Small-scale switch in cover-perimeter relationships of patches indicates shift of dominant species during grassland degradation

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Abstract

Aims Grasslands are globally threatened by climate changes and unsustainable land-use, which often cause transitions among alternative stable states, and even catastrophic transition to desertification. Spatial vegetation patch configurations have been shown to signify such transitions at large spatial scale. Here, we demonstrate how small-scale patch configurations can also indicate state transitions.

Methods The whole spatial series of degradation successions were chosen in alpine grasslands characterized as seven typical communities. Patch numbers, and perimeter and cover of each patch were recorded using adjacent quadrats along transects in each type of the communities. Species abundance within each patch was measured.

Important Findings Across seven grazing-induced degradation stages in the world’s largest expanse of grassland, from dense ungrazed turf to bare black-soil crust, patch numbers and perimeters first increased as patch cover decreased. Numbers and perimeters then decreased rapidly beyond an intersection point at 68% of initial continuous vegetation cover. Around this point, the vegetation fluctuated back and forth between the sedge-dominated grassland breaking-up phase and the herb-dominated phase, suggesting impending shift of grassland state. This study thus demonstrates how ground-based small-scale vegetation surveys can provide a quantitative, easy-to-use signals for vegetation degradation, with promise for detecting the catastrophic transition to desertification.

Keywords: grassland degradation, state transition, Tibetan Plateau, trade-off, vegetation patchiness
INTRODUCTION

Grassland ecosystems are experiencing increasingly unsustainable land-use and climate changes, which could drive catastrophic shifts in their structure and in the services they can provide (Kéfi et al. 2007a,b; Scheffer et al. 2001; Scheffer et al. 2009; Dakos et al. 2019). Catching signals for regime shifts are important to anticipate and take measures to prevent a desertification state, through recovery strategies that promote the sustainability of grasslands (Reynolds et al. 2007; Scheffer et al. 2009). Vegetation patchiness and patch self-organization have been proposed to depict the process of vegetation fragmentation and degradation (Malamud et al. 1998; Pascual et al. 2002; Rietkerk et al. 2004; Alados et al. 2007; Kéfi et al. 2007a). Empirical evidence has shown that the patch size – patch number relationship follows a power law with the increase of grazing pressure in degraded rangeland (Kéfi et al. 2007a). Moreover, modeling has revealed that high grazing pressure drives deviation from the power law, which could signal the approach of a catastrophic shift to desertification (Kéfi et al. 2007a). Regime shifts can be signified by particular spatial configurations, particularly in ecosystems that have self-organized regular patch patterns (Scheffer et al. 2009). It would be practical to catch signals for grassland state shift by pinpointing the relevant patch attributes, and their specific variations, along the entire series of degradation stages. This would provide a particularly useful monitoring tool if it could be done by direct and simple vegetation measurements at small spatial scale (e.g. Rietkerk et al. 2004).

