Vegetation-environment relationships in a South Asian tropical montane grassland ecosystem: restoration implications

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Abstract: We studied the role of environmental factors driving species distributions, community structure, and ecosystem properties in an endangered montane grassland ecosystem in the Nilgiris, Western Ghats. We examined plant composition, ecosystem properties and environmental factors in one of the largest grassland sites in the Nilgiris. Ordination analysis showed that environmental gradients, mainly slope and aspect, controlled the distribution of the dominant plants. Some of the abundant species showed mutually exclusive distributional patterns along gradients, and some species exhibited distinct association with other species suggesting similar environmental tolerances. Classification analysis identified four community types, but ordination revealed that these communities formed a continuum along environmental gradients. Slope and soil depth strongly influenced aboveground biomass while species composition was influenced by the aspect. This study provides baseline data on grassland communities in the Nilgiris, and the results suggest that restoration activities should factor in environmental preferences of the plants as well as natural species associations.

Resumen: Estudámos o papel dos fatores ambientais influenciando a distribuição das espécies, a estrutura da comunidade, e as propriedades do ecossistema num ecossistema de pastagens montanhosas ameaçadas de extinção no Nilgiris, Gates Ocidentais. Examinámos a composição de plantas, as propriedades do ecossistema e os fatores ambientais numa das maiores estações de pastagem em Nilgiris. A análise de ordenação mostrou que os gradientes ambientais, principalmente declive e o aspecto, controlavam a distribuição das plantas dominantes. Algumas das espécies abundantes apresentaram padrões de distribuição mutuamente exclusivos ao longo dos gradientes, e algumas espécies exibiram uma associação distinta com outras espécies, sugerindo tolerâncias ambientais similares. Análise de classificação identificou quatro tipos de comunidades, se bem que a ordenação revelou que essas comunidades formavam um continuum ao longo dos gradientes ambientais. O declive e a profundidade do solo influenciaram fortemente a biomassa aérea, enquanto que a composição de espécies foi influenciada pelo aspecto. Este estudo fornece dados de base sobre as comunidades de pastagem em Nilgiris, e os resultados sugerem que as atividades de recuperação deve levar em consideração as preferências ambientais das plantas, bem como as associações naturais das espécies.

Resumo: Estudiamos el papel de los factores ambientales que determinan la distribución de especies, la estructura de la comunidad y las propiedades ecosistémicas en un ecosistema

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amenazado de pastizales montanos en los Nilgiris, Ghats Occidentales. Se examinó la composición de plantas, las propiedades de los ecosistemas y los factores ambientales en uno de los sitios más grandes de pastizal delosNilgiris. Un análisis de ordenación mostró que los gradientes ambientales, principalmente de pendiente y orientación, controlan la distribución de las plantas dominantes. Algunas de las especies abundantes mostraron patrones mutuamente excluyentes de distribución a lo largo de los gradientes, y algunas especies exhibieron asociacionesclaras con otras especies, lo que sugiere que tienen tolerancias ambientales similares. Un análisis de clasificación identificó cuatro tipos de comunidades, pero la ordenación mostró que estas comunidades forman un continuo a lo largo de los gradientes ambientales. La pendiente y la profundidad del suelo influyeron fuertemente la biomasa aérea, mientras que la composición de especies estuvo influenciada por la orientación. Este estudio proporciona datos de referencia sobre las comunidades de pastizal en losNilgiris, y los resultados sugieren que las actividades de restauración deben tener en cuenta las preferencias ambientales de las plantas, así como asociaciones naturales de especies.

Introduction

Whittaker's (1975) community continuum model presents plant species in a defined area as widely overlapping species response curves along environmental gradients. The community continuum concept contrasts with the community-unit model of Clements (1936), which stated that a plant community is a distinct unit consisting of coevolved species. The community-unit idea is regaining value as evidence mounts for positive interactions at finer spatial scales (Callaway 2007). Therefore, the mechanistic understanding of both the effects of environmental gradients, and species interactions in the assembly of reference communities is key to developing a sound restoration plan (Suding & Hobbs 2009).

The montane ecosystem of the Nilgiris in southern India are known for their high degree of diversity and endemicity across plant and animal taxa (Gurukula Botanical Sanctuary 2005; Mohandass & Davidar 2009). The Nilgiris is an important region in the Western Ghats, which is one among the top 8 of the 34 global biodiversity hotspots (Myers *et al.* 2000). A majority of the Nilgiris landscape, originally under native grass cover, has been urbanized, farmed, submerged by large reservoirs, or converted to commercial plantations of tea and exotic trees, *viz.*, Black wattle (*Acacia mearnsii* De Wild.), Blue gum (*Eucalyptus globulus* Labill.) and pine (*Pinus patula* Schltdl. & Cham.). The remaining grasslands are mainly threatened by local disturbance events such as grazing (Puyravaud *et al.* 2012), and by natural expansion of these plantation species and other introduced woody exotic shrubs such as Scotch broom (*Cytisus scoparius* (L.) Link) and Gorse (*Ulex europaeus* L.) (Srinivasan *et al.* 2007). Loss of native plant diversity following Scotch broom invasion has been documented (Srinivasan 2012; Srinivasan *et al.* 2007), and the loss of grassland species is apparent even under sparse stands of commercial plantations. Conversion of grassland to tree plantations has been widely shown to reduce streamflow volume, and negatively impact streamflow rate and duration (Dye & Jarmain 2004; Jackson *et al.* 2005; Zhang *et al.* 2012), besides increasing soil salinity and acidity (Jackson *et al.* 2005; Jeeva & Ramakrishnan 1997). Restoring the grasslands will contribute towards maintenance of ecosystem services in the region.

The aim of this research was to create a systematic quantitative inventory of a montane grassland in the Nilgiris and to highlight the scope of restoration planning based on vegetation-environmental gradient relationships. Thus, one of the objectives of our study is to describe species distributions along easily measurable environmental gradients. We tested whether the community composition can be explained by multiple environmental gradients. Further we examined how abundance of the common species varied with specific environmental gradients. Since the

ultimate goal is to restore communities, it is ideal to restore plants along with their natural neighbours. This is in the context of increasing evidence for facilitative associations in natural communities (Brooker *et al.* 2008; Callaway 2007). Thus, we used numerical classification to identify community types and assessed their environmental preferences. We use the phrase 'community type' to refer to a group of vegetation samples that are compositionally alike. Finally, we examined the role of environmental factors in driving community structure i.e. species richness and diversity, and an ecosystem property i.e. aboveground biomass.

