of 5

**Table 1:** the physical and chemical characteristics of soil from the three background communities in areas A, B and C

Parameters	Areas		
	A	B	C
pH	7.2 ± 0.03	7.22 ± 0.07	7.43 ± 0.06
Organic carbon	mg*g <sup>-1</sup> 36.79 ± 0.75	33.80 ± 0.9	32.49 ± 1.29
Total nitrogen	mg*g <sup>-1</sup> 4.02 ± 0.02	3.88 ± 0.06	3.65 ± 0.06
Total phosphorus	mg*g <sup>-1</sup> 0.41 ± 0.01	0.4 ± 0.01	0.38 ± 0.01
Soil moisture	% 27.52 ± 0.55	25.4 ± 0.54	20.58 ± 0.54
Bulk density	g*cm <sup>-3</sup> 1.41 ± 0.01	1.45 ± 0.02	1.51 ± 0.05



**Figure 1:** the three experimental areas on the Tibetan Plateau, China. Areas A was abandoned and dominated by a later-successional native species *Festuca sinensis*, area B was abandoned and dominated by a mid-successional species *Leymus secalinus* and area C was experienced natural succession since 2001.

age groups were selected and labeled: (a) 1 week to 3 months old, (b) 1-, (c) 2-, (d) 3- and (e) 4-year-old mounds. It was not always possible to find six zokor mounds at each stage in all three areas. We selected and marked 27 mounds in area A, 26 in B and 27 in C. All selected mounds were of similar size ( $\sim 2500 \text{ cm}^2$ ) and intact since the time the rodents built them.

In addition, six  $50 \times 50 \text{ cm}^2$  permanent quadrats (f) that did not include any mounds were randomly placed in each plot to sample the background community. All vascular plants rooted in the quadrats were recorded, and the ground cover of each species estimated visually. Due to logistical limitations, each management regime was applied in only one field, so, like many studies on succession, our experiment design has no replication at the background community treatment level.

### Statistical analyses

We analyzed species composition, relative cover and species richness and five life forms: annual forbs (AF), biennial forbs (BF), perennial forbs (PF), leguminous plants (L) and graminaceous plants (G) on each mound. Regression analysis was used to test effects of the successional stages on species richness, and the relative cover of mound communities.

We used quantitative classification and ordination methods to analyze the overall structure and distribution pattern of mound communities during secondary succession. TWINSpan (two-way indicator species analysis) in program WinTwins (Hill and Šmilauer 2005) was used to identify major vegetation types from these data. Because the relative cover values of plant species ranged from 0.1% to 58.8%, the cutoff levels were defined as 0, 5%, 20% and 50% in our TWINSpan analysis. Detrended correspondence analysis (DCA) was used to compare the overall changes of species composition at each successional stage of mound vegetation and the reference community (Oksanen and Minchin 1997). Principal component analysis was not used because it exhibits a strong 'horseshoe effects' (Legendre and Legendre 2012). Ordination was performed with the 'vegan' package (Oksanen et al. 2011) in the R statistical program (version 2.13, R Development Core Team 2011). The species dataset was down-weighted to reduce the influence of rare species.

The checkerboard score (C-score; Gotelli and McCabe 2002; Oksanen et al. 2011) was used to estimate co-occurrence patterns among colonizing species within each mound age group. The C-score was obtained by calculating the average number of C units in a species presence/absence matrix. The C unit (cu) for each species pair was calculated as

$$cu_{ij} = (O_i - S)(O_j - S),$$

where  $O_i$  and  $O_j$  are the total number of quadrats occupied by species  $i$  and  $j$ , and  $S$  is the number of quadrats occupied by both species. A null model was established to ask whether the observed C-score differs from random expectations according to the method of Cutler (2010). A C-score greater than null model expectations is support for negative co-occurrence patterns (Diamond 1975), whereas a C-score less than that of the null model is support for positive co-occurrence. All calculations used functions loaded from the 'bipartite' package (Poisot et al. 2011) in the R environment.

The degree of divergence/convergence of sequentially assembled plant communities (stages a to f) was our measure of community dissimilarity. We calculated community

dissimilarity for all possible pairs of mounds within each age group as well as all possible pairs of a mound and its reference community with two beta-diversity indices. The Jaccard dissimilarity index is based on presence/absence data only, while Bray–Curtis distance index uses quantitative relative coverage values for each species. Both indices are widely applied into community studies because they are good at evaluating differences among communities (Faith *et al.* 1987). Distance analyses were computed using the “Vegan” package in R.

## RESULTS

### Species richness and plant cover

Many plant species were recorded in the study area: 90 species belonging to 26 families were observed in the 80 mounds + 18 background vegetation quadrats (see online supplementary Table S1). Of these, 52 species were perennial herbs, 10 biennial herbs, 26 annual herbs and 2 shrubs. Most species belonged to nine plant families: *Cyperaceae* (3 species), *Poaceae* (7 species), *Asteraceae* (18 species), *Fabaceae* (6 species), *Lamiaceae* (8 species), *Polygonaceae* (6 species), *Ranunculaceae* (5 species), *Gentianaceae* (5 species) and *Rosaceae* (7 species).