There are mounting efforts to find associations of ecosystem degradation with patch attributes following self-organization theory (Aguir and Sala 1999; Pascual et al. 2002; Alados et al. 2004; Alados et al. 2006; Crotty et al. 2018). It has been shown that the attributes of patch configurations, such as number, size, area, edge and connectivity could signify the intensity of stress from external perturbations and indicate the degradation levels of grassland (Brown et al. 2002; Kéfi et al. 2007a). Patch perimeters can be used to indicate the degree of vegetation exposure to stressful environmental conditions, and the edge effects (Crotty et al. 2018; Oñatibia et al. 2018). Patch connectivity could indicate states of ecosystem functioning (Ravi et al. 2010, Okin et al. 2015). Greater inter-patch distance diminishes the capacity to retain propagules for regeneration, thereby increasing the erosion risk (Aguir and Sala 1994, 1997; Pueyo et al. 2008; Augustine et al. 2012; Oñatibia et al. 2018). Furthermore, such attributes are also related to changes in biodiversity and the associated stability and multifunctionality of ecosystems (Rietkerk et al. 2004; Kéfi et al. 2007b; Maestre and Escudero 2009; Berdugo et al. 2017; Crotty et al. 2018). Both trade-offs and coordination among attributes could occur regarding state shifts during grassland degradation. Much progress has been made to seek information from patch configurations at larger spatial scales which could be used as signals for regime shifts, but a key question is whether such a predictive framework system could also be developed at relative small scale, i.e. the scale at which land managers could take simple ground-
based vegetation patch measurements. Here we propose a framework and try to test it in an alpine grassland ecosystem in the southeastern Qinghai-Tibetan Plateau. These grasslands, like many other alpine grasslands in the world, provide multiple important ecosystem services at local to global scales. However, these services are severely threatened by unsustainable land use and climate changes (Hopping et al. 2018; Miehe et al. 2008; Babel et al. 2014; Klein et al. 2014), leading to widespread degradation and desertification; and ultimately often persistent black-soil crust (Babel et al. 2014; Klein et al. 2014; Hopping et al. 2018). This is especially typical in Qinghai province, China, where overgrazing of the typical *Kobresia pygmaea* sedge pasture induces a reduction in vegetation cover and species richness, and soil organic matter (Lin et al. 2015; Babel et al. 2014). In addition, the severe cold and dry climate accelerates grassland degradation. Moreover, freeze-thaw cycles in the sod layer drive cracking of the *K. pygmaea* turf (Cheng and Wu 2007). This process is further exacerbated by the strong wind causing erosion in the cracks and accelerating the catastrophic shift to black-soil crust (Babel et al. 2014). Numerous studies have provided information of species composition, biomass, and soil nutrient concentration during this degradation sequence (Li et al. 2011; Chen et al. 2013; Dong et al. 2013; Babel et al. 2014; Hopping et al. 2018). However, such information is insufficient to understand and accurately predict the state shifts. Here we argue that it is critical to integrate spatial configurations and attributes of patches into the process of grassland degradation.

Grassland degradation driven by grazing pressure is recognized as the fragmentation and patchiness process starting from continuous vegetation cover (vegetation cover is close to 100%). Based on our field observations, the entire process of increasing vegetation patchiness goes through several typical stages, i.e. patch appearance (few large patches), patch development (transition of large patches into many moderate-size patches), patch self-organization (regular configurations), and patch disappearance (few small patches). In the initial stage of vegetation fragmentation, patches are characterized by large size, small patch numbers, high connectivity and small total perimeter per unit area. Then an increase of grazing pressure causes continuous fragmentation of large patches into regular patch patterns characterized by large patch numbers, moderate size, and large total perimeter. Finally, still heavier grazing pressure drives the collapse of patches. Patches will disappear rapidly and few small patches with small perimeter remain (Fig. 1). The cover of vegetation patches may show a gradually decreasing trend with patch appearance and self-organization, then reach the tipping point to transit to a rapid decline with patch collapse. Total patch perimeters could show an increasing trend with patch appearance and self-organization, then a decline with patch disappearance (Fig. 1). Based on these hypothesized variations of patch attributes, vegetation cover should show trade-offs between patch numbers and perimeters in the early transition stages of degradation, and then a switch to coordination between these attributes in the post-transition stages. Bringing all this together, we
hypothesized that a switch in patch cover-perimeter relationships could signify a transition to an alternative state of grassland.

Furthermore, in the case of the Qinghai-Tibetan Plateau, plant functional groups usually shift during grazing-driven degradation of *Kobresia pygmaea* C. B. Clarke pastures, with decreasing abundance of palatable graminoids (especially sedges) within increasingly smaller patches; and increasing abundance of unpalatable forbs (i.e. broad-leaved herbs) in such patches (Lin *et al.* 2015) until they also decline with grazing pressure increasing further. We hypothesized that the dynamic equilibrium of patch numbers between those dominated by graminoids versus by forbs should correspond to the switch of relationships among patch attributes, indicating the incoming state shift of graminoid dominance to forb dominance driven by grazing pressure.