Materials and methods

Study area

The Nilgiri Hills, an integral part of the Western Ghats of peninsular India, is located between 11° 10′ - 10° 30′ N and 76° 25′ -77° 00′ E (Fig. 1). The altitude in the upper areas of the Nilgiris range from 1800 to 2600 m asl. April is the warmest month with a mean maximum temperature of 25 °C, and January is the coolest month with a mean maximum temperature of 5 °C. Frost occurs at night on several days from November to March. The Nilgiris experiences two wet periods; the first receiving rain from the southwest monsoon between June and September, and the second from the northeast monsoon between October and December. The rainfall in the western regions of the plateau (including our study site) ranges from approximately 2500 mm to 5100 mm, (see Caner *et al.* 2007 for detailed meteorological information). The bedrock of the Nilgiris consists of Precambrian rocks, chiefly gneisses, charnockites and schist. The soils are classified as non-allophanicandisols (Caner *et al.* 2000).

Vegetation in the upper Nilgiris consists of patches of stunted tropical evergreen forests (locally called *shola*) surrounded by grasslands (Fig. 2a). According to recent vegetation nomenclature (Ashton 2003; Whitmore 1984), the *sholas* are categorized as 'tropical upper montane rain forest' and the surrounding grasslands as 'montane grasslands'. The grasslands are mainly composed of perennial C4 tussock grasses. The origin of these mesic grasslands was long believed to be due to anthropogenic fires and livestock grazing (see Thomas & Palmer 2007), however, more recently, it has been shown that the grasslands were present in the Nilgiris for at least 40,000 years BP (Caner *et al.* 2007; Vasanthy 1988), long before human occupation of this landscape. The current accepted

view is that the strong monsoon winds and frost during winter preclude expansion of the trees into the open slopes (see Caner *et al.* 2007; Thomas & Palmer 2007).

Sampling was done in November 2008 (during the second wet period of the year). This was nearly 21 months after a wildfire had swept through parts of the reserve; hence the sampled vegetation was the regrowth after the fire. A parallel study at the site showed that there were no notable differences in grassland community structure and composition between burned and unburned grasslands (Srinivasan 2012). This suggests that the ecosystem had recovered appreciably at the time of the survey.

Vegetation sampling

The vegetation was sampled in eighty-one 6 m^2 plots in 27 grassland sites spread across an area of nearly 3 km^2 in the Lakkadi region of the Nilgiris South Division Reserve Forest. This was the largest representative grassland site in the Nilgiris where we were permitted to sample.While large tracts of this grassland were covered by exotic woody plants (Fig. 2b), their distribution was patchy; hence uninvaded grassland patches were available for sampling. We defined a site as a visually homogenous grassy slope which was at least 30 m wide. Rocky patches, stream and *shola* edges, and marshy habitats were not sampled. The visual appearance of these grassy patches, lend themselves to colloquial naming based on plant height: short, mixed (a mix of short and tall bunch grasses), tall and lush (dense and homogenous) communities. Each of these assemblages is readily distinguishable from the others. This was the very approach adopted by earlier workers (Blasco 1970; Gupte *et al.* 1967; Gurukula Botanical Sanctuary 2005; Shankaranarayan 1958). We identified sites along nine transects, which were somewhat equally separated, to cover the study area. Each site was at least 100 m away from the next closest site, except for two instances (about 75 and 90 m apart). Within each site, three 6 m^2 plots were located. At each plot, community composition was sampled in six contiguous non-overlapping 1 m^2 quadrats. A 1m x 1m gridded-frame (divided into 100 units of equal size) was placed on the ground over the herbaceous vegetation to estimate the relative abundance of plant species in each quadrat. The abundance estimate of each species was arrived at by counting the number of units occupied by each species. This generated a list of plants with their percent cover for each plot, which

Fig. 1. (a) Location of the study area (the Nilgiris) in south India. (b) Spatial distribution of the sampling plots at the study sites in the Nilgiris South Division Reserve Forest.

we call a community sample. Plants were identified to the species level using a regional Flora (Fyson 1915); the same was used as a reference for botanical authorities and nomenclature.

Plant height was measured with a meter rule at 10 points uniformly distributed within each plot; at each point the height of the tallest clump was measured and averaged across the plot. The above-ground biomass was measured in each plot by clipping two -0.1 × 1 m strips of vegetation to the ground. Clipped biomass was sorted into

graminoids and forbs, and weighed after oven drying at 60 °C for 72 hours.

The following environmental variables were recorded at each plot. Slope inclination was measured using a clinometer. Soil depth was measured at 10 random points in each plot by gently pushing a 2 mm metal probe into the ground until no further easy penetration was possible. Elevation was recorded using a Trimble Geo Explorer GPS unit; the values were confirmed by plotting the coordinates on a Survey of India

Fig. 2. Upper panel (a): Pristine *shola*-grasslands in Mukurthi National Park, the Nilgiris. *Shola* is the local word for stunted tropical montane forest. Lower panel (b): Invaded *shola*-grasslands in the foreground, dense plantation of black wattle and blue gum, reservoirs and intensively farmed slopes in the far ground.

topographic map. The elevation of the sampled sites ranged from 2286 to 2380 m asl. Aspect was recorded using a compass. Aspect was used to create a proxy variable called the heat load index (equation 1; McCune & Keon 2002). This rescales aspect to a scale of 0 to 1, corresponding to the coolest (northeast) and warmest (southwest) slopes in the northern hemisphere, respectively. However, this index does not factor in the slope angle. Steeper slopes facing the direction of the incident radiation intercept more radiation than gentler slopes (Bennie *et al.* 2008). We applied a correction to the heat load index by multiplying equation 1 by the sine of the slope angle ϕ, producing the adjusted heat load index (equation 2).