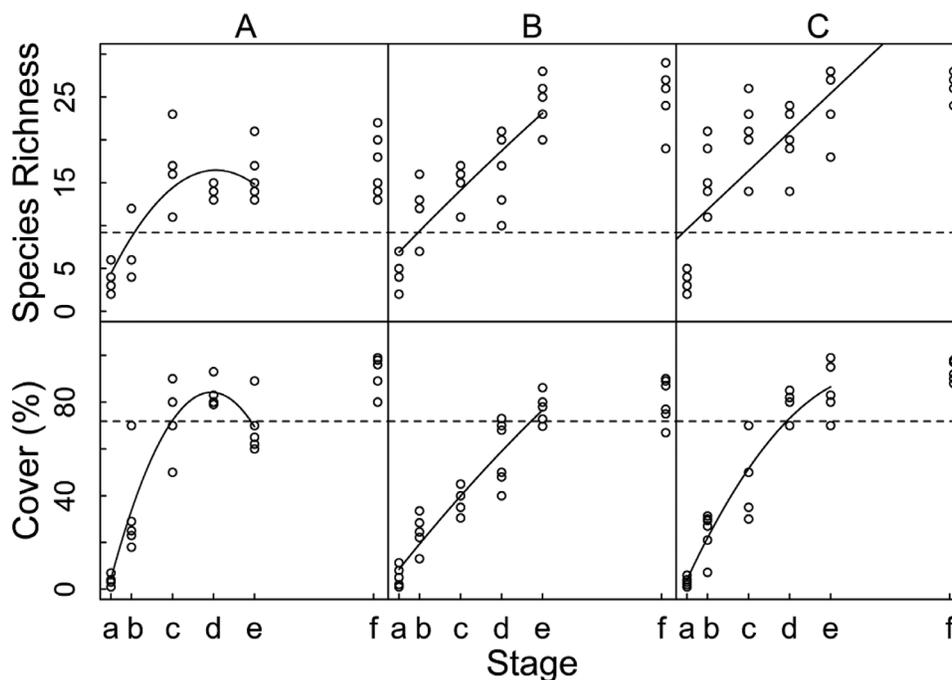
In 2009, species richness on mounds that we labeled in our study area ranged from 2 to 29, and total plant cover from 1% to 99%. The changes trend of total plant cover on a mound generally followed patterns of species richness within each plot (Fig. 2). Both species richness and plant cover of mound communities were low at stage a but then increased greatly within each plot (Fig. 2). Species richness and plant cover of

mound communities in plots B and C increased continuously over time, but that in plot A increased and then leveled off (Fig. 2, see online supplementary Table S2). From stage b onwards, species richness of mound communities was higher in plot C than in the other two plots (Fig. 2). The total cover of mound communities was higher in plot A than the other two plots from stage b to d (Fig. 2). Species richness and total plant cover of the background community were higher than that of any stage in the mound communities.

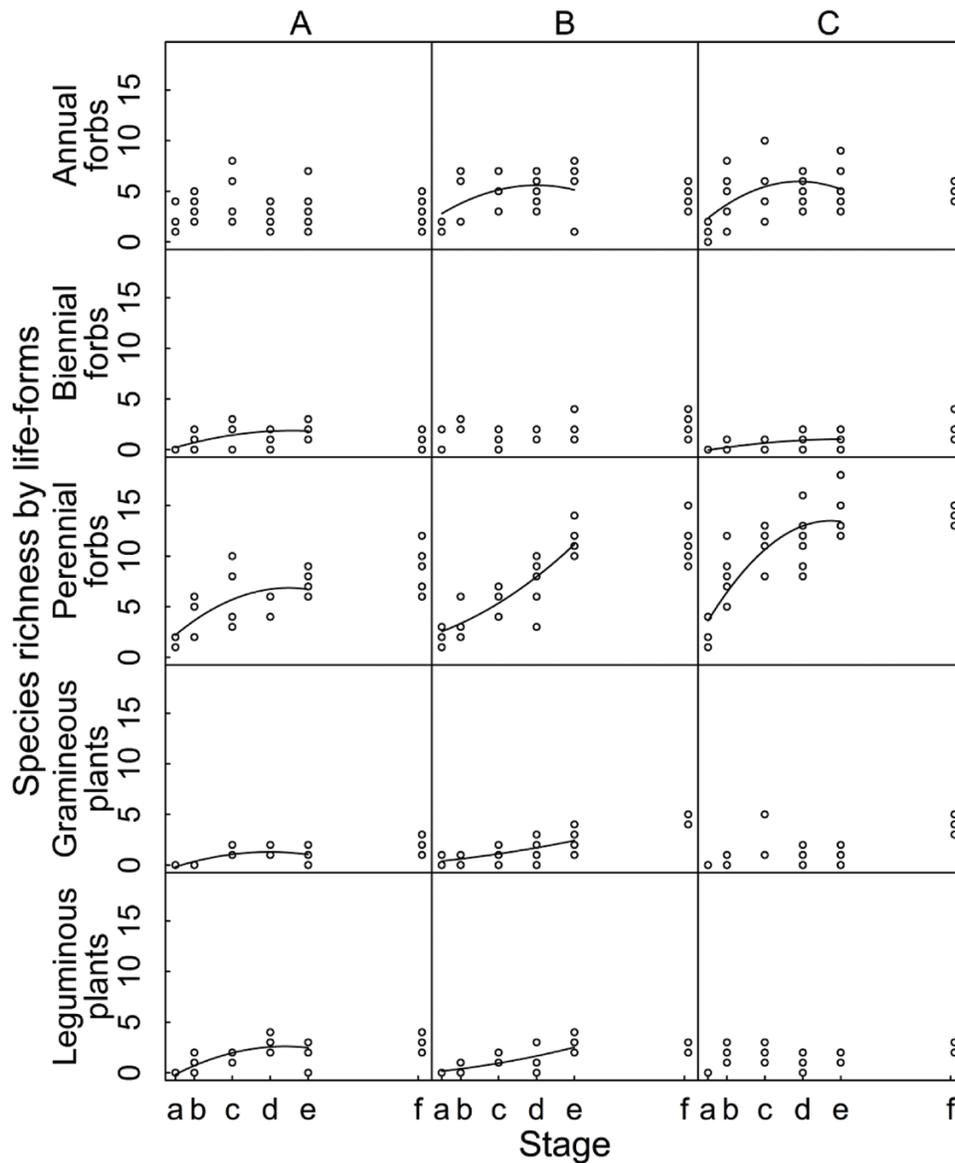
Species composition of the different life forms showed different patterns over time (Figs. 3 and 4, see online supplementary Table S2). Early stages of mound communities had high relative cover of annual forbs with low species richness. Over time, relative cover and species richness of mound communities increased for perennial forbs and legumes. In addition, species richness but relative cover of biennial forbs and gramineous plants of mound communities increased with succession stage. In background community, relative cover of perennial groups and species richness of annual forbs were lower than older mound communities.

