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THE ECOLOGY OF DISTURBANCES AND GLOBAL CHANGE IN THE MONTANE GRASSLANDS OF THE NILGIRIS, SOUTH INDIA

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ABSTRACT OF DISSERTATION

Madhusudan P. Srinivasan

The Graduate School
University of Kentucky

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THE ECOLOGY OF DISTURBANCES AND GLOBAL CHANGE IN THE MONTANE GRASSLANDS OF THE NILGIRIS, SOUTH INDIA

ABSTRACT OF DISSERTATION

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Biology at the University of Kentucky

By

Madhusudan P. Srinivasan
Lexington, Kentucky

Director: Dr. Scott K. Gleeson, Associate Professor of Biology
Lexington, Kentucky

2011

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ABSTRACT OF DISSERTATION

THE ECOLOGY OF DISTURBANCES AND GLOBAL CHANGE IN THE MONTANE GRASSLANDS OF THE NILGIRIS, SOUTH INDIA

Biodiversity rich regions worldwide face threats from various global change agents. This research quantifies environmental influences on vegetation, and the impacts of exotic woody plant invasion and anthropogenic nitrogen (N) deposition in a global biodiversity hotspot. The study was conducted in the montane grasslands of the Nilgiris, Western Ghats, and outlines potential management options for this region. Specifically, I examined (1) the role of environmental factors in influencing native plant distribution and ecosystem properties, (2) the status and impact of exotic shrub (Scotch broom, henceforth broom) invasion, (3) the role of disturbances in the success of broom, (4) the role of fire in restoring invaded grasslands, and (5) the impacts of terrestrial N loading on the grassland ecosystem. I used experiments and surveys to assess these. Distributions of several key species were explained by a few complex environmental gradients. In invaded-grasslands, broom populations consisted mainly of intermediate size and age classes, with no clear indication of population decline. Invasion negatively impacted plant community structure and drastically changed composition, favoring shade-tolerant and weedy species. However, invasion did not greatly alter ecosystem function. Fire successfully eliminated mature broom stands, but resulted in a short-term increase in broom seedling recruitment. At the end of 18 months, the fire effects on uninvaded-grasslands were not apparent, but there was no conclusive evidence of the formerly invaded patches attaining the composition of uninvaded-grasslands following burning. N fertilization strongly influenced soil N dynamics, and shoot N concentrations, but effects on aboveground production were weak. Surprisingly, N enrichment had positive effects on diversity in the short-term. It is clear that these grasslands need immediate management intervention to forestall degradation from invasion. Fire could be used to eliminate mature broom stands and deplete persistent seedbanks, which will facilitate colonization by shade-intolerant grassland plants. Active restoration should be mindful of environmental preferences of framework species. Long-term studies of the impacts of N deposition in the context of disturbances will help determine realistic critical thresholds and utilize disturbances to buffer the potential adverse effects of increasing N loading.

Keywords: community composition, ecosystem function, nitrogen (N) deposition, Scotch broom (Cytisus scoparius), shrub invasion

Madhusudan P. Srinivasan
April 15, 2011
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Dissertation

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This doctoral project has been an ambitious undertaking and my field experiences have been rather challenging. Yet, strangely, I feel ready to take on another such endeavor. I hope that if I do, I will have the kind of help that I did during this long process.

I want to thank my wife, Kausalya Shenoy, the most; she has helped me at every stage of this project and been a constant source of support, emotionally and academically. She put much time into reading my (at times) incoherent dribble and suggesting improvements, and providing inputs with data analysis. During my time in the field, she was my link to the outside world to coordinate and liaison with the academic circles here in the US. She also took a semester off from her program to support me in the field. I am indebted to my parents, Shanthi and Srinivasan, for all the time, effort and resources that they put into this project to help make it happen in this remote location. Though they understood my research poorly, they believed in me and worked to help this project succeed. They took it upon themselves to renovate a rundown shack in the middle of nowhere to make it a habitable and fully functional field station. My parents and my in-laws, Mithra and Mohan Shenoy, arranged the logistics for all kinds of equipment and supplies. My father-in-law put much effort into fabricating equipment to help with the fieldwork. I was very happy to have visits from friends and family which made my reclusive lifestyle in the mountains saner!

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PREFACE

Tropical montane grasslands are well known for their rich biodiversity and high levels of endemicity; montane ecosystems also provide a host of services to people in the mountains and plains. These habitats are among the ecosystems that are most vulnerable to global change agents, such as habitat destruction, climate change, invasion, terrestrial nitrogen (N) deposition and elevated CO₂ levels. Yet, these issues remain poorly studied in montane grasslands compared to lowland grasslands. The shola-grasslands of the Nilgiris are a mosaic of tropical evergreen tree patches (the sholas) interspersed in grasslands. This ecosystem is a tragic example of a speciose landscape visibly ravaged by habitat destruction and woody plant invasion.

