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Species diversity contributes to productivity – Evidence from natural grassland communities of the Himalaya

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The impact of species diversity on ecosystem functioning has generated considerable research and tremendous debate in view of the accelerated depletion of biodiversity worldwide. A number of recently conducted experiments based on synthetic assemblages of plant species indicated that ecosystem productivity declines with loss of species. The problem with acceptability of this hypothesis is that in spite of best efforts, conditions created in the experiments fall short of natural conditions. The present study, which was carried out in alpine grasslands of Himalaya, is from natural ecosystems to lend support to the above hypothesis. It emphasizes that with the depletion of biodiversity, we are going to lose some of the life-supporting ecosystem services.

Keywords: Biodiversity, ecosystem, grassland, Himalaya.

IN recent years, concern for the extinction of species and populations due to human activities has stimulated a number of observational and experimental studies on the relationships between species richness and ecosystem functioning. In observational studies, the impact of species richness on ecosystem function was examined by comparing different ecosystem types varying in species richness or similar ecosystems distributed at different locations[1,2]. The problem with these comparisons is that the ecosystems differing in species richness also differ in environmental conditions, such as precipitation and soil type. Clearly, in these situations, the response to the variation in species diversity cannot be separated from the response to environmental variation. To address this problem, a number of experimental studies were carried out in which species richness was designed by investigators as the sole independent variable, holding the physico-chemical environmental factors constant[3,4]. A number of these experiments conducted in North America and Europe showed that productivity increased with increase in species richness[5–7]. These investigators emphasized that with more species comes more complete harvesting of resources and, hence, more production[8]. A species-rich ecosystem would have more species in complementary roles (more niche differentiation and facilitation), and therefore, more niche space occupied than one with fewer species[7].

Serious weaknesses have been pointed out in the design and interpretation of experiments with synthesized model species assemblages[9,10]. Units of vegetation differing in species richness were synthesized by making random draws from a species pool, thus making it difficult to establish the causes of increase in productivity. In some experiments, more species communities that were created contained more productive species that were absent from the experimental assemblages of less species richness[9]. Furthermore, at least in some cases, the device employed to cause variation in species richness affected the result itself. For example, in a Minnesota grassland experiment[11], a supply of nitrogen was used to bring about changes in species richness. Consequently, it was not possible to ascertain whether the low stability in the species-poor sample was because of the low species richness or because the species adapted to high nitrogen levels were vulnerable to drought, the response to which was used as a measure of stability.

Another flaw was that it was not established whether the experiments were carried out under environmental conditions in which the component species naturally occur[10]. In specific cases, soils were sterilized and sand/fertilizer mix was used in place of soil.

There is a need for studies based on natural ecosystems, involving comparative approaches that control variation of all factors except diversity[12]. It is challenging to combine the positive features of both observational and experimental studies, in order to remove confounding effects of the physio-chemical environment in the observational studies and remove problems associated with the constitution of synthetic species assemblages of experimental studies. In the present study, we addressed the question whether species

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diversity contributes to ecosystem productivity, by sampling a large number of adjoining pairs of plots differing in species richness, in a natural alpine site in Uttaranchal (UA) in the Indian Himalaya. By limiting the comparison to adjoining plots, we minimized the confounding factors that have plagued the observational studies meant for showing the contribution of species diversity to ecosystem functioning. Stochastic and patchy occurrence of incidents leading to the loss in biomass, such as local herbivory and drought, can cause difference in species richness between adjoining plots, even when their soil condition is the same[13]. For example, such a difference in the present study site may result from carry-over effect of patchy/selective grazing in the past. An alpine meadow in Himalaya is generally foraged by a variety of domestic (sheep, goats, cattle and horses) and wild animals, which differ in their behaviour[14]. Soils of the pairs showed non-significant difference for all the soil parameters investigated (C, N, P and pH; Table 1). We assumed that if members of plot pairs with high species richness had higher net primary productivity than those having lower species richness, it would prove that species diversity contributes to ecosystem functioning. In accordance with our sampling design, we applied a paired *t*-test in order to examine whether the productivity in plots having higher species richness was greater than that in adjacent plots with lower species richness. It did not allow us to examine the correlation between a wide range of species richness and their productivity values, as was done in some experimental studies[7], in which the environment of plots was kept constant, species diversity being the sole variable. In our study, such an environmental control existed only with respect to the pairs of adjacently located plots; however, it permitted us to determine whether the magnitude of difference in the productivity of adjacent plots was correlated with a difference in their species diversity.