### TWINSPAN classification

In the TWINSPAN cluster analysis, younger communities were the first to segregate and older communities were the last (Fig. 5A). Similarly, the species growing on fresh mounds clustered separately from those on older mounds and the background communities (Fig. 5B, see online supplementary Fig. S1 and Table S1). Early-successional species, such as *Elsholtzia densa*, *Polygonum nepalense*, *Pedicularis chinensis*, *Chenopodium*



**Figure 2:** changes in species richness (above) and total cover (below) of mounds/quadrats during succession within three background communities (A, B and C). The dotted reference line on the y-axis was the mean of species richness at stage b (above) and cover at stage c (below) in plot A. a–e are 1 week to 3 month-, 1-, 2-, 3- and 4-year-old mounds, respectively, and f is the background community. Lines show significant regressions over the succession period a–e. Parameters and statistics for these are in supplementary Table S2.



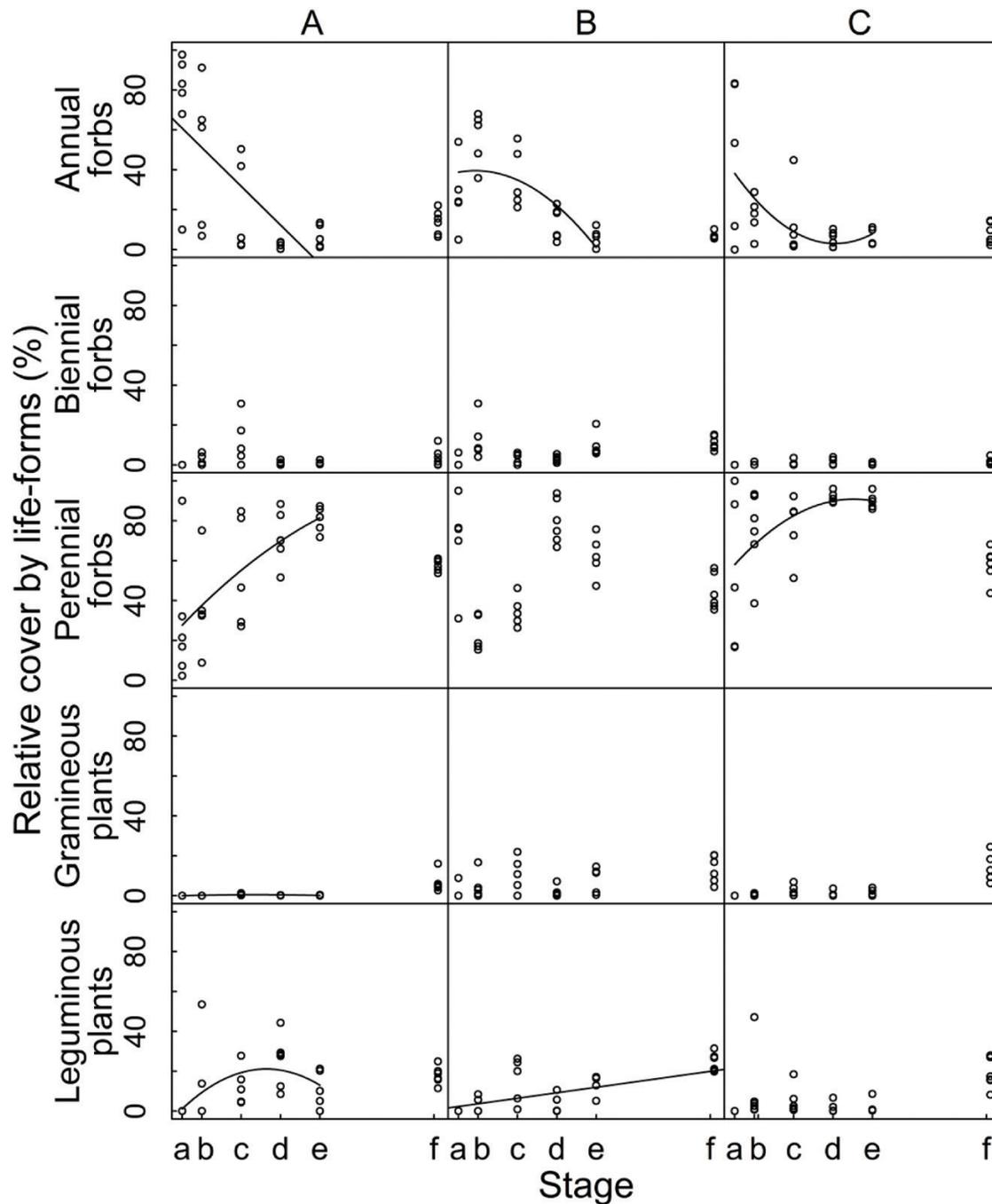
**Figure 3:** changes in species richness of different life-forms during succession on Zokor mounds in three background communities (**A**, **B** and **C**). a–e are 1 week to 3 month-, 1-, 2-, 3- and 4-year-old mounds, respectively, and f is the background community. Lines show significant regressions over the succession period a–e. Parameters and statistics for these are in supplementary Table S2.