To empirically test and quantify our conceptual framework based on qualitative observations, we carried out an extensive field investigation in alpine grasslands, quantitatively assessing patch attributes along three independent transects, each hosting the entire sequence of grazing-induced grassland degradation, across Qinghai province, China.

**METHODS**

**Study area**

The experimental sites were selected in alpine grassland dominated by sedge species *Kobresia pygmaea* C. B. Clarke. The target grasslands were distributed in three counties, i.e. Haibei (N 37.80°, E 100.48°; 3603 m a.s.l.), Huangnan (N35.01°, E101.54, 3700 m a.s.l.), and Guoluo county (N34.46°, E100°25, 3740 m a.s.l.) in Qinghai province, China. These sites are characterized by a typical alpine climate with similar annual average precipitation ranging from 509.2 to 523.7 mm, and mean annual temperature ranging from 0.4 to 1.0 °C. The elevation ranges from 3670 to 3860 m a.s.l. Details of the positions of succession stages sampled within sites are shown in Figure 2. These alpine grasslands are mostly used for pasture and have a long grazing history. Grazing management is extensive, in large continuously grazed paddocks.

**Patch configurations**

Field survey was carried out during plant growth peak from the middle of July to the middle of August in 2017. In each site a transect of each community in degradation sequence was selected. The study area was summer grazing pasture managed by different farm households. The variations in grazing pressure in different households had induced the distinct extents of degradation. We selected the spatial series of communities in different stages of grassland degradation succession based on regional knowledge (Lin *et al.* 2015; Liu *et al.* 2018) as well as on information about livestock quantities and pasture area in each of the three counties. The seven types of communities during the
degradation succession are typically (1) the ungrazed *K. pygmaea* community dominated by the sedge *K. pygmaea*, accompanied by the forbs *Ajania tenuifolia* (Jaq.) Tzvel. and *Oxytropis ochrocephala* Bunge; (2) light grazing pressure *K. pygmaea* community dominated by *K. pygmaea*, accompanied by the forbs *Leontopodium nanum* (Hook.f.et Thoms.) Hand. and *Medicago ruthenica* (L.) Trautv.; (3) moderate grazing pressure *K. pygmaea* community dominated by *K. pygmaea*, accompanied by the forbs, such as *L. nanum*, *Saussurea superba* Anthony f. and *O. ochrocephala*; (4) the cracking *K. pygmaea* community driven by heavy grazing pressure dominated by *K. pygmaea*, with the forbs *S. tenuifolia*, *Potentilla anserine* L., and *Elscholtzia ciliata* (Thunb.) Hyland.; (5) the erosion community composed of patches of *K. pygmaea* and forb species, including *P. anserine*, *Ligularia rockiana Hand.-Mazz.*, *A. tenuifolia*, *Artemisia myriantha* L.; (6) the severe-erosion community dominated by the forbs *L. nanum*, *E. ciliata*, *P. anserine*, *Lonicera semenovii* Regel, and small remaining patches with *K. pygmaea*; (7) the bare black-soil crust with few forb species including *L. semenovii*, *A. tenuifolia*, *L. nanum* and *Polygonum sibiricum* Laxm.. The ungrazed *K. pygmaea* communities were located within the enclosed meteorological observation stations where livestock were excluded. The succession series were selected in areas with rather flat ground surface and slopes less than 5° in each county. One 2 m x 30 m area was laid out in each community type in each county (Figure 2). Fifteen adjacent quadrats of 2 m x 2 m were set up within each 2 m x 30 m area. In each quadrat we recorded the number of vegetation patches, and measured the perimeter and percentage vegetation cover of each patch. Composition in terms of individual species’ cover of vegetation patches in each quadrat were also recorded. Vegetation patches within each quadrat were mapped as polygons at 1:10 scale and then we took a picture of the quadrat. The maps and pictures were digitalized, and % cover and perimeter of each patch were calculated in order to check the in situ measurements. We established and performed measurements in 315 quadrats in total.

