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Plant Species Diversity in the Kashmir Himalayan Grasslands Along an Elevational Gradient

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ABSTRACT

In view of paramount significance of species diversity to community structure and function, the present study was aimed at a comparative assessment of plant species richness, evenness, and aggregate diversity of the Kashmir Himalayan grasslands occurring at different elevations. Rarefaction method that takes into account nonlinearity of species and area combined with a fitting procedure, and non-parametric estimators were used to compute the expected number of species. All the estimators of species richness used in the present study performed reasonably well, but the ICE (Incidence-based Coverage Estimator) and Chao2 were particularly useful even at low sampling effort. Highest number of 26 species was recorded in the valley-plain grassland and lowest number of 17 species was recorded in the alpine grassland. Evenness and Shannon index of diversity, due to dominance of the grass *Themeda anathera*, in the sub-alpine grassland were lowest compared to the valley-plain and alpine grasslands. SHE analysis clearly indicated variable contribution of richness and evenness components to the aggregate measure of species diversity in these grasslands. Computation of the complementarity of species composition between the grasslands, analysed through use of the different indices, revealed more or less distinct species assemblages in the grasslands. We suggest that a separate but simultaneous measurement of diversity components using standardized sampling protocols and appropriate diversity estimators, as adopted in the present study, are obligatory for clear understanding and better interpretation of the patterns of plant diversity in the natural plant communities, such as grasslands.

Key Words: Rarefaction, Non-Parametric Species Richness Estimators, SHE Analysis, Species Diversity Indices.

INTRODUCTION

Spatial variability in vegetation and climate along elevational gradients is one of the fundamental features of a mountain ecosystem (Lomolino 2001). In fact, this gradient is complex in nature (Austrheim 2001) as several other environmental variables co-vary with it (Austin et al., 1996). Among the many biological attributes, components of species diversity are also known to be influenced by altitude (Austrheim 2002). For example, several investigators have reported decreasing trend in species richness with increasing elevation (Wolda 1987, Navarro 1992, Patterson et al. 1998), whereas others have reported hump-shaped relationship (Rahbek 1995, Fleishman et al. 1998, Odland and Birks 1999, Grytnes and Vetaas 2002). Though climatological, biological, geographical and historical factors have been implicated in varied species richness patterns along elevational gradients (Rahbek 1995, Rosenzweig 1995, Lomolino 2001), no universal explanation exists (Colwell and Hurtt 1994, Rahbek 1997). While the mechanisms that underlie such patterns are still being hotly-debated under broader framework of the biogeography and macroecology (Rhode 1992, Rosenzweig and Sandlin 1997, Brown 2001), quantifying plant species diversity is important, not only for basic comparisons among sites, but also for addressing the saturation of local communities colonized from regional source pools (Cornell 1999). Further, the need to document and understand patterns in species diversity is increasingly important as threats to biodiversity escalate (Sanders et al. 2003). Notwithstanding availability of several diversity indices (Magurran 2004), no single index fully captures the complex patterns of species richness and relative abundances (evenness) inherent in natural communities (Hurlbert 1971, Small and McCarthy 2002). Resultantly, little consensus has been reached as to how the diversity should be *best* measured and then *realistically* interpreted (Austin 1999). Given the suite of diversity measures and sampling protocols commonly used in biodiversity studies (Magurran 2004), an attempt is made in the present study to determine the choice of diversity estimators and sampling procedures ideal for the characterization of plant diversity in the Kashmir Himalayan grasslands that occur at different elevations and also to compare these grasslands in respect of species richness, evenness and community complementarity.

MATERIALS AND METHODS

Study Area

The present study was carried out in the Dachigam National Park area that represents the last abode of threatened Kashmir Stag (*Cervus elaphus hanglu*). The park is located 21 km north-east of Srinagar city in the state of Jammu and Kashmir, India and extends between 34^0 5' to 34^0 3' north latitudes, and 74^0 4' to 74^0 5' east longitudes. The park lies towards the southerly face of the Zanaskar mountain range of the Himalayas. It is roughly rectangular in shape with an area of 141 sq km. It is approximately 22.5 km in length and 8 km in breadth ranging in altitude from 1,600 meters to 4,400 meters above mean sea level (amsl). A sizeable portion of the park sustains grasslands which are used by the Kashmir Stag as its feeding grounds.

