PLANT COMMUNITIES

Ecosystem stability in Inner Mongolia

Arising from: Bai, Y., Han, X., Wu, J., Chen, Z. & Li, L. *Nature* **431,** 181–184 (2004)

Bai *et al.*[1] suggest that in China's Inner Mongolia steppe, community-level stability arises from compensatory effects among the principal components at both the species and plant functional group (PFG) levels. By analysing a consistent 19-year data set (1980–98), we show here that their analysis of a 24-year field data set (1980–2003) is called into question by inconsistencies in sampling location and numbers after 1998; the authors' findings are further undermined because they do not distinguish temporal variation from spatial heterogeneity in analysing compensatory effects among species or PFGs. We believe that rigorous reanalysis is needed for a better understanding of grassland stability.

The 24-year biomass data used by Bai *et al.*[1] are inconsistent owing to changes in sampling area and numbers after 1998, which accounts for the discrepancy with our reanalysis of a consistent 19-year data set covering the same period but ending in 1998 (Table 1). We also excluded some extraordinarily wet years (see Methods), as do Bai *et al.*[1], who assert that January–July precipitation was the primary climatic factor causing fluctuation of community biomass production. However, we found that correlations were greatest between, on the one hand, the community biomass (measured by live above-ground biomass (LAB), as in Bai *et al.*[1]) on both 15 and 31 August, and on the other, precipitation during the plant growing season (15 April to 15 August) ($r = 0.682$ and 0.705, $P < 0.001$). We also found that annual precipitation was significantly correlated both with LAB on 15 August and with the annual peak LAB ($r = 0.547$ and 0.556, $P < 0.05$) in the *Leymus chinensis* community. We found no significant correlations between LAB or peak LAB and precipitation in the *Stipa grandis* community ($P > 0.05$). Furthermore, we found no compensations between dominant and subdominant, or between subdominant and non-dominant, species and PFGs in the *L. chinensis* community. The compensatory effect between dominant and subdominant PFGs was not evident in either site (Table 1).

Second, even neglecting the change of sampling location and resampling of the 5 quadrats from the 20 quadrats in the period 1999–2003, Bai *et al.*[1] do not convincingly demonstrate the existence of specific compensatory effects on the community stability — these are generally measured by temporal variation[2–5]. Bai *et al.*[1] analysed data on relative figures for LAB to demonstrate compensations between PFGs or species (Figs 2 and 3 in Bai *et al.*[1]). However, the relative mass of one PFG or species in a community would inevitably rise (or fall) if the relative mass of the other PFGs or species fell (or rose), irrespective of whether true compensation exists between them.

Bai *et al.*[1] also illustrate the compensatory effects by showing the negative correlations between species or PFGs (Table 1 in Bai *et al.*[1]), but they pooled data for all 120 quadrats (5 quadrats per year for 24 years), which included both the temporal variability (generated by the 24 years) and the spatial variability (generated by the 5 replicates and the change of sampling location after 1998). Spatial heterogeneity alone can produce significantly negative correlations between some species, especially between dominant and subdominant species in both communities (Table 2), that are even stronger than those that Bai *et al.*[1] find in the bulk data set. Similar results for dominant–subdominant PFGs were also observed in both sites ($r = -0.500$, $P = 0.025$ in *L. chinensis* site and $r = -0.901$, $P < 0.001$ in *S. grandis* site). Furthermore, correlation does not imply causation[6]. The small proportion of significantly negative correlations in Bai *et al.*[1] (10 in 231 species pairs and 15 in 120 species pairs in sites A and B, respectively) is almost exactly what would be expected by chance, with a criterion of $P < 0.05$. It is not robust evidence for specific compensation effects.

Shiping Wang*†, Haishan Niu‡, Xiaoyong Cui‡, Shu Jiang*, Yonghong Li*, Xiangming Xiao§, Jinzhi Wang*, Guojie Wang*, Dehua Huang*, Qiuhui Qi*, Zonggui Yang*

*Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
†Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China
‡Graduate School, Chinese Academy of Sciences, Beijing 100049, China

Table 1 | Number of significant correlations in species and plant functional group levels.