Heat load index = $[1 - \cos(\theta - 45)]/2$, where θ is the aspect in degrees   ...1

Adjusted heat load index = $\sin(\phi) * [1 - \cos(\theta - 45)]/2$ ...2

Data analysis

We used Canonical Correspondence Analysis (CCA) to test for the relationships between grassland plant community composition and the measured environmental variables: slope, soil depth, elevation, northness ($\cos(\theta)$, where θ is the aspect in degrees) and eastness ($\sin(\theta)$). The correlation coefficients of the species-environment relationship along with the CCA diagrams allows the assessment of the individual, as well as combined effect of environmental factors, on species, community samples, or both. CANOCO v. 4.5 (ter Braak & Smilauer 2002) was used to run the CCA. With the exception of downweighting rare species, we used the default settings. Monte Carlo permutation test with 499 permutations was used to test for the significance of the species-environment relationship. Biplots of species and environmental vectors were created to understand the environmental basis for the species distribution, and triplots were used to visualize classified community samples in the species-environment space. To improve clarity, low frequency species were not shown in the diagram by adjusting the species weight range in Cano Draw v. 4.0 (Smilauer 1999-2002), a supplementary graphing program with CANOCO. Two-way indicator species analysis (TWINSPAN, Hill 1979) based on a divisive clustering algorithm was used to group community samples that were compositionally alike into community types. In the TWINSPAN software (Win TWINS, Hill & Smilauer 2005) the cut levels (to set abundance scales) were adjusted to 0, 2, 4,

8, 16, 24, and 36 to better suit the abundance range in our data. Species that had five or fewer occurrences were excluded from the analysis. A chi-square test was used to test if the number of community samples identified by TWINSPAN for each of the community types was significantly different from the number identified by visual classification in the field; this will indicate whether our visual classification came close to the TWINSPAN classification. A non-parametric Kruskal-Wallis ANOVA was used to test for differences in cover of the dominant grasses between the classified communities because of non-occurrences of species in several samples. Parametric one-way ANOVA was used to test for differences in plant community structure (species richness, diversity, and evenness) and ecosystem properties (plant height and above ground biomass of graminoids and forbs) between community types. The data for the following variables were transformed to meet the assumptions of parametric statistics: plant height (log 10), Shannon index (cubic), graminoid biomass (square root), forb biomass (log 10 (forb biomass +1)).

Regression analysis was used to illustrate species response curves along environmental gradients *viz.*, adjusted heat load index, slope and soil depth, to demonstrate the nature and magnitude of the response of the most abundant species to environmental factors. Slope and soil depth were considered to be independent factors as they were not significantly correlated ($r = -0.183$, $P = 0.102$). PROC REG (SAS v. 9.2) was used to determine the appropriate fit for the response curves.

The adjusted heat load index, which was used in regression analyses of individual species with the environment, was not used as an environmental variable in the CCA as northness, eastness and slope were individually used. These variables have ecological relevance besides serving as heat load indices. Including both the heat load and aspect would have confounded the results due to variance inflation, which occurs when mutually correlated variables are input.

Multiple regressions, with step-wise backwards elimination, were used in SAS v. 9.2 to examine the strength of environmental factors as drivers of community and ecosystem processes. The dependent variables-species richness, Shannon diversity, total plant biomass, graminoid biomass and forb biomass-were each regressed on the same environmental variables included in the CCA.

Results

Seventy-seven herbaceous vascular plant species were recorded in the sampled area; of these, 76 species represented 29 angiosperm families. *Pteridium aquilinum* (L.) Kuhn was the only fern recorded. *Dichanthium polyptychum* A. Camus, *Themeda tremula* Hack., *Ischaemum indicum* (Houtt.) Merr. and *Eulalia phaeothrix* Kuntze were the most abundant grasses, and *Hypochaeris glabra* L., *Anaphalis leptophylla* DC. and *Swertia corymbosa* Wight ex Griseb. the most abundant forbs (Appendix Table 1). Of the 77 species recorded, 56 were forbs; however, they represented only 3.4 % of the total aboveground biomass.
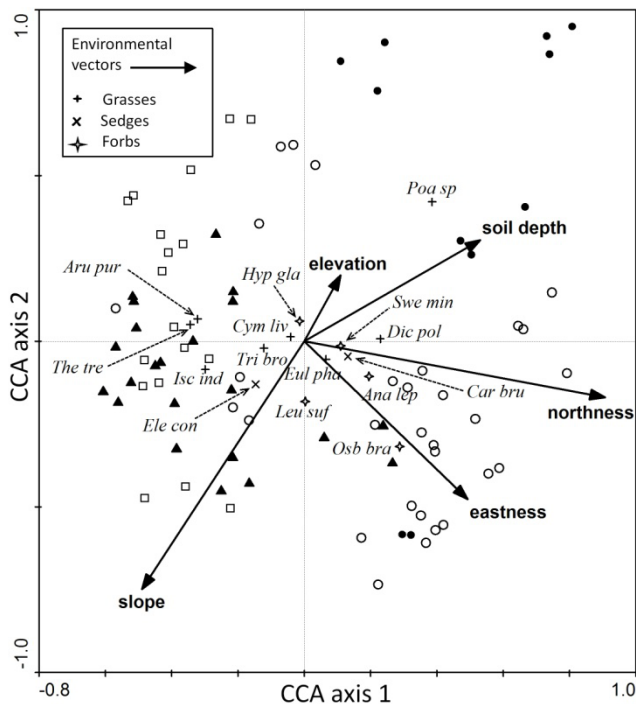
Fig. 3. CCA ordination triplot of 15 important plant speciesin the Nilgiris grasslands and the 81 sampled plots distributed and environmental variables. Species are represented by first three letters of the genus and species: *Anaphalis leptophylla, Arundinella purpurea, Carex brunnea, Cymbopogon lividus, Dichanthium polyptychum, Eleocharis congesta, Eulalia phaeothrix, Hypochaeris glabra, Ischaemum indicum, Leucas suffruticosa, Osbeckia - brachystemon, Poa* sp., *Swertia corymbosa, Themeda tremula, Tripogon bromoides*. The plots are classified into the four communities *viz.*, short (open squares), mixed (filled triangles), tall (open circles), and lush (filled circles).

Ordination of species and environment

The CCA ordination significantly explained 34.8 % of the total inertia in the species environmental matrix (Monte Carlo test: $F = 8.257$, $P = 0.002$). The first and second CCA axes accounted for 29.7 % and 2.6 % of the variation in the dataset respectively. Slope, northness, eastness and soil depth (in decreasing order of importance) were the prominent variables in determining species composition as indicated by the length of the respective environmental vectors (Fig. 3). The range of variation in elevation was low among the sampled sites; hence elevation was not a major driver of species composition in this dataset. Northness and slope were the most important in determining species composition patterns along the CCA axes 1 and 2 respectively, as indicated by the intraset correlations (Table 1). The intraset correlations are a measure of the strength of the association between community composition and environmental variables, when

Table 1. Intraset correlations of environmental variables with the first two axes of canonical correspondence analysis (CCA); see Data Analysis section and ter Braak 1986 for explanation of the analytical terms.