*glaucum*, *Geranium sibiricum*, *Polygonum convolvulus* and *Hypocoum erectum*, were abundant on open patches but distributed sporadically on older mounds. The later-successional group was classified into two sub-groups: (i) species found on newly established communities and abundant on older mounds, such as *Artemisia tangutica*, *Potentilla anserina* and *Lancea tibetica* and (ii) species that occurred mainly on older mounds and in the background communities, such as *Elymus nutans*.

### Detrended correspondence analysis

DCA ordination diagrams of mound communities with increasing age illustrate relationships among plant communities during succession (Fig. 6). Community composition changed over time after mound formation. Almost all new

mounds are scattered in ordination space, but with increasing age mounds showed higher aggregation in all plots (Fig. 6, see online supplementary Table S3). Over the sequence of successional stages, the DCA of species composition produced eigenvalues ( $\lambda$ ) of 0.849, 0.618, 0.525, 0.437, 0.417 and 0.284, and gradient lengths (GL) of 5.122, 3.083, 3.261, 2.785, 2.488 and 1.851 SD units from axis I of each diagram. These community species scores exhibited notable changes from one succession stage to the next. In the first stage, the high-cover species, *E. densa*, was located close to the center of DCA ordination graph (Fig. 6A). Most species with high scores at the second stage belonged to seed bank species and bud bank colonizers, such as *E. densa* and *P. anserina*. As time progresses, the scores of annuals gradually decreased, while the scores of perennial



**Figure 4:** changes in relative cover of life forms during succession on Zokor rodent mounds in three background communities (**A**, **B** and **C**). a–e are 1 week to 3 month-, 1-, 2-, 3- and 4-year-old mounds, respectively, and f is the background community. Lines show significant regressions over the succession period a–e. Parameters and statistics for these are in supplementary Table S2.

plants increased, and several perennial species coexist in the community (Fig. 6B–E). For example, *E. densa* gradually decreased from stage c, while *P. anserina* gradually increased. Perennial grasses gradually dominated after stage d.