		Leymus chinensis community				*Stipa grandis* community			
		Tested pairs	Number of PCs	Number of NCs	D–SD	Tested pairs	Number of PCs	Number of NCs	D–SD
Species	15 Aug	351	18	4	/	231	28	11	—
	31 Aug	351	16	12	/	231	18	5	—
PFG	15 Aug	28	2	0	/	28	0	1	/
	31 Aug	28	0	0	/	28	1	1	/

PC, positive correlation; NC, negative correlation; D–SD, correlation between dominant–subdominant species or PFGs; PFG, plant function group, as in Bai *et al.*[1]. Forward slashes, no correlation ($P > 0.05$); dashes, significant negative correlation ($P < 0.05$).

Methods. Study sites have been described[1,7–9]. Every year the sampling started on 1 May, ended on 30 September and was done at 15- or 16-day intervals. For the period of 1980–98, five 1 m × 1 m quadrats were sampled randomly[7] within the 100 m × 100 m permanent site; however, since 1999 the field-sampling design for *Leymus chinensis* community was changed and 20 quadrats were sampled in a new site (60 m north of the original site). The new and old *L. chinensis* sites differ in plant community structure: for example, *L. chinensis, Stipa grandis, Achnatherum sibiricum* and *Axyris amaranthoides* accounted for 43.1%, 12.4%, 8.7% and 0%, respectively, of community above-ground biomass at the old site in 1993, and 2.2%, 36.0%, 14.9% and 10.7%, respectively, in the new site in 2003. Both 1993 and 2003 had comparable amounts of precipitation over January–July and during the plant-growing season (15 April to 15 August). Over the 1980–98 and 1999–2003 periods, transects were not designed, nor were there five equally sized replicate blocks, as Bai *et al.* claim. Bai *et al.*[1] do not detail changes in sampling area and methods as they were not personally involved in data collection before 1998, neither do they describe how 5 out of the 20 samples collected each year after 1998 were selected. To retain consistency in the data set and avoid the effect of spatial heterogeneity, we used only a 19-year data set (1980–1998; 18 years in some cases because only total biomass was available for 15 August 1986 in the *L. chinensis* community and there were no data for 31 August 1998 in the *S. grandis* community). Meanwhile, the data of 20 quadrats in 2002 were used to analyse spatial variation in *L. chinensis* and *S. grandis* communities. All analyses were done as described[1]. At the species level, only commonly found species (those present in more than 50% of total sampling quadrats or years) were included. To analyse correlations between live above-ground biomass and precipitation, we excluded the extremely wet years (January–July precipitation, 1990, 1991, 1992 and 1998 excluded; precipitation in plant growing season, 1981, 1990, 1992 and 1998 excluded; and annual precipitation, 1981, 1986, 1990, 1992 and 1998 excluded), as suggested in Bai *et al.*[1].

Table 2 | Significant correlation coefficients between species in 20 quadrats in each site in 2002.

Leymus chinensis community				*Stipa grandis* community	
Species pair†	Correlation coefficients (r)	Species pair	Correlation coefficients (r)	Species pair	Correlation coefficients (r)
1 × 9	−0.539*	1 × 14	0.462*	1 × 3	−0.893**
8 × 19	−0.520*	10 × 12	0.599**	3 × 5	−0.708**
1 × 17	−0.512*	10 × 13	0.558**	3 × 8	−0.559*
8 × 13	−0.503*	12 × 16	0.500*	3 × 7	−0.546*
1 × 2	−0.490*	13 × 19	0.667**	4 × 8	−0.521*
8 × 9	−0.450*	14 × 20	0.463*	5 × 9	0.510*
3 × 16	0.444*	5 × 16	0.447*	7 × 10	0.532*
7 × 18	0.446*	8 × 15	0.578**	5 × 10	0.603*

Single and double asterisks indicate significance at the 0.05 and 0.01 levels, respectively.
† Numbers indicate the rank of the species in relative above-ground biomass in each site.

§Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, New Hampshire 03824, USA

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PLANT COMMUNITIES

Ecosystem maturity and performance

Arising from: Bai, Y., Han, X., Wu, J., Chen, Z. & Li, L. *Nature* 431, 181–184 (2004)

The effect of maturity, or successional stage, on ecosystem performance (measured as productivity or stability, for example) is important for both basic ecology and ecosystem management. On the basis of the results of a long-term study of two different plant communities at two sites in the Inner Mongolia grassland[1], Bai *et al.* claim that these communities simultaneously achieve high species richness, productivity and ecosystem stability at the late successional stage[1]. However, I question their interpretation of the data and suggest that this claim is undermined by evidence from other empirical and theoretical studies.