Environmental variables	Correlation coefficients	
	Axis 1	Axis 2
Elevation (m)	0.1096	0.1982
Soil depth (cm)	0.5307	0.3049
Northness[1]	0.9068	-0.1697
Eastness[2]	0.4923	-0.4775
Slope (in°)	-0.4893	-0.7489

[1]Northness = cos(θ)
[2]Eastness= sin(θ), where θ is the aspect in degrees

the environmental variables covary with each other (ter Braak 1986). But it must be noted that though slope has a high intraset correlation on the second CCA axis, the inertia explained by this axis is much lower compared to the first, and so its strength in structuring species composition is not necessarily the highest. *D. polyptychum* and *T. tremula* were the two most abundant grasses that were clearly discriminated by aspect (Fig. 3). *D. polyptychum* had a high preference for northern facing slopes while *T. tremula* seemed to prefer the opposite aspects (this can be inferred by extending the northness vector in the opposite direction). Similarly, the environmental affinities of the

different plotted species can be deciphered. For example, *Poa gamblei* Bor was most abundant in sites with deeper soil and less slope, while the opposite conditions were more conducive to *Eleocharis congesta* D. Don and *I. indicum*. Species distributed near the origin of the graph (e.g. *Cymbopogon lividus* (Thwaites) Willis, *H. glabra*, *S. corymbosa*, *E. phaeothrix*) have less specific environmental affinities.

Species responses to environmental gradients

Clear patterns of species distributions in response to environmental gradients were observed (Figs. 4 - 6). Some species co-occurred along the gradients, while others were negatively associated with each other. The abundance of the grasses *D. polyptychum* and *E. phaeothrix* and the forb *A. leptophylla* were negatively related to the heat load, while the grasses *T. tremula*, *I. indicum* and *Arundinella purpurea* Hochst. ex Steud. and the forb *H. glabra* responded positively (Table 2, Fig. 4). The response curves of these two groups in relation to heat load seem almost perfectly complimentary and compensatory. The cover of *I. indicum* was depressed at the values of the environmental gradient that coincided with intermediate abundances of *D. polyptychum* and *T. tremula* (Fig. 4a). Similarly, the concurrent increase and decrease in the cover of *H. glabra* and *S. corymbosa* closely tracked the responses of *I. indicum* and *A. purpurea*, but in a compensatory manner (Fig. 4 a,b).

Again, the decline in the abundance of *D. polyptychum* with increasing slope was compensated by the rise in the abundance of the *T. tremula*, *I. indicum* and *A. purpurea* (Fig. 5, Table 2). The same set of species exhibited opposite trends when their abundance was regressed with soil depth (Fig. 6, Table 2).

In general, the species distributional responses to environmental gradients were better explained by the regression models for the most abundant species as opposed to the low abundance species. The adjusted heat load index had the strongest influence on the examined species distributions, showing strong significant relationships with most species (Table 2).

Interestingly, multiple grasses co-occurred in appreciable abundances in adverse conditions; for example, *T. tremula*, *I. indicum* and *A. purpurea* co-occurred in sites characterized by greater heat load and slope, and shallow soils; conversely *D. polyptychum*, which thrived in more productive

sites, lacked such consistent co-occurrences with any other species (Figs. 3 - 6). These observations suggest the possibility of facilitative species associations in adverse environments; this remains to be experimentally tested.
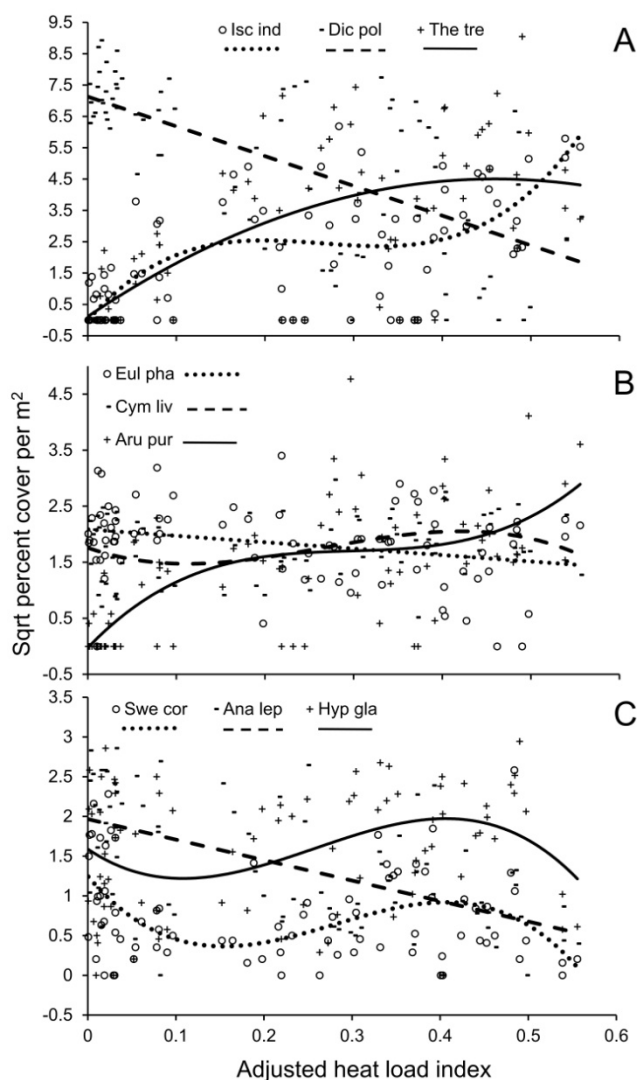