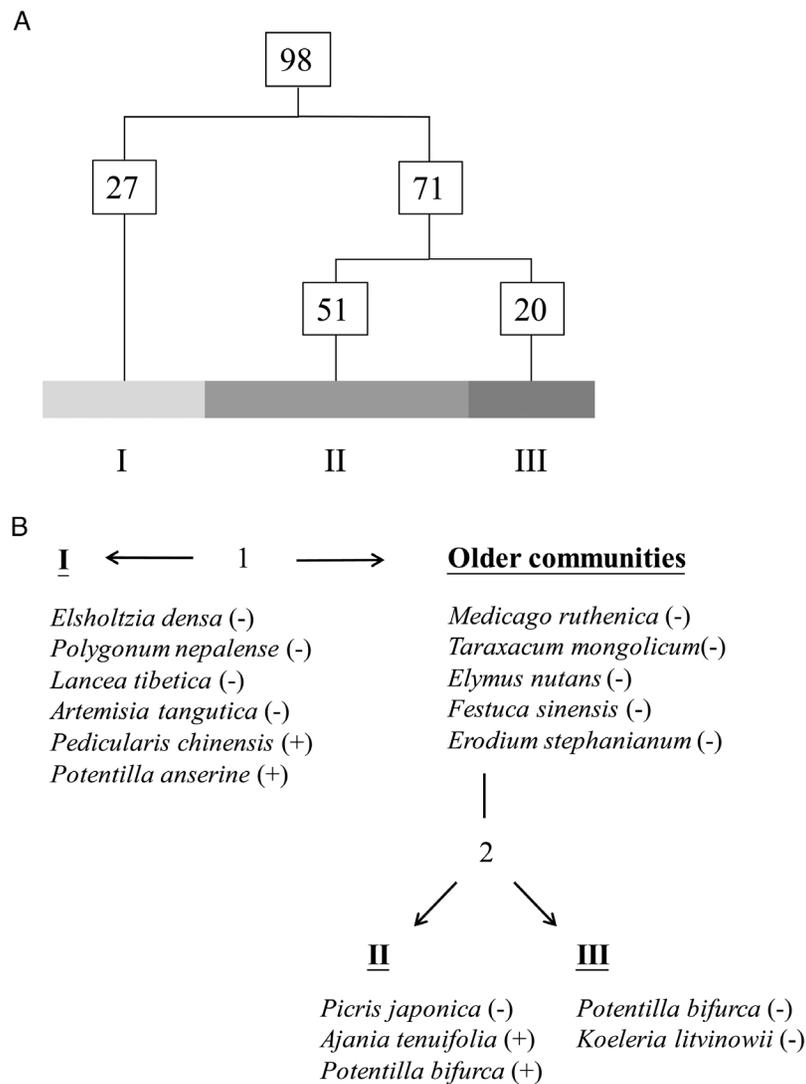
### Species co-occurrence patterns

The C-scores for the consecutive communities showed clear and progressive changes with increasing age within each plot

(Table 2). The C-scores for new mounds in plots B and C were significantly higher than random expectations. However, most C-scores of older mounds and ‘background’ communities had lower values than expected.

### Dissimilarity of mound communities

Based on presence-absence and cover data for species, four levels of community convergence during succession in the



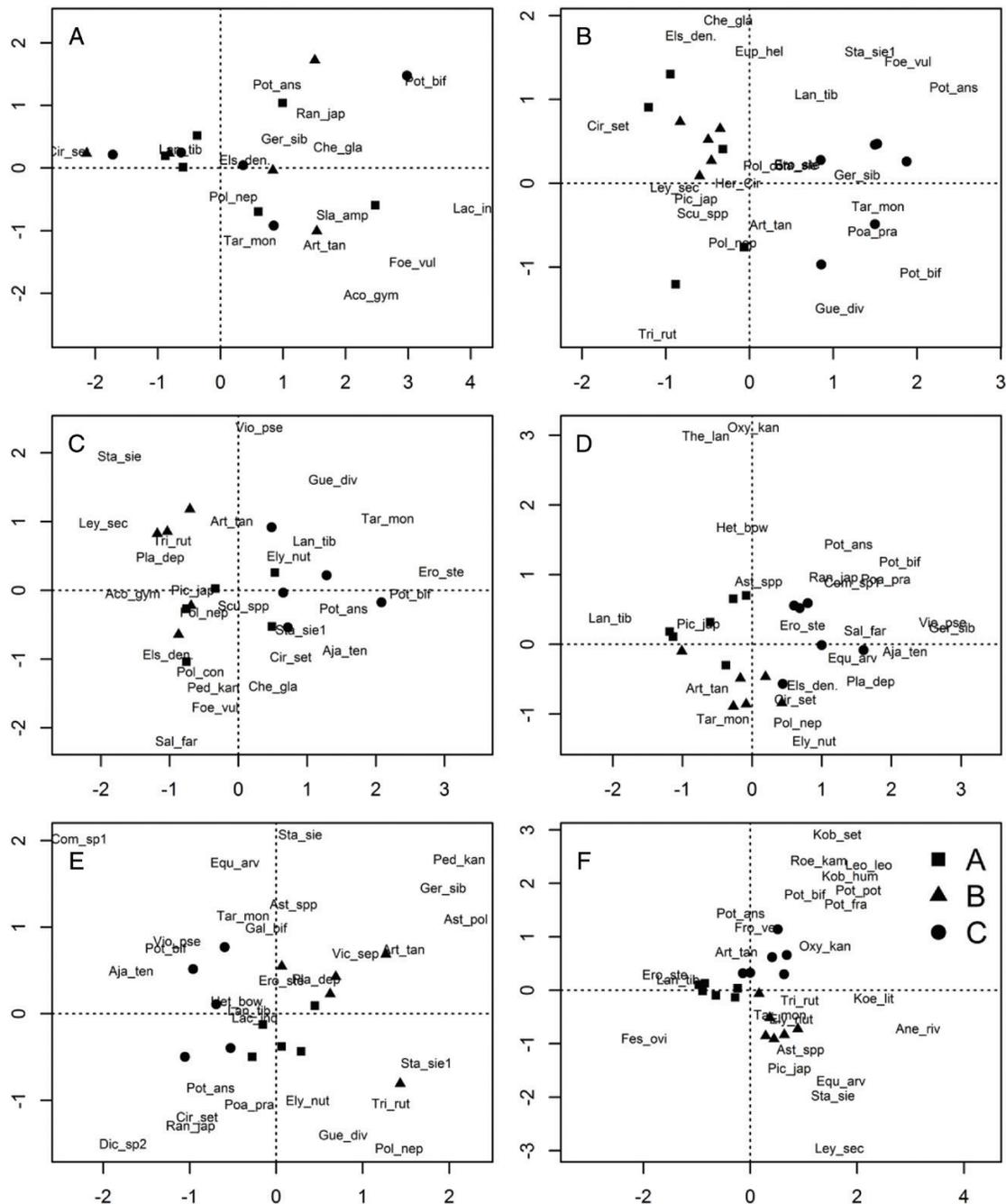
**Figure 5:** TWINSpan analysis for 98 communities in the study site. **A.** Dendrogram of TWINSpan classification. Community number of each group figure into textbox on each branch. **B.** Stepwise indicator species for the groups at each branch together with pseudospecies values. Underline parts indicate different groups. I: fresh mounds (younger than 1 year old); II: 2- to 4-year-old mounds; III: background communities. The sequence of branching is given with numbers. (+) denoting left arm preferential species, (-) denoting right arm preferential species.