Bai *et al.*[1] present data on above-ground biomass of the total community and on various plant groups, but they provide no time series to indicate how diversity, productivity and stability might have changed during succession.
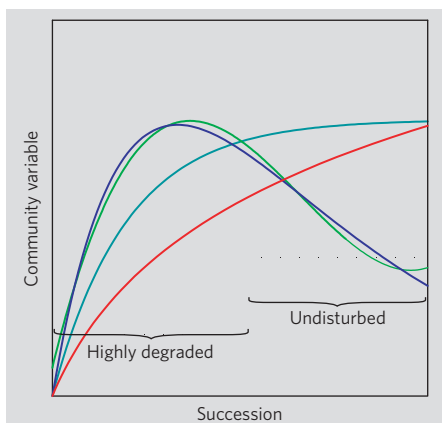

Figure 1 | Changes during succession. Model of temporal changes in diversity (species richness; green curve), productivity (blue), biomass (turquoise) and stability (red) during succession, based on an extensive literature review[5,6]. In the transitional stage, both early (short-lived) and late (long-lived) species coexist, leading to high species diversity. In this stage, biomass is relatively low and resource level is still high, promoting higher productivity. In the late stage, stability may be high but diversity and productivity may be low because of competitive exclusions[7] and sequestration of limited resources by accumulated litter and biomass[5,12].

The two communities compared at their site A represent two extreme degrees of disturbance: one undisturbed and the other heavily degraded. Although the undisturbed community did support relatively higher diversity and above-ground biomass than the highly degraded community, intermediate amounts of disturbance or transitional stages, which may well support even higher diversity and productivity, were not accounted for[2–6] (Fig. 1).

Over space (that is, within one habitat), the 'intermediate disturbance' hypothesis[7] predicts that diversity will be highest at an intermediate level of disturbance[2,3]. Extensive evidence[2–12] in support of this hypothesis is not in agreement with the conclusions of Bai *et al.*

Finally, over time at one locality, successional studies from various ecosystems — particularly those covering entire successional cycles — reveal that biodiversity and productivity are highest in the mid- or transitional-stage of succession, when both early- and late-stage species coexist. The high diversity and productivity then gradually decline owing to accumulated biomass and litter and therefore to increasing competition[2–12] (Fig. 1).

Although each particular case would be expected to show some deviation from the general patterns in Fig. 1, because of the life history of dominant species, less destructive disturbance, or variation in resources available over time[13], for example, it is not clear why the Inner Mongolia grassland should be so different[1]. If community stability, whose estimate depends on how it is measured, and biomass both increase with succession and are really high in undisturbed mature ecosystems, then the contrasting patterns between diversity and stability call their relationship into question.

The high stability in mature, or late-stage succession, grassland may be at least in part caused by the longer lifespan of the remaining, competitive perennial species (unlike annuals or short-lived plants in early succession) and by the high accumulated biomass, rather than by species diversity. For example, if community stability is measured as the coefficient of variation in biomass (CV, variance/mean)[1], then the CV, which is not independent of mean biomass[14], will be lower when the biomass is higher, so the stability should be higher. Long-term, simultaneous monitoring of these variables in both above- and below-ground communities over the entire successional cycles of the grassland would help to clarify this point.

Qinfeng Guo
US Geological Survey, NPWRC, Jamestown, Nevada 58401, USA
e-mail: qguo@usgs.gov

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Wu et al. *reply*

Reply to: Wang, S. *et al. Nature* doi:10.1038/nature03862 (2005) and Guo, Q. *Nature* doi:10.1038/nature03583 (2005)

Some of our findings[1] are questioned by Wang *et al.*[2], on the basis that we use inconsistent data and fail to distinguish spatial heterogeneity effects. Here we show that both claims are unfounded. We also address the questions raised by Guo[3] concerning how the steppe communities vary as they mature.

In 1998 (not in 1999, as Wang *et al.* indicate), the sampling transect in our site A (the

Leymus chinensis community) was moved about 60 m northward within the same fenced plant community in a fairly uniform environmental setting to allow for more replicates and other sampling activities. To assure data consistency, we chose 5 quadrats in the new location at exactly the same distance interval as in the old transect. Our reanalysis of the 1980–97 data confirms our previous result[1] that live