**Grazing pressure survey and calculation**

The main types of livestock in this regions are yak and sheep. Livestock quantity was investigated using questionnaire surveying through home visits in each community type in each county. Besides livestock, common herbivores in the region are pikas. These rodents primarily feed on plant roots. The number of pika caves was recorded and the cover of each cave openings was measured in each 2 m x 2 m quadrat and used as a proxy for destroyed vegetation cover by pikas.

To quantify grazing pressure in different communities, we developed herbivory indices. Firstly, we converted yak mass into sheep-unit according to the mean mass of yak and sheep respectively. Then livestock grazing indices in each degradation stage were calculated by converting livestock quantity into sheep units via the grassland area that had been used as pastures (Fig. S1c). This procedure yielded a discrete variable that ranged from 0 in ungrazed communities to 6.69 sheep units ha\(^{-1}\) in the erosion communities (Fig. S1d). For pika grazing indices, we calculated the destroyed vegetation
cover by the openings of the pika caves in each area (Fig. S1A, B and a, b), and calculated aboveground biomass destroyed by pikas according to the mean aboveground biomass in the corresponding communities. Then pika grazing indices in each community type was calculated as the ratio of aboveground biomass destroyed by pikas to the mean aboveground biomass in each community type which yielded a discrete variable ranging from 0.011 to 0.092. In order to quantify the herbivory indices by integrating livestock and pika grazing indices in each community type, we used livestock grazing index multiplied by the difference between one and pika grazing index, which yielded a discrete variable that ranged from 1.98 in the light grazed communities to 6.36 in the erosion communities (Fig. S1e). We converted the aboveground biomass destroyed by pikas into grazing indices according to forage consumption by sheep during a year in the ungrazed communities, which yielded the value of 0.39.

**Statistical analysis**

ANOVARs followed by Tukey post-hoc tests were used to test for differences in numbers per m², % cover, and total perimeter per m² of vegetation patches, as well as for differences in livestock and herbivory indices in different community types during the degradation succession of grassland. We calculated frequencies of patch numbers regarding patch cover and total perimeters distributed within the three 2 m x 30 m areas in each type of communities during the degradation succession. In these analyses, the frequencies of patch numbers dominated by *K. pygmaea* and forb species respectively were calculated. Piece-wise regression analyses were used to test the relationships between total perimeters per area and % cover of vegetation patches across the series of grassland degradation. Specifically, the first equation was fitted through the data for these patch attributes in the early transition stages ranging from the ungrazed to the heavily grazed communities. The second equation was fitted through the data for these patch attributes where they varied sharply and rapidly in the latter transition stages during the degradation, i.e. from the erosion community to the bare black-soil crust. We tried different functions to fit the data and selected the two unitary quadratic equations that could best characterize the relationships between total perimeter and % cover in the two respective periods. After confirmation of non-significance of any correlation of temperature, precipitation and altitude with the attributes of vegetation patches, regression analyses were performed to test relationships of numbers, total perimeter and % cover of vegetation patches with grazing indices in the spatial series from the ungrazed community to the erosion community. We did not consider the severe erosion and bare black-soil crust communities in these analyses, as herbivory indices decreased significantly as these communities did not have enough pasture area to support large number of herbivores. Furthermore, the rapid transition into the barren black-crust soil state did not rely on grazing pressure anymore. Then residuals of numbers, total perimeters and % cover of patches were calculated, and lag 1 autocorrelation and variance of their residuals were calculated to detect the trends close to the
critical threshold. All analyses were performed using SPSS version 16.0 (SPSS Inc. Chicago, Illinois, USA).