mound communities were identified (Fig. 7): (i) convergence of communities at the same stage within each area, (ii) convergence in species composition of zokor mounds and their background community within each area, (iii) convergence of communities at the same stage across the three sample areas and (iv) convergence in species composition of zokor mounds and their background community across the three sample areas.

## DISCUSSION

The results from TWINSpan classification and life-form groups analysis showed that recently disturbed mounds were closely associated with annual forbs (e.g. *E. densa*, *P. convolvulus*, *C. glaucum*, *H. erectum*, *P. chinensis*, *P. nepalense*) or perennial

forbs (e.g. *G. sibiricum*, *L. tibetica*, *A. tangutica*, *P. anserine*). These early-arriving and disturbance-sensitive colonists with the characteristics of *r*-strategists are short-lived annuals emerging from the seed bank or longer-lived perennials sporadically resprouting from root fragments in the soil of fresh mounds, or dispersing from adjacent habitats, establishing high-abundance populations with rapid growth rates because they can benefit from the resource-rich patches immediately after the disturbance (Houseman et al. 2008; Latzel et al. 2008). It was in line with some results from a seed addition experiment, which indicated that, in the case of unrestricted dispersal, superior colonizers profit from non-equilibrium conditions caused by small disturbances (Inouye and Tilman 1995; Lanta and Lepš 2009). Also, it provided evidence to Sheil and Burslem (2003)'s view, which pointed out that the significant



**Figure 6:** ordination diagrams from detrended correspondence analyses of data on Zokor mound communities at several successional stages. **A–E** are 1 week to 3 month-, 1-, 2-, 3- and 4-year-old mounds, respectively, and **F** is the background community. The scientific names of the species are abbreviated (see online supplementary Table S1).

increase in species richness following gap creation has been shown to arise primarily from regrowth of existing propagules and immigration. However, patterns at the life-form level showed trends different for early-colonizing annual versus perennial forbs. We found evidence that annuals are best at colonizing open habitats but have poor competitive ability, and are therefore not able to compete against more vigorous perennial species when the latter arrive, while perennial

forbs have an advantage in competition (Jones *et al.* 2008). This could account for the continuous increase in species richness and coverage of plant communities in the later period. This result was consistent with many studies on succession, in which pioneer species are replaced by more competitive taxa (Cutler 2010; Lanta and Lepš 2009; Lebrija-Trejos *et al.* 2010). However, it contrasts with the pattern seen in three meadows in the western Cascade Range of Oregon, where few

**Table 2:** observed and expected [mean (95% confidence interval)] values for C-scores for co-occurrence analyses of successional stages on Zokor rodent mounds within three background communities

	C-score	
	observed	expected
<b>A</b>		
a	6.7	6.32 (6.29, 6.35)
b	19.4	24(23.9, 24.1)
c	68.8	90.3 (90.04, 90.56)
d	22.3	43.13 (43.01, 43.25)
e	35.4	57.68 (57.49, 57.88)
f	32.1	64.67 (64.5, 64.84)
<b>B</b>		
a	13.8	9.63 (9.58, 9.67)
b	36.1	38.38 (38.24, 38.52)
c	26.2	48.31 (48.14, 48.47)
d	56.1	91.96 (91.75, 92.17)
e	97.2	130.28 (129.94, 130.63)
f	50.8	125.5 (125.23, 125.78)
<b>C</b>		
a	7.9	6.38 (6.35, 6.41)
b	39.2	72.02 (71.85, 72.2)
c	85.1	133.73 (133.38, 134.08)
d	59.3	102.13 (101.9, 102.36)
e	72.1	109.24 (108.94, 109.54)
f	74.3	163.86 (163.53, 164.2)

A, B and C are the three areas, and a–f are 1 week to 3 months, 1-, 2-, 3-, 4-year-old mounds and the background communities, respectively.