The 89 pairs of vegetation patches (82 pairs differing in diversity) that we sampled in this study were distributed across 30 grassland stands (each stand representing a relatively uniform species composition and habitat) between 3100 and 3900 m altitudes, in the Valley of Flowers, a national park located in the Indian Central Himalaya (30°41′–30°48′N lat., 79°33′–79°46′E long.). The adjoining patches differing in species richness were approximately between 3.2 and 5.8 m^2 in area.

Grazing of domestic animals, particularly sheep and goats, was formerly common in the study grasslands, but was stopped in 1982, subsequent to the establishment of the national park. The common herbivorous wild mammals of the grassland are bharal (*Pseudois nayar*), Himalayan musk deer (*Moschus chrysogaster*) and mouse hare (*Ochotona roylei*).

The Valley of Flowers remains snowbound for about six months each year, from November to April. There is no weather station, but data collected during 1994, indicated a rainfall of 1075 mm during three monsoon months (late June to late September)[15]. During the snow-free period in 1994, the mean maximum temperature ranged from 6.3°C in November to 15.5°C in August and the minimum from 1.2°C in November to 11.7°C in August[15].

The major growth forms in grasslands are tall forbs (TF; height >30 cm), short forbs (SF; height <30 cm), cushion and sprawling forbs (CSF), and grasses and sedges (GS)[16]. *Polygonum polysthycum*, *Impatiens sulcata*, *Impatiens racemosa*, and *Selenium tenuifolium* were common TF; *Bupleurum candolii* and *Ranunculus hirtellus* were common SF, *Bistorta affinis* and *Potentilla astrosanguinea*, the widespread CSF, and *Calamagrostis emodensis*, *Danthonia cachemyriana* and *Stipa roylei* the common GS[17,18].

We made several surveys of the study grasslands during May–June 2003, when green cover of plants was being reconstituted following snowmelt, and identified 30 stands to be measured. We then used detailed surveys within stands to locate pairs of adjoining vegetation patches or plots that apparently differed in species richness (a patch here is a piece of vegetation with a certain species richness and composition). We marked 89 pairs of vegetation patches with three pairs in each of the 30 stands, except one. A pair of patches apparently occupied similar topographical features and soil characters. Out of 89 such pairs, 82 pairs differed in species richness. In the remaining seven pairs, species richness was equal in the adjoining plots. Within each of the adjoining patches of vegetation we marked out a 1 × 1 m quadrat in which we listed species and measured their cover using the point-frame method[19], counting only the first hits of the descending needles. We sampled the marked quadrats (hereafter referred to as plots) in late August 2003 to estimate peak aboveground community biomass, which was taken as an estimate of aboveground net primary production. Plants were clipped at the ground surface, air-dried and collected in polyethylene bags and brought to the laboratory, where they were oven-dried at 80°C to constant weight. The time of peak biomass was

Table 1. Paired *t*-test for various soil parameters in 89 pairs of adjacently placed plots; all values were non-significant

	Paired differences				
Parameter	df	Mean	SE	*t*	*P*-value
pH	88	–0.0079	0.0205	–0.384	0.816
Organic matter	88	–0.0758	0.0609	–1.244	0.217
Phosphate	88	0.0034	0.0050	0.675	0.501
Total nitrogen	88	0.0080	0.0154	0.518	0.606