RESULTS

Cover, numbers, and perimeter of vegetation patches in degradation succession

Patch numbers and total perimeters both increased stepwise with grazing pressure along the sequence from the ungrazed community to the cracking community. Then they both decreased stepwise to the lowest values in the black-soil crust (Fig. 3a, b and Fig. S2A, B). In contrast, patch cover decreased stepwise slowly from the ungrazed community to the cracking community, followed by a steep decline to the bare black-soil crust (Fig. 3c and Fig. S2C).

Shifts in frequency of patches dominated by *K. pygmaea* and forbs in degradation succession

Regarding relative changes in the cover of the different growth forms, frequencies of (large) patches dominated by the foundation sedge species *K. pygmaea*, were the highest in the ungrazed community and then large patches were gradually transformed into steadily smaller patches as degradation proceeded until they completely disappeared in the severe erosion community and bare black-soil crust (Fig. 4a-g). Contrarily, frequencies of small patches, dominated by forbs, increased gradually and reached the highest value in the erosion community, then decreased gradually in the severe erosion community and the bare black-soil crust respectively (Fig. 4a-g). Frequencies of patches with small perimeter, dominated by *K. pygmaea*, decreased gradually from the ungrazed community to the severe erosion community, and then disappeared completely in the bare black-soil crust (Fig. 4h-n). In contrast, frequencies of patches with small perimeter, dominated by forbs, increased from the ungrazed community to the erosion community, and then decreased gradually from the severe erosion community to the bare black-soil crust (Fig. 4h-n). As regards both cover and perimeter, the frequencies of patches dominated by *K. pygmaea* were exceeded by the frequencies of patches dominated by forbs following the transition from the cracking community to the erosion community (Fig. 4d, e, k, l).

Switch of cover-perimeter relationships of patches in degradation succession

Two separate best-fit quadratic equations were derived to characterize the relationships between total perimeter and cover in transition stages ranging from the ungrazed to the cracking community, and the stages ranging from the erosion community to the bare black-soil crust, respectively (Fig. 5a). The intersection point combined a total perimeter of 3.69 m² with a relative vegetation cover value of 68% (Fig. 5a). The patch cover-number relationship showed a corresponding abrupt shift from negative to positive slope along transition stages from ungrazed communities towards black soil crust, although patch numbers showed large variability within each degradation stage (Fig. 5b). Perimeters
were positively correlated with patch numbers, and they increased with patch number in the early and middle transition stages, to then decline with patch numbers in the late stages (Fig. 5c). The point, which was positioned at 68% of initial continuous vegetation cover, corresponded to the transition from the cracking to the erosion community, where the abundance of the sedge *K. pygmaea* and forb species fluctuated back and forth. From there, any further increase of grazing pressure could result in the catastrophic transition to the bare black-soil crust (Fig. 6a, b).

**DISCUSSION**

Our empirical findings are consistent with our conceptual framework, i.e. we have convincingly demonstrated that the combination of 68% of initial continuous vegetation cover, and a total patch perimeter of 3.69 m² could be used as signal for the grazing-induced state transition in alpine *K. pygmaea* grassland. These results also support our hypothesis that the switch of relationships among patch attributes is corresponded to a dynamic equilibrium of patch numbers dominated by graminoids as the pre-transition representative versus forbs as the post-transition one. Such forb dominated patches indicate any further increase in grazing pressure would result in transition of grassland to bare black-soil crust (Fig. 6).