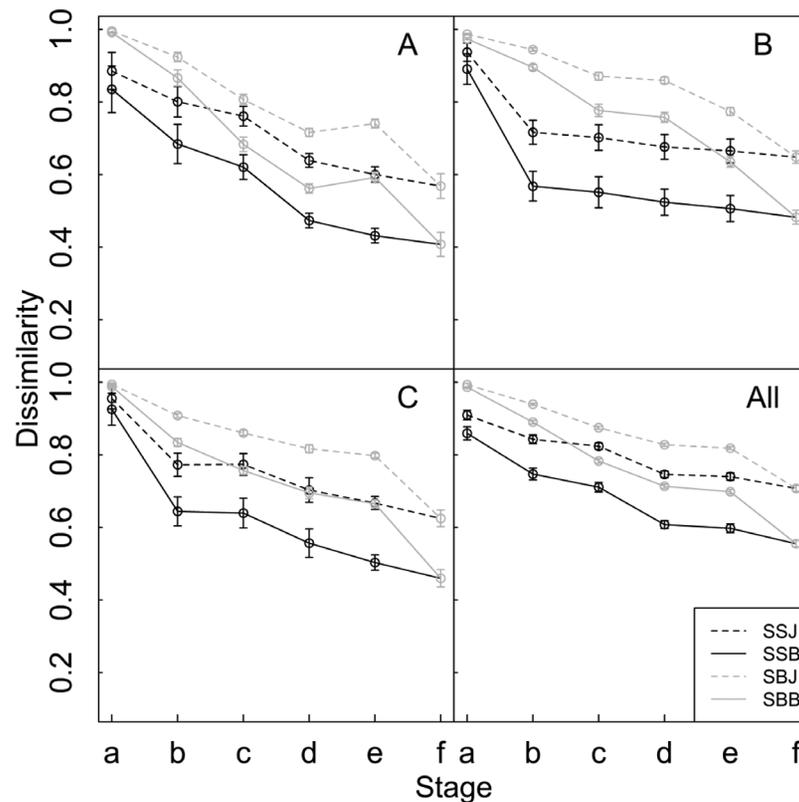
annuals and little evidence of competitive exclusion of subordinate species appeared on gopher mounds (Jones et al. 2008). Several factors may help to explain why competitive exclusion occurred on zokor mounds in our meadow, including a competition–colonization tradeoff, sensitivity of different life-forms and the presence of a seed bank and/or below-ground organs (Cadotte 2007; Jones et al. 2008; Questad and Foster 2007). For example, early-appearing annual forbs (such as *E. densa*) declined before the slower growing superior competitors (such as *P. anserina*) became dominant or reached their maximum abundances, probably in part because the crust formed on the mound surface as time passes prevented seedlings from germinating (Collins and Smith 2006).

Three observations support the conclusion that disturbed systems can contain species with both good colonization and strong competitive ability (Limberger and Wickham 2012). First, *E. densa*, an annual forb with high dispersal ability, dominates on younger mounds but persists in older mounds and in background communities. The relevant mechanism may be a mass effect, which helps regulate and maintain annual forbs appearing in mound and non-mound communities (Chase et al. 2005). This is consistent with previous reports in which

ephemeral plants with wind-dispersed seeds and fast growth can grow in unoccupied habitats in a wide variety of locations (Questad and Foster 2007; Schiffers et al. 2010), but contrary to the study by Jones et al. (2008), in which forbs were virtually absent from communities with little gopher disturbance. Second, our results also show that some perennial forbs that are good at colonizing empty mounds also dominated later, outcompeting other species. This could be explained by regenerative strategies by which perennial rhizomatous forbs with rhizomes, roots and tubers recolonize empty habitats (Latzel et al. 2008, 2009). Third, we also observe that the perennial grass *L. secalinus* regenerated sporadically on young mounds in plot B. This could be because (i) *L. secalinus* was the dominant species in the background community and was not limited by dispersal there, (ii) the soil is loose in newly formed mounds or (iii) some buried individuals of *L. secalinus* regenerated. Taken together, our observations imply either (i) that there is not always a tradeoff between these two abilities, or (ii) that dispersal does not always limit colonization by more competitive species, even if they lack long-distance dispersal ability.

The C-scores within the community-level matrix increased with successional stage, implying that species interactions become more obvious over time, similar to the results of Cutler (2010). The negative co-occurrence patterns in the first stage may occur due to low population densities, resulting in unoccupied niches and weak interspecific interactions. In contrast, positive co-occurrence patterns were formed in later stages, indicating greater aggregation of species than expected by chance due to a change in the balance between competition and localized dispersal.