The present study was conducted on three grasslands lying at three different altitudes. The valley-plain grassland was at an elevation of 1,600 m (amsl). The sub-alpine grassland was in the Pahlipora area at an altitude of 2,500 m (amsl), while as the alpine grassland was in the Dugwan area of the National Park at an elevation of 3,400 m (amsl). The grassland sites chosen for the present study were protected from grazing for last 30 years. The valley-plain grasslands are located in the alluvial plain basin of the Kashmir valley; the sub-alpine grasslands occur in patches below timberline interspersed with coniferous forests and alpine grasslands (meadows) occur beyond the timberline.

Sampling Procedure

Angiosperm species richness, evenness and diversity in the three above described grasslands were investigated during summer (June-August). In each grassland, 30 quadrats (0.5 m^2) were randomly laid to record presence/absence of the species in each quadrat. In addition, abundance of species was also calculated after Curtis and Cottam (1956). In case of runners, each node was taken equivalent to an individual and in respect of other rhizomatous species each upright shoot was considered as an individual (Singh 1969). Community diversity was evaluated as: a) observed richness, which was quantified both as number of species accumulated versus sampling effort and as rarefied species richness; b) estimated total richness, calculated from a suite of non-parametric richness estimators; c) species evenness, using Hurlbert's probability of intraspecific encounter (PIE); d) Simpson's and Shannon's indices of diversity, to capture overall heterogeneity; and e) complementarity of communities, to quantify dissimilarity among communities with respect to species identities and abundances.

Computation of Rarefaction Curves

Individual-based rarefaction curves for the three grasslands were computed using mathematical expression based on combinatoric theory following Hurlbert (1971), Heck et al. (1975). It was used to calculate the number of species expected in a sub-sample of individuals selected at random from a larger sample.

$$E(S) = \sum_{i=1}^{s} \left\{ 1 - \left[\binom{N-N_i}{n} \Big/ \binom{N}{n} \right] \right\}$$

where, *E(S)* is the expected number of species in the rarefied sample,
n is the standardized sample,
N is the total number of individuals in the sample to be rarefied, and
N_i is the number of individuals in the i_{th} species in the sample to be rarefied, summed over all species counted.

The term $\binom{N}{n}$ is an important "combination" because it allows to calculate all the possible number of unique species combinations.

Rarefaction curves and 95% confidence intervals for the three sites were estimated using EcoSim7.0 (Gotelli and Entsminger 2003). Rarefied estimates of richness were calculated after 1000 iterations.

Species Richness Estimators

Statistical estimates of total species richness were calculated using the EstimateS, Version 7 (Colwell 2004). EstimateS uses curve fitting models to predict asymptotes of species accumulation curves and computes richness estimates based on a variety of non-parametric estimators and, in many cases, their associated standard deviations. Different estimators differ with respect to how they deal with rare species (Chazdon et al. 1998). Input data were formatted as species (rows) by samples (columns) abundance matrices. Individuals within a species were randomly assigned to samples, which removes patchiness due to temporal differences in abundance when the patchiness parameter is set to zero. Sample order was randomized with replacement and mean richness estimates were calculated after 100 iterations of the random sampling algorithm. Following species richness estimators were computed.