Fig. 4. Regression plots of the cover of the important grassland species with adjusted heat load index: (A) the three most abundant grasses, (B) medium abundance grasses, (C) most abundant forbs. The fitted regression lines are intended to represent the species response curves for that environmental gradient. See Table 2 for the coefficient of determination (R^2) and other relevant statistics. Species are represented by first three letters of the genus and species, see legend of Table 2 or Fig. 3 for full botanical names of species.
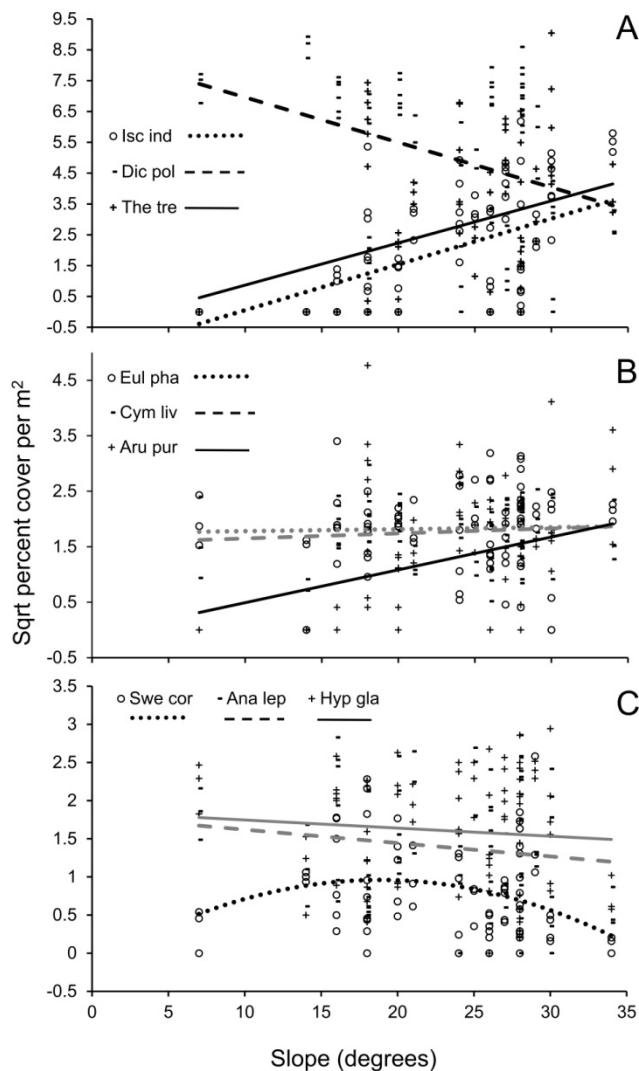
Fig. 5. Regression plots of the cover of the important grassland species with slope: (A) the three most abundant grasses, (B) medium abundance grasses, (C) most abundant forbs. The fitted regression lines are intended to represent the species response curves for that environmental gradient. Lines for non-significant relationships are coloured grey. See Table 2 for the coefficient of determination (R^2) and other relevant statistics. Species are represented by first three letters of the genus and species, see legend of Table 2 or Fig. 3 for full botanical names of species.

Classification of the community in relation to the environment

TWINSPAN was used to delineate four communities from the 81 plant community samples. The TWINSPAN assignment of the community samples to the four community types viz., *T. tremula - I.*

indicum, *D. polyptychum - T. tremula*, *D. polyptychum - E. phaeothrix* and *D. polyptychum*, agreed well with the visual classification of the communities in the field as short, mixed, tall and lush respectively. The term community is used here to describe a seemingly homogenous assemblage of plant species that can be distinguished from other such homogenous patches. Ninety-one percent of the plots were classified under the same community type by both the TWINSPAN classification and the visual classification in the field.

Table 2. Regression statistics of the important species with the environmental factors. The first six species are grasses and the last 3 are forbs. Species are listed in the order of decreasing abundance, except that *Hypochaeris glabra* was more abundant than *Arundinella purpurea*. Species are represented by first three letters of the genus and species: *Dichanthium polyptychum, Themeda tremula, Ischaemum indicum, Eulalia phaeothrix, Cymbopogon lividus, Arundinella purpurea, Hypochaeris glabra, Anaphalis leptophylla, Swertia corymbosa.*

| Species	df	F	P	R^2
Adjusted heat load index				
Dic pol	1, 79	61.7	< 0.0001	0.4385
The tre	2, 78	32.18	< 0.0001	0.4521
Isc ind	3, 77	19.21	< 0.0001	0.428
Eul pha	1, 79	6.96	0.01	0.081
Cym liv	3, 77	3.01	0.0353	0.1049
Aru pur	3, 77	20.41	< 0.0001	0.443
Hyp gla	3, 77	2.97	0.0368	0.1038
Ana lep	1, 79	38.64	< 0.0001	0.3284
Swe cor	3, 77	5.19	0.0026	0.1683
Slope				
Dic pol	1, 79	10.62	0.0017	0.1185
The tre	1, 79	9.27	0.0032	0.105
Isc ind	1, 79	22.94	< 0.0001	0.225
Eul pha	1, 79	0.07	0.7971	0.0008
Cym liv	1, 79	0.71	0.4025	0.0089
Aru pur	1, 79	8.39	0.0049	0.096
Hyp gla	1, 79	0.55	0.4591	0.007
Ana lep	1, 79	1.4	0.2409	0.0174
Swe cor	2, 78	3.45	0.0368	0.0812
Soil depth				
Dic pol	1, 79	19.48	< 0.0001	0.1978
The tre	1, 79	12.02	0.0009	0.132
Isc ind	3, 77	5.43	0.0019	0.1746
Eul pha	1, 79	1.68	0.1991	0.0208
Cym liv	1, 79	1.68	0.1991	0.0081
Aru pur	1, 79	9.12	0.0034	0.1035
Hyp gla	1, 79	1.04	0.3119	0.0129
Ana lep	1, 79	1.96	0.1659	0.0242
Swe cor	1, 79	0.01	0.9405	0.0001
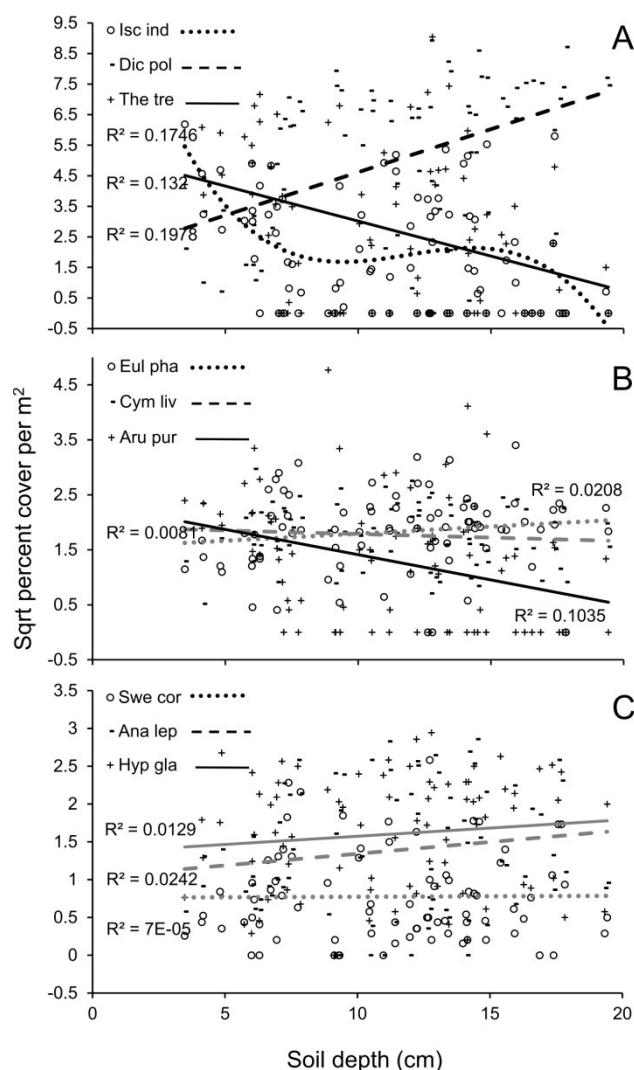
Fig. 6. Regression plots of the cover of the important grassland species with soil depth: (A) the three most abundant grasses, (B) medium abundance grasses, (C) most abundant forbs. The fitted regression lines are intended to represent the species response curves for that environmental gradient. Lines for non-significant relationships are coloured grey. See Table 2 for the coefficient of determination (R^2) and other relevant statistics. Species are represented by first three letters of the genus and species, see legend of Table 2 or Fig. 3 for full botanical names of species.