In our study, two different diversity patterns were observed during post-disturbance succession on zokor mounds. Species richness and plant cover increased continuously in plots B and C. This is consistent with previous findings in other small-scale disturbed grassland ecosystems (Cutler 2010; Jones et al. 2008; Wang et al. 2008). Unlike plots B and C, however, species richness and plant cover in plot A quickly increased to a peak, followed by a slight subsequent decline. This could be due to a limited species pool in area A where the total species richness was much lower than in the other two areas. Our study showed mound communities accumulate species immediately following disturbance: both species richness and cover increased quickly, consistent with results of Wang et al. (2008). High species accumulation rates without competition exclusion could account for this observation (e.g. Hubbell et al. 1999; Tilman 1994). On the other hand, species accumulation on empty patches during secondary succession can also be slow (Cutler 2010; Sheil and Burslem 2003). After individuals fill the mound community, it is no longer in a ‘gap’ state. It has been hypothesized that if mound communities provided intermittent empty niches for colonization, diversity might rise continuously (Debra et al. 2014; Sheil and Burslem 2003). Alternatively, species diversity can decrease through competitive exclusion (Chesson 2000; Limberger and Wickham 2012).



**Figure 7:** changes in mean plant community dissimilarity among plant communities pairs of Zokor mound and/or background quadrat along 6 successional stages in three background communities, **A**, **B** and **C**. All refers to the meta-community of all three background communities. SSJ (black dotted line): Jaccard dissimilarity between community pairs at the same stage; SSB (black solid line): Bray–Curtis dissimilarity between community pairs at the same stage; SBJ (grey dotted line): Jaccard dissimilarity between mound community and their background community; SBB (grey solid line): Bray–Curtis dissimilarity index between mound community and their background community. Mean  $\pm$  SE,  $n = 6\text{--}153$  pairs of communities.

Thus, we conclude that two patterns in our study may reflect transient changes in species accumulation rates.

None of our results support the hypothesis of historical contingency and climatic determinism (Clements 1916; Egler 1954). Initial mound communities are highly variable (Lepš and Rejmánek 1991; Schiffers *et al.* 2010). Only a small number of individuals occurred on the mounds in the first few days, and the identities of the first colonists to arrive on newly formed mound communities are highly variable, so stochastic factors may dominate. Alternatively or in addition, small-scale disturbance can lead to fluctuations in micro-environmental conditions, resulting in colonization by fugitive species (Collins and Smith 2006; Questad and Foster 2007). In our study area, both annual and perennial forbs have the chance to occur on new zokor mounds, but species richness was low on each mound, resulting in communities with negative species co-occurrence patterns at this stage. This result contrasts with recent study in California grasslands (Larios *et al.* 2013), in which observed annual exotic dominant species appeared in the first year after an extreme disturbance.

Zokor mound communities at the same stage became more similar to each other and to their background communities dominated by gramineous species over time. Previous studies

of long-term primary succession on lava flows (Cutler 2010) and secondary succession in tropical forests (Lebrija-Trejos *et al.* 2010) have produced similar results. We also observe a decline in eigenvalues and GLs of DCA ordination with increasing age, suggesting that community structure of all the quadrats tended to converge over time. Such community patterns resulted from the combination of a sharp decline of few dominant pioneer species (annual forbs) and a gradual increase of species from the background community (perennial forbs) from a limited species pool. This is not consistent with the historical contingency hypothesis, which holds that community is determined by the order and timing that individual species entered the system, even if environmental conditions and species pool are similar.

Our results suggest that regeneration from broken roots and germination from the seed bank drive early succession, but background-based species pool and competition exclusion become more important over time. Our results provide one of the first examples of zokor mound community convergence over time, whereas mound communities among the three plots at the same stage apparently diverged later in succession. In other words, older mound communities in different background communities diverged due to background-based

assembly, while mounds in the same 'background community' and even the whole study area converged. This is partially consistent with results from a 5-year container experiment in meadow and floodplain communities, in which final composition converged in each site but diverged between the two habitats (Lanta and Lepš 2009). Different background vegetation resulting from three restoration treatments is one of the potential explanations for our result. As in most studies of succession, the absence of replication at the background-community level limits the strength of our inferences. Future studies should use randomized blocks for background-community treatment, and include a broader spectrum of grassland types. Also, our study has focused on vegetation colonization within the first four years after disturbance in a sub-alpine meadow, but longer term studies are needed. Ongoing and future studies on zokor disturbance communities can help us test theories of succession, as well as helping us to develop strategies for the management of grassland ecosystems.

## CONCLUSIONS

In our 4-year field experiment on plant succession on zokor mounds, we observed two different patterns of plant community diversity over time: (i) continuously increasing and (ii) an initial increase followed by a later decline. The relative cover changes in life forms do not correspond with patterns in species richness. Succession of zokor mound communities was initially consistent with 'multiple alternative states', whereas later succession moved towards 'non-random community structuring by background-based assembly'. Species composition on newly formed mound communities was primarily determined by species' dispersal colonization abilities and regenerative strategies, while species co-occurring later were primarily the outcome of species interactions. Tradeoffs between competition and colonization, characteristics of different life-forms and mass effects in a limited species pool are mechanisms that could explain the convergent development pattern under low disturbance frequency. Small-scale disturbances by rodents provide unique opportunities to investigate and test theories of secondary succession and increase our ability to manage the degraded grasslands.

## SUPPLEMENTARY MATERIAL

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

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