Besides grazing as the key biotic driver, and interacting with it, the principal abiotic drivers underlying the spatial configurations of vegetation patches were considered to be the limiting resources, such as soil water and nutrients (Rietkerk *et al.* 2004). Increased resource scarcity leads to spatial reorganization of plants and nutrients in ecosystems with harsh abiotic conditions, and ecosystem states develop with localized structures, such as gaps, labyrinths, stripes, and spots (Pascual *et al.* 2002; Alados *et al.* 2007; Pueyo *et al.* 2008). Such patterns are commonly observed in arid, savanna and peatland ecosystems (Alados *et al.* 2004; Kéfi *et al.* 2007; Pueyo *et al.* 2008; Oñatibia *et al.* 2018). Hence, the positive plant-resource feedback drives the spatial patch configurations via self-organized patchiness where nutrients accumulate locally and are recycled around plants, thereby forming “islands of fertility” (Schlesinger *et al.* 1990). Regular spatial patterns usually indicate smaller perimeter-area ratios, and low edge exposure of vegetation cover can decrease the risk of large patches being eroded (Crotty *et al.* 2018). Moreover such regular patterns can also reduce inter-patch distances thereby maintaining connectivity, which is facilitates positive feedback among vegetation patches (Ravi *et al.* 2010; Okin *et al.* 2015). Once resource scarcity reaches a threshold, the ecosystem shifts toward a homogeneous state following the complete loss of plants (Rietkerk *et al.* 2004). In the alpine grassland, soil resources (i.e. nutrients and water) decrease along the decline of vegetation cover during the entire series of grassland degradation (Lin *et al.* 2005; Liu *et al.* 2018), which may be due partly to a reduction in plant litter and soil organic matter and
partly to surface crust formation and soil compaction. Patch numbers and total perimeters reach the highest values at the cracking *K. pygmaea* community where patch cover starts to decline rapidly. Both trade-offs and coordination relationships between cover and perimeter were observed, as hypothesized. Moreover, the switch of those relationships was at 68% of the initial continuous vegetation cover (Fig. 6), where the vegetation composition fluctuated between predominance of *K. pygmaea* sedges in the cracking community and that of forb species in the erosion community; and subsequently shifted to the latter through the positive feedback between plants and limiting soil nutrients via self-organized patchiness (Lin *et al.* 2005; Dong *et al.* 2013; Liu *et al.* 2018). Such phenomena were recorded by simple ground-based measurements in small plots set out over short distances. This makes our study the first *in situ* demonstration of self-organized patch dynamics with state transition at small spatial scale which could provide new perspectives for fine-scale prediction of regime shifts in ecosystems (Rietkerk *et al.* 2004).

Alternative state transitions are usually driven by a complex, combination of several factors with a high degree of stochasticity (Scheffer *et al.* 2001). In our experimental sites, overgrazing by livestock as well as harsh conditions of the climate and relatively young soil profiles are the main forces driving alpine grassland degradation (Miehe *et al.* 2014) but we also identified an important role for a second biotic player, i.e. pikas. Ungrazed *K. humilis* grasslands were selected within enclosed areas to exclude livestock, where pikas are the main herbivores. These rodents can be rather abundant especially in *K. pygmaea* grassland (Fig. S1). When heavy grazing aboveground by livestock causes grassland cracking by freeze-thaw cycles due to the large volume of the matted epipedon belowground (Cheng and Wu 2007; Niu *et al.* 2019), pikas can accelerate this process especially because they are predominantly root herbivores. The cracking *K. pygmaea* community has commonly been recognized as the stage most sensitive and vulnerable to external perturbations and climate changes, which is easily eroded and transformed into the bare black-soil crust (Dong *et al.* 2013; Babel *et al.* 2014; Lin *et al.* 2015; Liu *et al.* 2018). It is easy to understand that the combination of aboveground and belowground herbivores likely adds to this vulnerability even more than aboveground grazing alone. Once the width of cracks has increased to 4-5 cm, these grasslands are at high risk of further erosion under severe climate conditions and then a catastrophic shift of grassland to the barren state may take happen rapidly even in the absence of mammalian grazing (Dong *et al.* 2013). Results from three grazed Mediterranean arid ecosystems in Spain, Greece, and Morocco showed similar factors driving rangeland degradation (Kéfi *et al.* 2007a). Arid rangelands are the most sensitive ecosystems to human activities and climate fluctuations. High grazing pressure often pushes arid rangelands towards desertification, and raised aridity can accelerate desertification in a discontinuous way, and propel the system towards the edge of collapse (Kéfi *et al.* 2007a). Although, we also observed other signals in our study which could imply the approach to the catastrophic shifts of grassland toward desertification, such as the deviation in perimeter-cover ratio (Fig. S3a), shifts in growth rates of the
patch numbers from positive to negative (Fig. S2a), and increases of variances in the residuals as well as the coefficients of the lag 1 autocorrelations of patch numbers, cover and total perimeter lengths during the approach towards the erosion community (Fig. S3b-g; Carpenter and Brock 2006; Scheffer et al. 2009). Identifying the critical transition to desertification and testing early warning signals are far from being achieved in this study. However, our research provides useful information toward revealing critical transition by extensive data collection ranging from the cracking K. pygmaea community to the erosion community. Furthermore, modeling the dynamics of plant and resource during degradation succession is essential to accurately catch early warning signals for the critical transition to the desertification.