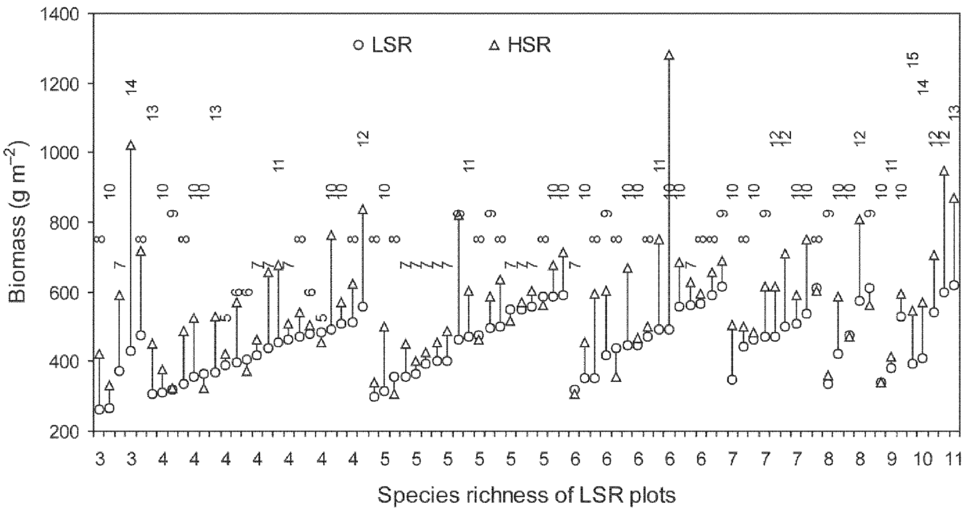

Figure 1. Aboveground biomass in 82 adjacently placed high species richness (HSR) and low species richness (LSR) plots. Each connecting bar represents a pair of adjacent plots. Numbers on x-axis represent species richness of LSR plots, and those above the triangles indicate species richness of HSR plots.

based on sequential biomass sampling investigated earlier[20]. Their study has shown that the peak aboveground plant biomass is a fairly good measure of aboveground net primary production in alpine grasslands of Himalaya, as aboveground biomass at the beginning of growth in spring is zero and species in general attain peak biomass simultaneously. We have also belowground biomass values, but we did not use them because belowground net production values are significantly lower than peak belowground biomass values in alpine grasslands of this Himalayan region[21,22]. This difference is largely because a sizeable part of belowground biomass is carried over from one year to another; its amount varies from one species to another[23]. Moreover, analysis of total biomass (sum of peak aboveground biomass + peak belowground biomass) produced the same conclusions as that of aboveground biomass. Here we have used peak aboveground biomass values as estimates of net primary production.

Apart from species richness, we also calculated species diversity, as human activities affect species evenness long before they affect species richness[22]. Within each 1 × 1 m plot we counted species number and calculated species diversity, using Brillouin Index (HB) (described by Pielou[23] and reviewed by Magurran[24]), which is similar to the Shannon–Weiner diversity index, but is more appropriate when the randomness of the sample is suspect.

If there are S species, n_i is the crown cover of individuals of the ith species and N is the total cover of all individuals in a sample area (quadrat), then Brillouin's Index (HB) of diversity is:

$$HB = \frac{\ln(N!) - \sum_{i=1}^{S} \ln(n_i!)}{N}.$$

We also calculated growth form diversity using the above index. Here S was the number of growth forms, n_i the sum of crown cover of all species belonging to ith growth form, and N the total cover of all individuals of all growth forms.

The species richness varied from 3 to 11 m^{-2} in the lower species richness (LSR) plots and 5 to 15 m^{-2} in higher species richness (HSR) plots (Figure 1), the mean values (of 82 plots) 5.7 and 9.2 respectively, being significantly different. A paired t-test analysis of the study pairs indicated that the mean aboveground biomass was significantly greater ($t = 15.413$; $P < 0.001$) in HSR plots (567.7 ± 18.56 g m^{-2}) than in LSR plots (451.8 ± 10.12 g m^{-2}) of 82 pairs (Table 2). As for the means of three replicates in each of the 30 stands (except one), in 29 stands HSR plots had greater aboveground biomass than LSR plots. In seven of these 29 stands, differences were statistically significant. In one stand (no. 16) in which the pattern was reversed (i.e. LSR plots showing higher aboveground biomass), the difference in aboveground biomass was not significant. Out of 82 pairs having unequal species richness, in 70 pairs aboveground biomass was greater in HSR plots than in LSR plots and in the remaining 12 it was greater in LSR plots (Figure 1).