ICE: Incidence-based Coverage Estimator of species richness (Lee and Chao 1994)

$$S_{ice} = S_{freq} + \frac{S_{infr}}{C_{ice}} + \frac{Q_1}{C_{ice}}\gamma_{ice}^2$$

while the sample coverage estimate based on incidence data is:

$$C_{ice} = 1 - \frac{Q_1}{N_{infr}}$$

where

$$N_{infr} = \sum_{j=1}^{2} jQ_j$$

and the estimate of coefficient of variation of the Q_j's, is:

$$\gamma_{ice}^2 = \max\left[\frac{S_{infr}}{C_{ice}}\frac{m_{infr}}{(m_{infr}-1)}\frac{\sum_{j=1}^{2} j(j-1)Q_j}{(N_{infr})^2} - 1, 0\right]$$

Chao2: An incidence-based estimator of species richness (Chao 1987) and the full, bias-corrected formula is:

$$S_{Chao2} = S_{obs} + \frac{Q_1^2}{2(Q_2+1)} - \frac{Q_1 Q_2}{2(Q_2+1)^2}$$

The variance estimator that Estimate S used to compute standard deviation for Chao2 is:

$$\mathrm{var}(S_{Chao2}) = Q_2\left[\frac{G^4}{4} + G^3 + \frac{G^2}{2}\right]$$

Where $G = \frac{Q_1}{Q_2}$

Jacknife 1: First-order jacknife estimator of species richness (Burnham and Overton 1979, Heltshe and Forrester 1983)

$$S_{jack1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right)$$

Jacknife 2: Second-order jacknife estimator of species richness (Smith and Van Belle 1984)

$$S_{jack2} = S_{obs} + \left[\frac{Q_1(2m-3)}{m} - \frac{Q_2(m-2)^2}{m(m-1)}\right]$$

Bootstrap: Bootstrap estimator of species richness (Smith and Van Belle 1984)

$$S_{boot} = S_{obs} + \sum_{k=1}^{S_{obs}}(1-p_k)^m$$

Key to variables of the above mentioned nonparametric species richness estimators

S_{obs}	Total number of species observed in all quadrats
S_{freq}	Number of species occurring in > 10 quadrats
S_{infr}	Number of species occurring in ≤ 10 quadrats
Q_j	Number of species occurring in j number of quadrats
m	Total number of quadrats
m_{infr}	Number of quadrats having at least one S_{infr}
p_k	Proportion of quadrats containing species k
S_{obs}	Total number of species observed in all quadrats

Evenness

We compared evenness of the three grasslands using Hurlbert's probability of intraspecific encounter (PIE) which is the probability that two randomly sampled individuals from the community are two different species (Hurlbert 1971). PIE is calculated as:

$$PIE = \left(\frac{N}{N-1}\right)\left(1 - \sum_{i=1}^{s} p_i^2\right)$$

where, N is the total number of species in the assemblage, and p(i) represents the proportion of the entire sample represented by species i.

Unlike most other evenness indices, this metric has several advantages and was preferred because it is not influenced by sample size and number of species in a sample (Peet 1974, Ludwig and Reynolds 1988).

Species Diversity

Indices of diversity integrate both species richness and evenness into a single measure in an attempt to capture overall heterogeneity at a site. We calculated the Shannon-Wiener diversity index

$(H' = -\sum p_i \ln p_i$,

where p_i is the proportion of individuals of the *i*th species) using the software EstimateS, Version 7 (Colwell 2004). In order to assess independent yet simultaneous contributions of richness and evenness to community diversity, SHE analysis was carried out (Hayek and Buzas 1997, 1998). In SHE analysis, the relative contributions of richness and evenness to H' diversity are partitioned using the decomposition formula: $H' = \ln(S) + \ln(E)$. This decomposition equation is derived from the following conditions :(i) maximum H' diversity occurs when all species are equally distributed ($H'_{\text{Max}} = \ln(S)$), and (ii) E is related to H' by the equation $E = e^{H}/S$. Thus, the SHE decomposition formula, $H' = \ln(S) + \ln(E)$, indicates that H' diversity equals its maximum value, $\ln(S)$, less the amount of unevenness, $\ln(E)$ (subtracted because evenness ≤ 1 and $\ln(E)$ will be ≤ 0), in the sample. In this way, SHE analysis partitions H' diversity into richness and evenness components and allows an independent evaluation of their contributions to H'. Using SHE analysis, $\ln(S)$, $\ln(E)$, and H' values were calculated cumulatively, with the addition of each sample. Results were examined graphically to evaluate relationships among diversity measures. SHE analysis was also used to infer the species abundance distribution best representing each sample community, based on Hayek and Buzas (1997, 1998).