Also, the number of community samples in TWINSPAN classification versus field classification was not significantly different ($\chi^2 = 0.909$, df = 3, $P = 0.8232$). Because growth form differences among conspecifics in burned and unburned areas were not obvious at the time of the survey, we believe the following community characterizations apply to the un-burned grass-lands as well.

T. tremula - I. indicum communities were dominated by *T. tremula*, *I. indicum* and *A. purpurea* (Table 3). These species are short and are characterized by growth that hugs the surface; hence we refer to these as "short" communities. This was the least productive of all communities (see Table 4), but appears to better endure harsher environmental conditions such as the warmer southwestern aspects, steep slopes and shallow soils; hence this assemblage occupies such environments (Fig. 3).

D. polyptychum - T. tremula communities appeared to have a mixed height structure due to the appreciable cover of taller species such as *D. polyptychum* and *E. phaeothrix*, as well as the dominant grasses of the short communities (Table 3). This community had the highest species diversity (Table 4). "Mixed" communities were found in topographies that were comparable to short communities, except that these sites were not in the extreme south-western aspects (Fig. 3).

D. polyptychum - E. phaeothrix communities: The "tall" communities had appreciable cover of *D. polyptychum* and *E. phaeothrix* (Table 3). These species thrived on cooler and wetter northeast-facing, gentler slopes with deeper soils (Fig. 3). This community had high species richness, supported the most number of common forbs and also had the highest forb biomass compared to the other communities (Table 4).

D. polyptychum communities were distinguished by the luxuriant growth of *D. polyptychum* (Table 3); these were the most productive (hence we refer to them as "lush"), but also the least diverse communities (Table 4). The dominant grasses in the short communities, *T. tremula* and *I. indicum*, were completely absent and limited to one occurrence, respectively. This community was strongly correlated with flatter slopes and greater soil depth but was unaffected by aspect (Fig. 3).

The Gurukula Botanical Sanctuary (2005) recognizes the same set of species as the defining species of the grassland. The structural appearance of the communities described in their report concurs with our observations. This concurrence holds particularly for the composition of lush communities. However, the report did not describe the species composition of the short, mixed and tall communities.

Table 3. Cover (mean ± 95% confidence interval) of the important grasses in the four grassland communities, listed in the order of their overall abundance. Non-parametric ANOVA (Kruskal-Wallis) was used to test the differences in cover of each species between the community types.[*] Communities which do not differ significantly are denoted by the same superscript letters; comparisons are within species only. Species are represented by first three letters of the genus and species, see legend of Table 2 or Fig. 3 for full botanical names of species.

	Short N = 18	Mixed N = 22	Tall N = 30	Lush N = 11	Kruskal-Wallis H, P
Dic pol	2.15 ± 0.95[a]	18.59 ± 4.54[b]	47.16 ± 3.39[c]	60.83 ± 5.95[c]	68.31, <0.0001
The tre	40.97 ± 6.64[a]	14.8 ± 2.66[b]	1.83 ± 1.07[c]	0[d]	68.24, <0.0001
Isc ind	15.65 ± 4.89[a]	14.14 ± 3.62[a]	1.21 ± 0.75[b]	0.18 ± 0.24[c]	51.69, <0.0001
Eul pha	1.43 ± 0.54[a, d]	4.07 ± 0.81[b, c]	5.28 ± 0.74[b]	3.46 ± 1.82[c,d]	36.14, <0.0001
Cym liv	4.39 ± 1.03[a]	3.20 ± 0.75[a, b]	3.63 ± 0.56[a, b]	2.07 ± 1.18[b]	9.64, 0.0219
Aru pur	7.56 ± 2.48[a]	3.86 ± 1.11[a]	0.68 ± 0.34[b]	0[b]	60.22, <0.0001

[*]Short = *T. tremula-I. indicum* communities; mixed = *D. polyptychum-T. tremula* communities; tall = *D. polyptychum-E. phaeothrix* communities; lush = *D. polyptychum* communities.

Table 4. Community and ecosystem variables (mean ± standard error) in the four grassland communities. One-way ANOVA was used to test the differences in each variable between the community types.[*] Communities which do not differ significantly are denoted by the same superscript letters; comparisons are within variables only. All variables except species richness have been back transformed for presentation.

Variables	Short, N = 18	Mixed, N = 22	Tall, N = 30	Lush, N = 11
Species richness	19.39 ± 0.76[a]	21.45 ± 0.73[a, b]	22.77 ± 0.72[b]	18.91 ± 0.67[a]
		df = 3,77; F = 5.32; P = 0.002		
Shannon index	1.55 ± 0.07[a]	2.09 ± 0.04[b]	1.61 ± 0.05[a]	1.16 ± 0.09[c]
		df = 3,77; F = 50.42; P = <0.0001		
Evenness	0.53 ± 0.02[a]	0.69 ± 0.01[b]	0.52 ± 0.02[a]	0.39 ± 0.03[c]
		df = 3,77; F = 46.16; P = <0.0001		
Plant height (cm)	22.43 ± 0.81[a]	28.59 ± 1.49[b]	42.19 ± 1.99[c]	53.16 ± 3.31[d]
		df = 3,77; F = 43.28; P = <0.0001		
Graminoid biomass (g m^{-2})	256.48 ± 15.32[a]	323.52 ± 20.11[a, b]	355.77 ± 24.12[b]	477.18 ± 50.25[c]
		df = 3,77; F = 8.17; P = <0.0001		
Forb biomass (g m^{-2})	6.35 ± 2.01[a]	9.80 ± 1.87[a, b]	16.59 ± 3.19[b]	13.55 ± 3.07[a, b]
		df = 3,77; F = 5.04; P = 0.003		

[*]Short = *T. tremula-I.indicum* communities; mixed = *D. polyptychum-T. tremula* communities; tall = *D. polyptychum-E. phaeothrix* communities; lush = *D. polyptychum* communities.