The regression analysis suggests that difference in productivity between adjoining LSR and HSR plots tended to increase with increasing difference between these plots, both in species richness ($r^2 = 0.1628$; $P < 0.001$) and species diversity (Figure 2), emphasizing in another way, the role played by species richness in increasing productivity. The index of diversity closely followed species richness ($r = 0.978$, $P < 0.001$); even a difference of one species of richness invariably caused a marked difference in diversity.

Across all the 178 plots, productivity was significantly correlated with species richness as well as species diversity ($r = 0.508$, $P < 0.001$ and $r = 0.485$, $P < 0.001$ respecti-

Table 2. Paired *t*-test between high species richness (HSR) and low species richness (LSR) plots for various parameters; only parameters having significant differences are given. Values are both on the basis of 82 pairs of plots differing in species diversity and 30 stands, each sampled by three pairs of plots (except one in which number of plots was two)

	$n = 30$				$n = 82$			
Parameter	HSR mean ± SE	LSR mean ± SE	*t*-value and significance (df = 29)		HSR mean ± SE	LSR mean ± SE	*t*-value and significance (df = 81)	
Species richness	9.106 ± 0.270	5.906 ± 0.285	12.776	0.001	9.17 ± 0.23	5.67 ± 0.21	15.413	0.001
Species diversity	1.894 ± 0.024	1.52 ± 0.037	12.012	0.001	1.897 ± 0.020	1.491 ± 0.028	14.51	0.001
Growth form diversity	0.782 ± 0.022	0.525 ± 0.042	7.374	0.001	0.794 ± 0.015	0.505 ± 0.033	10.027	0.001
Aboveground biomass	566.83 ± 27.40	454.99 ± 16.50	6.068	0.001	567.73 ± 18.55	451.82 ± 10.18	7.838	0.001
Total biomass	998.68 ± 49.11	796.62 ± 34.66	7.546	0.001	997.72 ± 31.38	790.04 ± 20.44	9.628	0.001
TF crown cover	47.28 ± 2.52	61.13 ± 3.48	–5.312	0.001	45.74 ± 1.90	62.52 ± 2.87	–6.241	0.001
SF crown cover	18.98 ± 2.23	13.77 ± 1.74	2.992	0.006	19.42 ± 1.59	13.29 ± 1.51	3.382	0.001
CSF crown cover	20.38 ± 1.65	13.34 ± 1.82	3.665	0.001	21.00 ± 1.34	12.11 ± 1.51	4.905	0.001

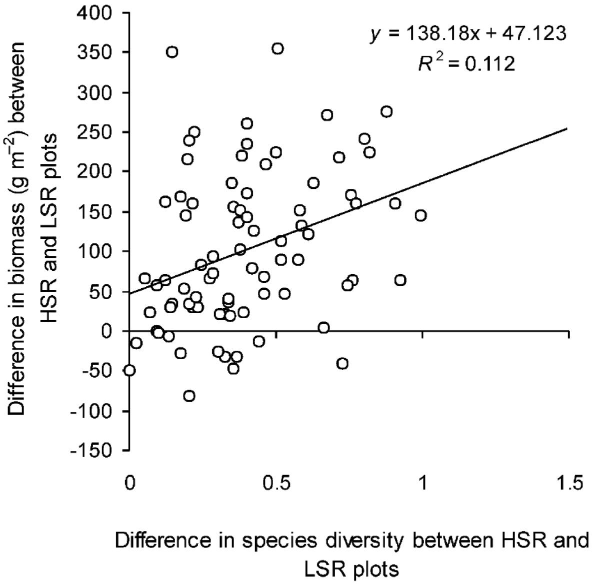

Figure 2. Difference in aboveground biomass between pairs of HSR and LSR plots in relation to difference in their species diversity. Difference between HSR and LSR plots was calculated as HSR – LSR. The relationship is significant at 0.002 level and follows linear trend (two outlier points are ignored that represented excessively high difference in biomass of 590 and 790 g between HSR and LSR plots).

vely). Multiple regression carried out on all the 178 plots, to observe the combined effect of species richness and growth form diversity on productivity, indicated a significant relationship ($F = 29.477$; $P < 0.001$). Across all the plots, correlations were significantly positive between species diversity and growth form diversity ($r = 0.776$; $P < 0.001$), and species diversity and species richness of each of the growth forms (TF, $r = 0.486$; SF, $r = 0.512$; CSF, $r = 0.765$; GS, $r = 0.332$; for all $P < 0.001$).