Simpson's (inverse) diversity index (1/D) was also calculated as it is one of the most robust and most easily interpreted, although no diversity index is considered a perfectly unified measure (Magurran 2004). Values for the Simpson index range from 1 to the number of species in the sample, with higher values indicating greater overall diversity (Krebs 1999).

Complementarity of community composition among sites was quantified using the Morisita-Horn index (Magurran 2004), in addition to classical indices of Jaccard, Sorensen and Bray-Curtis, which is generally recognized as the best overall estimate of similarity because it is less sensitive than others to changes in species richness and sample size (Magurran 2004). The Morisita-Horn index is computed as:

$$MHS_{ij} = \sum_{k=1}^{S} \left[x_{ik} x_{jk} / \left(d_i + d_j\right) N_i N_j \right]$$

where, S = Number of species, X_{ik} = Abundance of species *k* in sample *I*, N_i = Total individuals in sample *i*, and

$$d_i = \sum_{k=1}^{S} x_{ik}^{2} / N_i^2$$

However, no measure of similarity is free of limitations and the Morisita-Horn index is sensitive to changes in the abundance of the most common species (Magurran 2004).

RESULTS

Floristic Composition

The highest number of 26 plant species was recorded in the valley-plain grassland with dominance of grasses, such as *Bromus japonicus, Bothriochloa ischaemum, Cynodon dactylon* and *Poa pratensis* while *Themeda anathera* was the most dominant among the 22 species inhabiting the sub-alpine grassland. Lowest number of 17 plant species was recorded in the alpine grassland with the dominance of *Cynodon dactylon* (Table 1). While the valley-plain grassland shared 2 and 3 species with sub-alpine and alpine grasslands respectively; the sub-alpine grassland shared no plant species with the alpine one.

Table 1. Abundance (ind.0.5m^{-2}) of different species growing in the three grasslands.

Valley plain	Abundance	Subalpine	Abundance	Alpine	Abundance
Bromus japonicus	67.69	*Themeda anathera*	106.1	*Cynodon dactylon*	34.04
Bothriochloa ischaemum	61.58	*Arthraxon prionoids*	8.43	*Myosotis caespitosa*	18.13
Cynodon dactylon	56.4	*Androsace rotundifolia*	6.5	*Potentilla argyrophylla*	15.13
Poa pratensis	46.19	*Silene vulgaris*	5.7	*Trifolium repens*	12.13
Convolvulus arvensis	19.32	*Medicago polymorpha*	4.79	*Poa pratensis*	11.5
Arenaria serpyllifolia	15.73	*Stachys seriaca*	3.76	*Iris ensata*	9.95
Plantago lanceolata	13.81	*Clinopodium vulgare*	3.55	*Trifolium pratense*	9.35
Oxalis corniculata	12.77	*Nepeta laevigata*	3.33	*Thymus serphyllum*	5.6
Scandix pectinveneris	10.47	*Lespedeza elegans*	3.29	*Hackelia uncinata*	5.12
Vernonica persica	9.68	*Solidago virgaurea*	3.0	*Duchesnea indica*	4.85
Lespedeza cuneata	9.18	*Daucus carota*	2.5	*Arenaria griffithii*	4.69
Crepis sancta	7.61	*Artemesia absinthium*	2.45	*Galium aparine*	3.75
Lotus corniculatus	6.27	*Crepis kashmirica*	2.21	*Bistorta amplexicaule*	3.19
Trifolium pratense	5.95	*Indigofera heterantha*	2.2	*Polygonum affine*	2.84
Vicia sativa	5.17	*Euphorbia wallichii*	2.0	*Artemesia annua*	2.55
Euphorbia helioscopia	5.08	*Prunella vulgaris*	1.92	*Achillea millefolium*	2.15
Medicago polymorpha	4.32	*Lespedeza cuneata*	1.61	*Geranium pratense*	1.85
Erodium cicutarium	3.86	*Sium latijugum*	1.5		
Capsella bursapastoris	3.8	*Carpesium cernuum*	1.45		
Ranunculus arvensis	3.45	*Hypericum perforatum*	1.44		
Poa bulbosa	2.89	*Artemesia scoparia*	1.33		
Poa annua	2.8	*Myriactus wallichi*	1.29		
Lithospermum arvense	2.64				
Sisymbrium loesellii	2.43				
Taraxacum officinalis	2.07				
Tragopogon kashmirianus	1.6				