Effect of environmental variables on community and ecosystem properties

Elevation and eastness were eliminated in all the multiple regression models by the stepwise backwards elimination process. Among all the variables, the variance explained for species richness was the lowest (Table 5). Species richness significantly decreased with increasing soil depth, but increased with northness. In contrast, diversity was negatively related to northness, and positively related to slope. The effect of environmental variables on forb biomass was similar to that of diversity. Both total biomass and graminoid biomass were related to soil depth and slope; similar responses were expected for these variables because 96 % of the total biomass was composed of graminoids.

Discussion

Community-environment relationship

Although the measured environmental variables explained an appreciable amount of the variance in species composition, a large proportion

Table 5. Multiple regression statistics of the community and ecosystem variables with the environmental variables. Eastness and elevation were eliminated by the step-wise backwards elimination process.

Dependent Variable	df	F	model P	R^2	Standardized coefficient, ß (P value)		
					Soil depth	Slope	Northness
Species richness	2, 78	6.21	0.003	0.137	-0.275 (0.018)	-	0.372 (0.002)
Diversity	2, 78	7.93	0.001	0.169	-	0.254 (0.021)	-0.259 (0.019)
Biomass	2, 78	25.48	< 0.0001	0.395	0.525 (<0.0001)	-0.263 (0.004)	-
Graminoids biomass	2, 78	23.23	< 0.0001	0.373	0.526 (<0.0001)	-0.229 (0.014)	-
Forbs biomass	2, 78	10.09	< 0.0001	0.206	-	0.335 (0.002)	-0.225 (0.036)

remained unexplained (see results of the CCA). This could be attributed to unmeasured environmental variables such as slope position, soil chemistry, microclimate, and also biotic interactions such as competition and facilitation. Disturbances, depending on the severity, can also have a strong influence on community composition in grasslands (Jacobs & Schloeder 2002; Sankaran 2005; Veen *et al.* 2008). The changes in community composition due to the recent fire could have contributed to a portion of the unexplained variance. Nonetheless, environmental factors strongly structured the distribution of four highly abundant species. Aspect was the most important factor: the northern facing slopes were preferred by the dominant grass *D. polyptychum* and southern aspects by the *T. tremula - I. indicum-A. purpurea* association. In the northern hemisphere, northern aspects are cooler than the southern equator-facing aspects (Bennie *et al.* 2008). Also, plants on the west facing slopes are more stressed by the afternoon sun when the morning dew has dried. Thus plant ecologists have frequently encountered vegetation that is adapted to dry conditions on south-western slopes (Lakhani & Davis 1982; Perring 1960). Undeniably, a complex-composite gradient such as aspect encompasses other influences like the direction of monsoonal winds, which can interact with biotic (e.g. seed dispersal) and abiotic factors (e.g. soil temperature). To a large extent the distribution of the dominant species was governed by the insolation effects of aspect. This is clear from the strong significant response of the top three grasses to the adjusted heat load index (Table 2 and Fig. 4a). Pemadasa & Mueller-Dombois (1979) found *I. indium* and *T. tremula* in drier sites of a similar landscape- *Patanas* in the central highlands of southwestern Sri Lanka. Among the important species only *I. indicum* was strongly related to

increasing slope (Table 2 and Figs. 3 & 5a) suggesting an ability to tolerate lower soil nutrients and moisture characteristics of steeper slopes (Bennie *et al.* 2006). *D. polyptychum* dominated sites in cooler aspects, having deeper soil profiles and on relatively flat ground, thereby indicating its preference for nutrient rich and wetter soils. In grasslands, soil depth is positively correlated with soil organic matter (SOM) which increases plant nutrient supply, cation exchange and water holding capacity (Miller & Donahue 1990).

All this taken together suggests that *D. polyptychum* thrives in fertile soils and is less heat tolerant, while *T. tremula, I. indicum* and *A. purpurea* are adapted for relatively unfertile and drier environments. Thus *D. polyptychum* dominates the lush communities, and *T. tremula* and *I. indicum* dominate the short communities, representing two ends of a spectrum of communities ranging from the most nutrient rich to impoverished soil conditions. Although there are seemingly apparent sets of environmental conditions linked to each of the four grassland assemblages, the preference for the site conditions are by no means strict. Communities, like their constituent species, are better expressed within an environmental range that may be close to an optimum for that configuration of species. It is indeed such an expression of species that lends to the perception of communities. Thus communities are not discrete or definite associations of species, but rather, loose intergrading aggregations strewn along complex environmental gradients.

Trends in species response to gradients

The compensatory patterns in the response curves of *D. polyptychum* and the *T. tremula-I-indicum-A.purpurea* group highlights the compli-

mentary resource use by plants under environmental constraints. For example, the low abundance of the latter group when the former is abundant, and *vice versa*. Such patterns are also illustrated by the sudden decline in the abundance of *I. indicum* and *A. purpurea* when *D. polyptychum* and *T. tremula* are both highly abundant (Figs. 4a & 6a). A curious pattern that emerged from the species responses was that multiple species tracked one another: *I. indicum* and *A. purpurea*, and *C. lividus*, *H. glabara* and *S. corymbosa*. The species associations within a community type (Table 3 and Fig. 3) or at the ecosystem level (Fig. 3) may have resulted either from positive interactions between species, or a coincidence in environmental preference, or both. The gradually changing compensatory and complimentary patterns in species responses along the same range of environmental gradients suggest that species are continuously distributed, with individual species peaking at gradient values that are closer to their respective environmental optima. This follows the individualistic-continuum concept (Goodall 1963) based on Gleason's (1926) individualistic hypothesis and Whittaker's (1975) community continuum idea. Callaway (1997, 2007) has reviewed many points of evidence to show that in many instances species would not be present, or at least not at high abundances, if not for the positive interactions with benign species. One possible argument for the association of *T. tremula, I. indicum* and *A. purpurea* is that this association is a product of mutual facilitation in relatively adverse conditions; further experiments could be planned to test whether this hypothesis can be supported.