Data on aboveground biomass of 82 pairs of adjoining plots differing in species richness stress that species richness/species diversity was positively correlated with primary productivity in alpine grasslands of the Himalaya. There is evidence to indicate that species richness may contribute to primary productivity through proportionally greater niche occupancy and hence resource utilization.

There was greater aboveground biomass in plots of lower species richness in only 12 out of 82 pairs in which species richness differed. Among these, in 10 pairs the proportion of TF was greater, indicating that growth form, at least in some plots, can have an overriding influence. TF are reported to be particularly productive in the Himalayan alpine grasslands[25]. However, when we looked at the effect of presence of TF on biomass across all pairs of plots, the effect of species richness on productivity was more apparent than that of growth form. A pair-by-pair survey of growth form crown cover data indicates that the majority of HSR plots with higher biomass did not have a greater proportion of TF. Of the pairs of plots in which biomass was greater in plots of higher species richness (70 pairs), 30% had a greater proportion of TF. In brief, it is evident that though the contribution of a growth form to productivity was small compared to that of species richness, it cannot be absolutely negated. Since species diversity and crown cover of TF were negatively correlated ($r = –0.499$; $P < 0.001$), it is evident that when adjacent plots of natural communities are compared, the association between the presence of large and productive species (of TF) and high species richness is weak. It may be pointed out that in the Ecotron experiments, the supposed benefit to productivity associated with the greater biodiversity is attributable to the fact that the more diverse communities that were created contained larger and more productive species that were not included in experimental species assemblages of the less diverse communities[26].

The relative effects of species richness on productivity are the greatest at small to intermediate spatial scales, while at a regional scale where environmental heterogeneity is greater, effects of biological factors such as species diversity and individual species become less important[12]. Correlation between diversity and productivity at a regional scale is largely driven by non-biological environmental factors, such as soil fertility and climate[12]. Across all the 178 plots, productivity was significantly correlated with species richness as well as species diversity ($r = 0.508$, $P < 0.001$ and $r = 0.485$, $P < 0.001$ respectively). Multiple regression carried out on all the 178 plots to observe the combined effect of species richness and growth form diversity on productivity indicated a significant relationship ($F = 29.477$; $P < 0.001$).

Regression analysis suggests that difference in productivity between adjoining LSR and HSR plots tended to increase with increasing difference between these plots both in species richness and species diversity (Figure 2), emphasizing in another way the role played by species richness in increasing productivity. The regression relation between differences in aboveground production and species richness of 82 pairs of adjacent plots indicated that the difference of one species led to an average difference of 29 g m^{-2} yr^{-1} net production. The difference in diversity index also caused conspicuous difference in productivity. On an average a drop on 0.1 unit of diversity index suggests a reduction of about 23 g m^{-2} yr^{-1} in productivity.

The effects of diversity on productivity must come from interactions among individuals of different species[27], and in grasslands individual species interact within an area of 1–2 m^2. The significant difference in values of aboveground biomass in LSR and HSR plots suggests that there is the potential for increasing productivity of a site by realizing its potential alpha diversity. Compared to adjoining LSR plots, 17 HSR plots had aboveground biomass greater by >200 g m^{-2}. This indicates the importance of spatial patchiness in species diversity as a community character of grassland communities. Local patches that individuals and species form together make up a community[28,29]. Since these patches differ significantly in species richness[30], they can have a strong influence not only on internal community dynamics, but also on productivity and other ecosystem properties. In communities with stressful environment as alpine grasslands species, co-existence is more through niche differentiation and facilitation than antagonism and other such processes[31].

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