The use of spatial data to infer impending transitions is one of the most promising areas of predicting ecology. However, the complex and stochastic forces, such as climate, biotic factors and anthropogenic activities, make it hard to find straightforward spatial series (Clements and Ozgul 2018; Dakos et al. 2019). In this study, based on substantial body of knowledge about the entire succession of alpine grassland degradation (Chen et al. 2013; Babel et al. 2014; Lin et al. 2015; Liu et al. 2018), we used the space-for-time substitution approach by choosing the entire series of alpine grassland degradation to identify the signals for state shift. What are the mechanisms underlying the switch in cover-perimeter relationships and shift in growth forms of dominant species, and how such information could be linked to signify the impending critical transitions of grassland ecosystems need to be tested. Moreover, plant trait information has recently been suggested to be introduced into the early warning signal theory (Clements and Ozgul 2018; Dakos et al. 2019). Fitness-related phenotypic traits can be used to infer the stability and health of a population or ecosystem (Clements and Ozgul 2016). Therefore, one promising next step is to link trait-based and abundance-based signals with patch configurations not only at large scale (Clements and Ozgul 2018) but, based on this study, also at small scale.

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Figure legends

**Figure 1:** Conceptual framework describing the characteristics of vegetation patchiness and variation of patch attributes with increasing grazing pressure during the degradation of alpine grassland, with hypothesized trade-offs and coordination among patch attributes. The initial continuous vegetation within a certain area is fragmented into a few large patches with large vegetation cover and small total perimeter length under low grazing pressure (I). Large patches are continuously fragmented into a large number of small ones with increase of grazing pressure. Then patches with regular spatial configurations form via self-organization, leading to a large number of patches of moderate cover and long total perimeter (II). Finally high grazing pressure drives a catastrophic shift to desertification (III), characterized by few patches of low cover and small total perimeter. Along this trajectory, vegetation patches appear, increase in number, and disappear (panel a). Total vegetation cover decreases slowly at first, and then declines rapidly to virtually bare ground (b). Total perimeter length follows the same trend as patch numbers (c). Trade-offs between vegetation cover and numbers (panel d) and between vegetation cover and total perimeters (e) could occur during pre-transition phases I and II, while in phase III this pattern switches to coordination between these patch attributes.

**Figure 2:** The locations of sampling points in the spatial series representing the subsequent stages of grassland degradation. Communities under increasing grazing pressures included: NGK, Ungrazed *K. pygmaea* community; LGK, *K. pygmaea* community under light grazing; MGK, *K. pygmaea* community under moderate grazing; HGK, cracking *K. pygmaea* communities under heavy grazing; EKF, eroded *K. pygmaea* and forb community; SFK, severely eroded forbs and *K. pygmaea* community; BSB, black-soil crust with few forbs.