The environment and community structure and ecosystem properties

Overall species richness was largely determined by the richness of forbs, which was nearly threefold higher than that of grasses. The higher species richness on northern slopes may be attributed to cooler and wetter conditions there. Similarly, higher richness on wetter northern slopes was reported from hilly grasslands in Mongolia (Gong *et al.* 2008). Interestingly, the higher species richness of forbs did not necessarily translate to greater diversity or higher forb biomass. Perhaps the high abundance of *D. polyptychum* on northern aspects stifled the growth of the forbs. This also explains the seemingly contrary negative relationship of northness with

forb biomass. The negative relationship of species richness with soil depth (Table 5) can be attributed to the displacement of many forbs by matrix forming grasses, mainly *D. polyptychum*, which thrive in deeper soils, rich in SOM and nutrients (Miller & Donahue 1990). *D. polyptychum* clumps are generally large owing to their profuse clonal growth, and their size is particularly enhanced in more productive sites. Hence, to a large extent the relationship of the environmental variables with total biomass and graminoid biomass could be explained by increasing dominance of *D. polyptychum* with soil depth and flat terrain. Lush communities were virtually composed of *D. polyptychum*; these sites had the deepest soils and lowest species richness and diversity (Table 4). Based on observations in the field, lush communities often occurred at foot-slopes which had deeper soils due to poorer drainage (Fig. 3). Patterns of decreasing graminoid (C_4) biomass and increase in forb (C_3) biomass with slope, as seen in this study, was also reported by Gong *et al.* (2008); they found soil water and macronutrients to be the principal factors that limited the growth of C_4 grasses on steep terrain.

How do the shola-grasslands of Lakkadi compare with similar habitats elsewhere?

The *shola*-grassland-like vegetation characterized by natural mosaics of stunted tropical evergreen trees and open grasslands in the more "exposed" topographical settings is not unique to the Nilgiris. These ecosystems are also found in the adjacent Palni and Anamalai hills (Blasco 1970; Karunakaran *et al.* 1998); similar landscapes are also reported from south-central highlands of Sri Lanka (locally called Patanas: Pemadasa & Mueller-Dombois 1979) and mesic tropical locales of Afromontane archipelago (Meadows & Linder 1993). There was an overlap of five species when the eight most frequent species in our study were compared to those in the Eravikulam National Park (ENP) in the Anamalai hills (Blasco 1970; Karunakaran *et al.* 1998). *D. polyptychum* and *T. tremula* were not as common in ENP, while *Sehima nervosum* Stapf, a dominant grass in ENP (Karunakaran *et al.* 1998), did not occur in our site or elsewhere in the Nilgiris (Fyson 1915). However, *I. indicum* is common in the Nilgiris (based on our data and work by other authors, see: Gupte *et al.* 1967; Gurukula Botanical Sanctuary 2005), Anamalais (Karunakaran *et al.* 1998), *Patanas* (Pemadasa & Mueller-Dombois 1979) and presu-

mably the Palni hills. In the patanas, *E. phaeothrix* was found only in wetter sites, whereas *I. indicum* and *T. tremula* were found exclusively in drier sites. This is similar to the patterns from the current study. However, our study can be compared to the other two studies only to a limited extent because (1) we measured complex environmental gradients (e.g. aspect) while other studies measured direct gradients (e.g. soil potassium), (2) our study focused on characterizing the predominant grassland type, hence, we did not sample the minor habitats such as marshes, stream sides, rocky grassland, etc. The other two studies included minor habitats which harbour a host of species that are exclusive to such conditions. Though most of the original *shola*-grasslands have been decimated in the Nilgiris, Palnis and Anamali hills, for similar reasons, the *shola*-grasslands of the Nilgiris is the best remaining example of this ecosystem mainly because of its greater extent. Strict measures need to be taken to protect and augment the current extent of grasslands mainly through the removal of exotic woody plants coupled with active restoration of native species.

Conclusions

Despite the long botanical history of the Nilgiris, very few systematic ecological studies have been carried out, particularly in the grasslands. Systematic plant inventories need to be undertaken in the remaining grassland patches not protected by law in the upper areas of the Nilgiris to highlight the importance of these remnants. Where feasible, such fragments, which are often degraded, can be acquired by the state forest department and awarded protection status to initiate restoration activities.

Invasion by woody exotic plants - commercial trees and ornamental shrubs - are the principal threat to the remaining grasslands. Methods of exotic plant removal in grasslands have been discussed by various authors (Scotch broom: DiTomaso & Johnson 2006; Srinivasan *et al.* 2012; Swezy & Odion 1997); (wattle: Campbell & Kluge 1999; Wilson *et al.* 2011). Restoration can either be passive or active. Passive restoration would involve clearing patches of plantations and exotic shrubs thickets and maintaining such clearings by weeding the recruits. This would encourage species colonization from neighbouring seed pools, and also incorporate the environmental preferences of dominant species and species associations from neighbouring reference patches. Active restoration would require introduction of grassland plants through seeding and planting of ramets in accordance with the environmental preferences of species or local species associations. If vegetation inventories in nearby reference sites indicate affinities between multiple species, for instance the environmental response curves of dominant species is tracked by that of less dominant species, the association so observed needs to be maintained.

Restoration can be supported by initiating systematic grassland surveys that involve measuring of both complex and direct environmental gradients. Since distinct communities are easily recognized in this landscape by their structural appearance, ecologists can replicate the composition of such communities in potential restoration sites in tune with the environmental gradients that prevail in the reference communities. Complex gradients can be measured with minimal effort and are extremely meaningful to analyse and explain species distribution as seen from the current study. We need to invest in further experiments to conclusively test whether the associative patterns seen are indeed due to facilitative processes, which could further aid restoration management. Our study has presented a feasible model for interpretation of vegetation patterns along environmental gradients, using the best representative site in the Nilgiris. The reference data that we present here is directly applicable to restoration of invaded patches in this site. We recommend similar surveys be carried out throughout the district to understand regional variations in plant distribution patterns; these data will also serve as a reference for localized restoration projects.

Acknowledgements

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Appendix Table 1. Average percent cover and percent frequency of occurrence (freq.) of important plants in the four community types. Cover is based on plant cover in 1 m² quadrats; frequency is based on the proportion of plots the species occurred within a community type.

Species	Short		Mixed		Tall		Lush	
	cover	freq.	cover	freq.	cover	freq.	cover	freq.
Asteraceae								
Anaphalis leptophylla	0.41	78	2.25	100	4.00	97	2.67	100
Hypochaeris glabra	3.45	100	3.30	100	3.03	97	2.68	91
Gentianaceae								
Swertia corymbosa	0.20	78	0.94	95	1.64	100	0.40	73
Poaceae								
Arundinella purpurea	7.56	100	3.86	100	0.68	53		
Cymbopogon lividus	4.39	100	3.20	100	3.63	100	2.07	91
Dichanthium polyptychum	2.15	78	18.59	100	47.16	100	60.83	100
Eulalia phaeothrix	1.43	89	4.07	100	5.28	100	3.46	91
Ischaemum indicum	15.65	89	14.14	100	1.21	57	0.18	18
Themeda tremula	40.97	100	14.80	100	1.83	47		