Rarefaction

The expected numbers of species in the three grasslands plotted against number of individuals on the x axis is shown in Figure 1. The plots provide a measure of species diversity which is robust to sample size effects, permitting comparison between communities. Thus, valley-plain grassland shows high observed species richness compared to sub-alpine and alpine grasslands and the same is not a function of number of individuals sampled in the grasslands. Even if more individuals would have been sampled the number of species in the investigated grasslands would have remained same.

Species Diversity Patterns

Richness

The observed number of species in any sample of individuals from a community underestimates the true number of species present. In statistical terms, observed species richness (S_{obs}) is a biased estimator of true richness for the assemblage sampled. Thus, a critical element of evaluating the performance of a species rich-

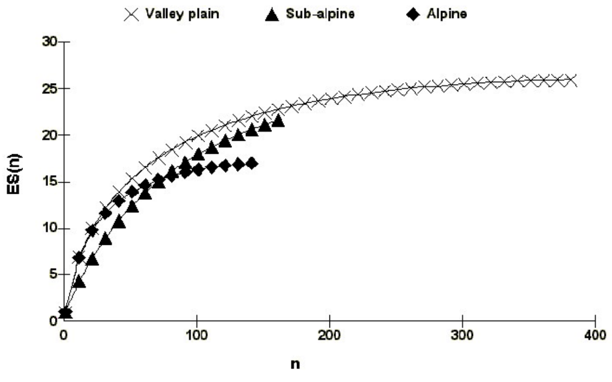

Figure 1. Rarefaction curves of the three grasslands

ness estimator is to assess how the estimator behaves as a function of the sample size. In the three grasslands studied during the present investigation (Figure 3), species accumulation curves computed using the Incidence Coverage Estimator (ICE) and Chao2 estimator showed that the number of species approach an asymptote only after sampling of 5 quadrats. Other species richness estimators also performed well.

Evenness

Evenness, or the relative distribution of individuals among species, was higher in valley-plain and alpine grasslands (0.90 and 0.89, respectively) and lowest (0.60) in sub-alpine grassland (Table 2).

Table 2. Diversity indices of the three grasslands.

Index	Grasslands		
	Valley-plain	Sub-alpine	Alpine
Shannon-Wiener (H)	2.63	1.75	2.50
Simpson's diversity (1/D)	9.67	2.52	9.38
Hurlbert's PIE	0.90	0.60	0.89

Diversity Indices

Data on various indices computed for the three grasslands are presented in Table 2. Shannon-Wiener index was highest (2.63) in valley-plain grassland and lowest (1.75) in sub-alpine grassland. Similar pattern was obtained when Simpson's diversity index (1/D) was computed for the grasslands under study.

SHE Analysis

SHE analysis (Figure 2) show significant differences in H' diversity patterns among the three grasslands with highest in the valley-plain grassland and lowest in the sub-alpine grassland. Cumulative ln(E)/ln(S) remained relatively constant in all the three grasslands.

Comparison of Grasslands

Data on the four computed indices of similarity based on shared species is presented in Table 3. All the indices reveal similar pattern of greater similarity between valley-plain and alpine grasslands, than between either of these grasslands and the sub-alpine grassland.

