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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.

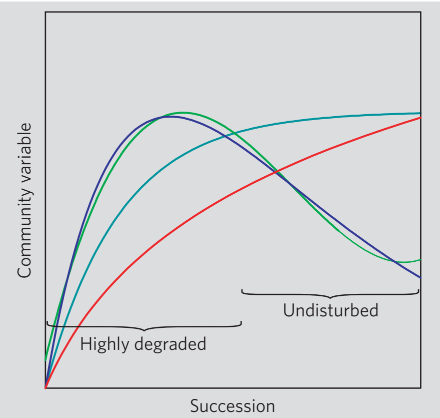

Figure 1 | Changes during succession. Model of temporal changes in diversity (species richness; green curve), productivity (blue), biomass (turquoise) and stability (red) during succession, based on an extensive literature review[5,6]. In the transitional stage, both early (short-lived) and late (long-lived) 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.

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PLANT COMMUNITIES

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 above-ground biomass (LAB) was significantly correlated with January–July precipitation, but not with annual precipitation.

By contrast, Wang *et al.* show that LAB is correlated with April–August and annual precipitation[2]. However, an earlier analysis[4] by some of these authors using 1980–89 data showed that peak LAB correlated to annual precipitation only in the *Stipa grandis* community (our site B), not site A, contradicting their result presented here[2]. Using the same 1980–89 data set, they reported that peak LAB of site A was significantly correlated with July precipitation and April–September precipitation[4], but later found that above-ground net primary production was correlated with neither annual precipitation nor April–September precipitation[5]. Differences in timescale, biomass variables and data analysis procedures may have contributed to these seeming discrepancies, and the results of Wang *et al.* do not therefore invalidate our findings.

We are aware that spatial heterogeneity and scale influence ecological analysis[6,7], but the fine-grained within-community heterogeneity of site A is unlikely to have significantly undermined our results. The LAB and species composition estimated from 5 and 20 quadrats show quite similar results (for example, $\text{mean}_{\text{LAB,5quadrats}} = 185.21$, $\text{s.d.}_{\text{LAB,5quadrats}} = 30.97$, whereas $\text{mean}_{\text{LAB,20quadrats}} = 188.05$, $\text{s.d.}_{\text{LAB,20quadrats}} = 31.09$, on 30 August 2001). Also, our correlation analyses treated the 5 quadrats as replicates, and each data pair was always from the same quadrat over the 24 years. This was not 'pooling' all quadrats together, as suggested by Wang *et al.* Spatial variability precludes neither compensatory effects nor statistical analysis using replicates: on the contrary, statistical power should increase with the number of replicates.

Wang *et al.* criticize the use of relative biomass for detecting compensatory effects, but our correlation analyses were based on absolute biomass (although our Fig. 3 in ref. 1 used relative biomass for visual clarity). They suggest that the relatively small number of species pairs showing negative correlations trivializes compensation effects, but this reasoning is flawed because the dynamics of even a few dominant species can significantly influence ecosystem productivity and its stability, as shown in our study[1].

Guo[3] questions our finding that plant communities in the Inner Mongolia grassland (site A and site B) achieve high species richness, productivity and ecosystem stability concurrently at late successional stages[1]. Although our focus was on the relationship between ecosystem stability and compensatory interactions in mature steppe communities, Guo's comments raise questions concerning species diversity and biomass production over the course of succession.

Our conclusion did not refer to species richness and productivity as being the "highest", nor did we suggest any particular relationship between richness and productivity along a succession gradient in space or time[1], so this cannot be in contradiction to the intermediate disturbance hypothesis. Existing studies in the same area indicate that species evenness (relative abundance), rather than richness (number of species), shows a hump-shaped response to a grazing gradient[8,9]. It is therefore necessary to distinguish between species richness and species diversity, which usually incorporates both richness and evenness.

Guo argues that the highest biodiversity and productivity should occur before plant communities reach their mature state, a point articulated several decades ago[6,10,11]. Relevant studies of the Inner Mongolia grassland[12,13] show that a hump-shaped relationship of species richness is not evident with respect to either succession stages or community biomass. We acknowledge that such relationships may depend on the timescale of observation. Could the species richness and biomass of our two study sites decline several decades from now if they continue to be enclosed against fires and grazing by large animals? They might, but this is only speculation.

We disagree with Guo's contention that the coefficient of variation (CV, variance/mean) in community biomass decreases with increasing mean biomass. Usually when mean biomass increases, so does the variance. Thus, CV does not necessarily decrease and, in general, the main reason for using CV instead of variance itself is to minimize bias introduced by changing the mean.

We concur that the longer lifespan of perennial species may contribute to the higher stability of mature steppes. But we note that both undisturbed mature and degraded successional communities in the Inner Mongolia grassland contain annuals as well as perennials[12,13], except in extreme situations where top soils are largely lost. We also agree that monitoring both above- and below-ground ecological variables is important for fully understanding the relationship between biodiversity and ecosystem processes.

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