**Figure 3:** Numbers per m² (a), total perimeter lengths per m² (b) and cover fraction (c) of vegetation patches in 2 by 2 m plots in the subsequent communities during grassland degradation with increasing grazing pressure. Means ± SE in different types of communities are given. Bars sharing the same letters are not different at the *P* < 0.05 level (by Tukey test). For community abbreviations see Fig. 2.

**Figure 4:** Frequencies of patches dominated by the sedge species *K. pygmaea* versus forb species regarding fraction of vegetation cover and perimeter of individual patch distributed within the three 2 m x 30 m transects in the seven subsequent communities representing the stages of grassland degradation. For community abbreviations see Figure 2.

**Figure 5:** Relationships of vegetation cover with total perimeter length per m² (a) and patch numbers per m² (b) and relationship of total perimeter length per m² with patch numbers per m² (c) in the communities during the grassland degradation succession. Dots with different colors represent the values of the seven subsequent communities during grassland degradation. For community abbreviations see Figure 2.
**Figure 6:** Framework summarizing the mechanisms underlying patterns of vegetation patchiness and its state transition with increase of grazing pressure. The dynamic equilibrium between sedge- and forb-dominated patch numbers is corresponded to the switch in cover-perimeter relationships from trade-offs to coordination of patch attributes during degradation. The relative patch cover at switch point is about 68% of the initial continuous vegetation cover. Grazing pressure drives fluctuation in abundance of sedges and forbs around the point. Further increase in grazing pressure could drive catastrophic transition to desertification.
Figure 1: Conceptual framework describing the characteristics of vegetation patchiness and variation of patch attributes with increasing grazing pressure during the degradation of alpine grassland, with hypothesized trade-offs and coordination among patch attributes. The initial continuous vegetation within a certain area is fragmented into a few large patches with large vegetation cover and small total perimeter length under low grazing pressure (I). Large patches are continuously fragmented into a large number of small ones with increase of grazing pressure. Then patches with regular spatial configurations form via self-organization, leading to a large number of patches of moderate cover and long total perimeter (II). Finally high grazing pressure drives a catastrophic shift to desertification (III), characterized by few patches of low cover and small total perimeter. Along this trajectory, vegetation patches appear, increase in number, and disappear (panel a). Total vegetation cover decreases slowly at first, and then declines rapidly to virtually bare ground (b). Total perimeter length follows the same trend as patch numbers (c). Trade-offs between vegetation cover and numbers (panel d) and between vegetation cover and total perimeters (e) could occur during pre-transition phases I and II, while in phase III this pattern switches to coordination between these patch attributes.
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Figure 3: Numbers per m$^2$ (a), total perimeter lengths per m$^2$ (b) and cover fraction (c) of vegetation patches in 2 by 2 m plots in the subsequent communities during grassland degradation with increasing grazing pressure. Means ± SE in different types of communities are given. Bars sharing the same letters are not different at the $P< 0.05$ level (by Tukey test). For community abbreviations see Fig. 2.
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Figure 6: Framework summarizing the mechanisms underlying patterns of vegetation patchiness and its critical transition with increase of grazing pressure. The dynamic equilibrium between sedge- and forb-dominated patch numbers informs about the approaching fold bifurcation, which marks the switch in cover-perimeter relationships from trade-offs to coordination of patch attributes during degradation. The relative patch cover at fold bifurcation is about 68% of the initial continuous vegetation cover, and feedback between sedge- and forb-dominated patch numbers exists around fold bifurcation. Grazing pressure drives fluctuation in abundance of sedges and forbs around the bifurcation. Further increase in grazing pressure ultimately drives the state transition to catastrophic desertification via the negative feedback between sedges and forbs.

Vegetation states - cover of patches
Grassland degradation succession
Shift of dominant species & state transition
Grazing pressure
Grazing pressure
Grazing pressure
Grazing pressure
Grazing pressure