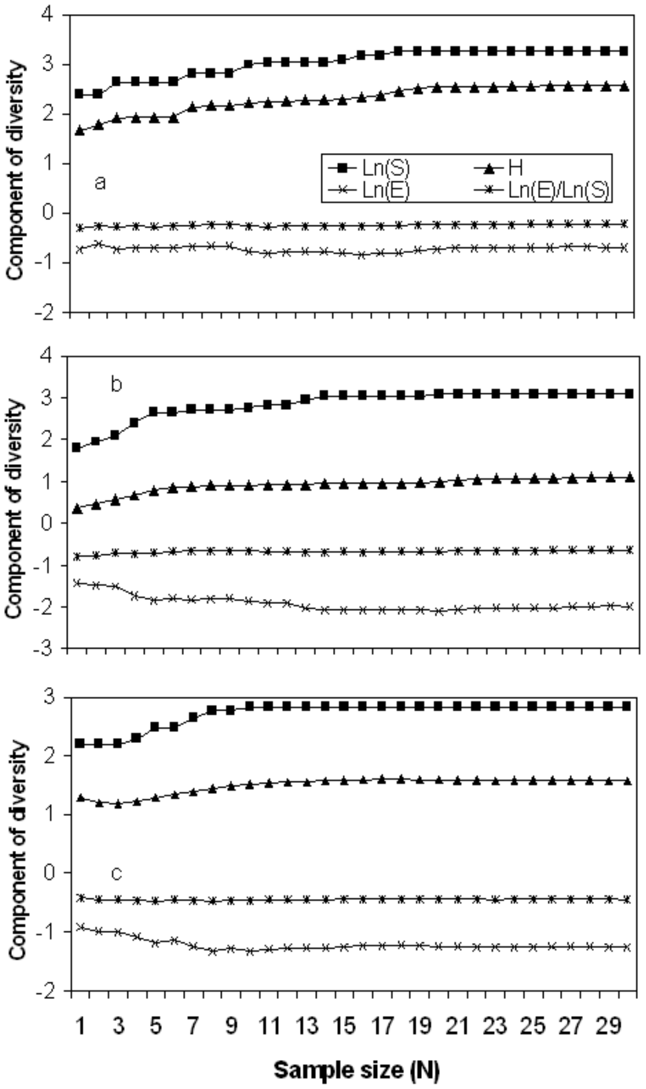

Figure 2. SHE analysis of Valley plain (a), sub-alpine (b) and alpine (c) grasslands

DISCUSSION

Our study of the three grasslands shows strong patterns of spatial variability, with significant changes in plant species composition and diversity relative to location of the grassland. The valley-plain grassland shares just two (*Medicago polymorpha* and *Lespedeza cuneata*) and three (*Cynodon dactylon, Poa pratensis* and *Trifolium pratense*) plant species with the sub-alpine and alpine grasslands, respectively. This very limited species compositional complementarity highlights the elevational vegetation

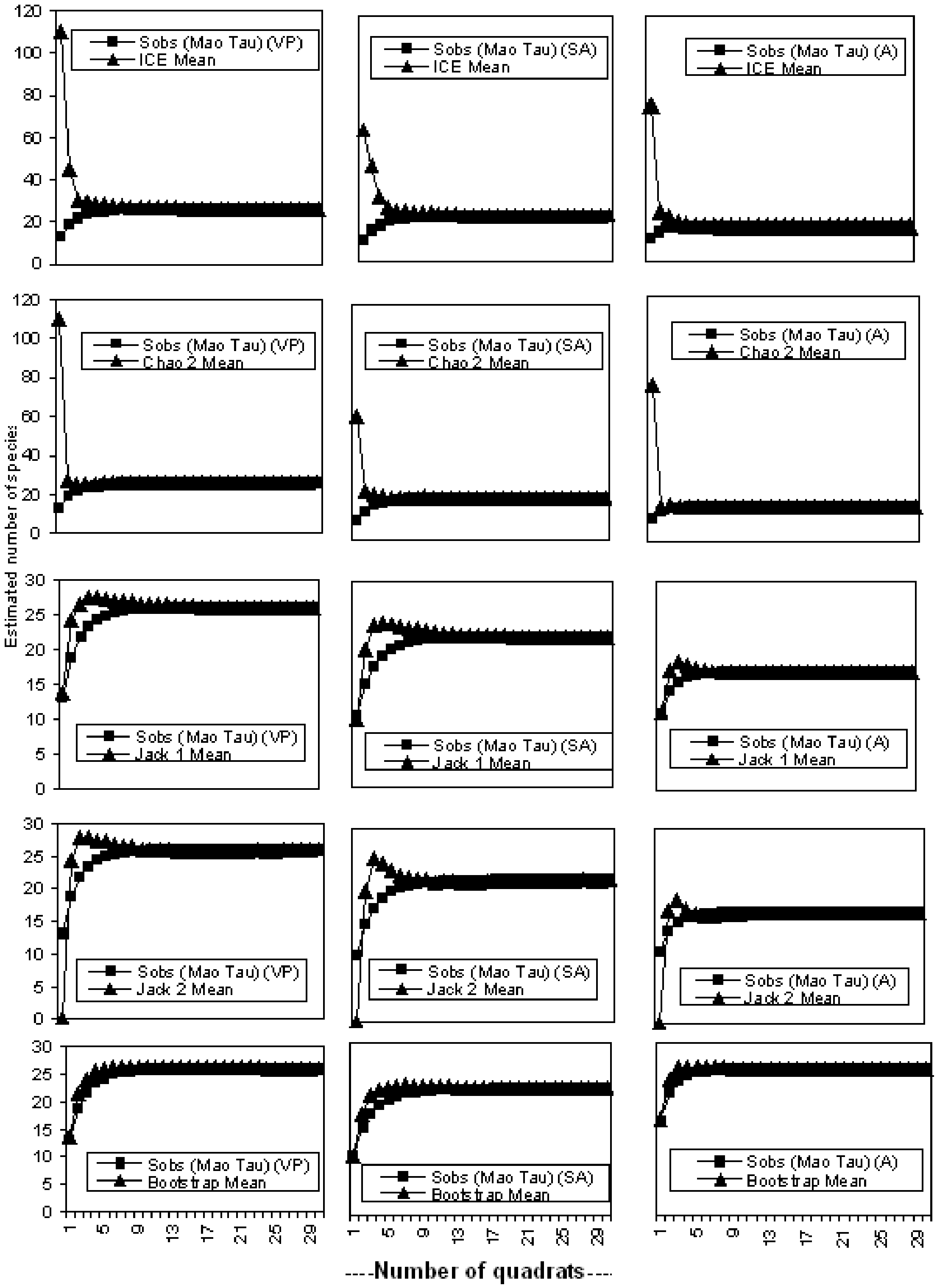

Figure 3. Performance of different species richness estimators for the valley-plain (VP), sub-alpine (SA) and alpine (A) grasslands

Table 3. Similarity indices of the three grasslands on the basis of shared species.

Grassland (1)	Grassland (2)	Similarity indices			
		Morisita-Horn	Jaccard	Sorensen	Bray-Curtis
Valley-plain	Sub-alpine	0.002	0.043	0.083	0.020
Valley-plain	Alpine	0.420	0.075	0.139	0.194
Sub-alpine	Alpine	0.000	0.000	0.000	0.000

zonation in Kashmir Himalaya. Special combination of ecological conditions may be deterministic factor shaping this observed pattern (Lomolino 2001, Brown 2001). In fact, any factor that limits species dominance may promote the coexistence of specialized species at the same time, thereby increasing overall diversity (Sánchez-González and López-Mata 2005). It holds particularly true for sub-alpine grassland where species diversity is low due to predominance of *Themeda anathera*. In addition, geological history could be another reason for lack of floristic similarity between sub-alpine and alpine grasslands as the former exist as a result of patch disturbances (fire, grazing, etc.), while as the latter are due to harsh climatic conditions prevalent in alpines. Lower levels of species richness in the alpine grassland can be explained as a function of ecophysiological pressures, such as low temperature, low productivity and shorter growing season (Rahbek 1995, Vetaas and Grytnes 2002). It is also likely that the harsh environmental conditions prevalent in the alpine habitats also contribute to limited species overlap between it and the low elevational grasslands as only the specialized plants that tolerate severe conditions occur in the alpine grassland. Few species that are shared by the three grasslands have a wide distribution range in the region.

Though the observed species richness is heavily dependent on the number and size of samples with an increasing numbers of species generally found with increasing sampling intensity (Small and McCarthy 2002), yet the rarefaction analysis carried out during the present study did not reveal any such increase thus suggesting that the number and size of quadrats laid in the grasslands to characterize the diversity patterns are sufficient (Figure 1). Species richness estimators used to approximate the actual number of species in the present study also indicate that 30 quadrats of 0.5 m^{-2} adequately captured the actual total number of species that exist in these grasslands. Comparison of the four non-parametric estimators of species richness reveals that ICE and Chao estimators provide an earlier bias reduction than Jacknife estimators and similar results have been obtained by Clémentine et al. (1998). The requirement of only presence/absence data for computation and insensitivity to sample size are the attractive features of these estimators and for many applications, it is believed that ICE is likely to prove a robust, multipurpose species richness estimator (Chazdon et al. 1998).

In our study, simultaneous plotting of evenness and richness data showed that the former did not vary significantly with increasing number of samples in valley-plain grassland but the latter registered an increase (Figure 2a). On the contrary, in the sub-alpine (Figure 2b) and alpine grasslands (Figure 2c) decrease in evenness was accompanied by moderate increase in richness. This decrease in evenness suggests that added species tend to be relatively uncommon or rare and such findings concur with those of Wilson et al. (1999) who found decreases in evenness with increasing spatial grain in herbaceous communities of New Zealand. In their analysis, Wilson et al. (1999) noted that species richness can only increase or remain constant with increasing spatial scale or sample size, whereas evenness may increase or decrease. Decrease in evenness with increase in grain size is supposed to be general feature of plant species abundance distribution and of vegetation response to environmental micro-heterogeneity (Wilson et al. 1999, Wang et al. 2002). While decrease in the evenness is noticeable in sub-alpine and alpine grasslands, it remained more less constant in the valley-plain grassland (Figure 2). In addition, constant cumulative ln(E)/ln(S) in all the grasslands suggests the data to be best fit by log normal distribution. However, constant H' indicates a log series distribution (Small and McCarthy 2002). More or less constant H' and ln(E)/ln(S) with increasing numbers of samples in sub-alpine and alpine grasslands indicates that the two grasslands may exhibit characteristics intermediate between log normal and log series distributions, which is expected of communities with a small number of abundant species (Magurran 2004). However, it needs to be emphasized that SHE analysis is able to discriminate only three species-abundance distributions, though many others have been fit to plant community data (Wilson 1991, Ulrich and Ollik 2005).

In conclusion, the present study clearly indicates that the location and sampling strategy are critical considerations in the assessment of richness, evenness, and diversity patterns in spatially variable communities, such as the grasslands occurring at different elevations. Based on the results of this and other studies, evaluation of both alpha- (within-habitat) and beta- (between-habitat) diversity at varying spatial scales seems essential for a comprehensive assessment of community diversity patterns. Besides, the present study also highlights that communities containing relatively small proportions of rare species may require smaller number and size of samples. Hence the understanding and assessment of natural patterns of plant diversity along elevation gradients, critical to management of such ecosystems, requires adequate sampling, 'right' choice of sampling protocol and the appropriate diversity estimator.

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