The first chapter of this dissertation was inspired by restoration intentions and makes the argument that quantifying vegetation patterns in the context of the environmental gradients can help develop a sound restoration plan for the region in question. Here, I describe the distribution of species and species associations along environmental gradients; also, I examine the role of environmental factors in structuring plant community and ecosystem properties. I believe this study can serve as a model to quantitatively characterize the vegetation in the Nilgiris grasslands to achieve conservation and restoration goals here.

Vast areas of the grasslands are currently under the cover of Cytisus scoparius (Scotch broom, henceforth broom) an exotic invasive shrub. Broom continues to make significant inroads into the remaining grasslands. The second chapter examines the population structure of broom stands in the grasslands to ascertain the health of the population. This chapter also provides some preliminary insights into the impacts of broom on the native grassland community.

Though not natural, indigenous people have used fire to manage the grasslands for centuries. However, the use of fire has been discontinued for the past several decades. The use of fire to control broom invasion is often discussed by managers, but is not implemented due to concerns over unintended consequences. Further, the effects of wildfires on broom populations have not been scientifically documented. In the third chapter, I use experiments and surveys to understand if fire can be used as an effective tool to eliminate mature scotch broom stands and also deplete soil seedbanks. I investigate the interactive effects of fire and grazing in open uninvaded grasslands, as grazers disperse broom seeds into the open grasslands. In chapter four, I quantify the impacts of scotch broom on the grassland plant community and ecosystem function. I then follow the recovery of invaded and uninvaded grasslands from a wildfire. I monitor the treatments over time to determine if fire can be used as a management tool to aid in the recovery of characteristic native grassland plants in invaded patches. This is particularly relevant if fire is effective in controlling the invasion, as suggested by data from chapter three.

One of the less apparent, yet important, global change agents is terrestrial N loading. The Western Ghats receives the highest deposition rates among all global biodiversity hotspots, and is projected to receive even more in the future. To date, the scientific community is unaware of what species we might lose due to high N enrichment rates. In the fifth chapter, I use an experiment to examine the impacts of N loading on the native grassland community and ecosystem. To my knowledge, this is the first study to document the impact of environmentally relevant N deposition in a natural ecosystem in India. This study will spark much needed long-term research on global change agents in conjunction with prevailing local disturbances.

Like many unique ecosystems, the shola-grasslands are fast disappearing. Sound basic and applied research is required to achieve conservation goals in the region, which will serve as the foundation for future research to build upon. Besides conserving the endemic flora and fauna here, conservation is important for the indigenous people who have strong socioeconomic and cultural ties to the grasslands. The findings from this project will influence how these grasslands will be managed in the future.
CHAPTER ONE

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

Summary
Understanding the role of environmental factors in shaping communities and ecosystems is indispensible for conservation planning and restoration. I studied the role of environmental factors in driving species distributions, community assembly, community structure, and ecosystem properties in an endangered montane grassland ecosystem in the Nilgiris, Western Ghats. I measured plant composition, ecosystem properties and environmental factors in 27 grassland sites in the Nilgiris mountains. Results from ordination analysis showed that environmental gradients, mainly slope and aspect, controlled the distribution of the dominant plants. Species varied in their environmental optima. Coenoclines of abundant species showed patterns of mutual complementarity. Some species tracked each other along gradients suggesting similar environmental tolerances. Classification analysis identified four community types, but ordination revealed a continuum of communities along environmental gradients. Environmental variables strongly influenced ecosystem properties rather than community structure. Aboveground biomass was explained mainly by slope and soil depth, while species richness and diversity were better explained by northern aspects. This study provides crucial 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.

Introduction
To a large extent, environmental factors control the distribution of plant species. Species that can tolerate a given range of environmental conditions occur in a defined area to form communities. Formation of communities and the semblance of structure in communities is due to (1) abiotic processes such as the interaction between species tolerances and heterogeneity in the environment, and (2) biotic interactions like competition, facilitation and predation (Daubenmire 1968). Hence it is vital to study the distribution of species and communities in the context of environmental factors. Whittaker's (1975) community continuum model presents plant species in a defined area as widely overlapping unimodal coenoclines along environmental gradients. This model is often referred to as the individualistic-continuum as it was inspired by Gleason's (1926) individualistic species hypothesis, i.e., species are distributed independently as a consequence of the interactions of their life history characteristics, physical environment and inter-specific interactions. The distinction between the two theories is that the former is a community level construct, while the latter is defined at the species scale. The community continuum concept emerged as the popular model over the community-unit model of Clements (1936), which stated that a plant community is a distinct unit consisting of coevolved species. But the community-unit idea is regaining value as evidence mounts for positive interactions at finer spatial scales (Callaway 2007). The goal of my study is to understand plant distributions in a montane grassland ecosystem based on underlying environmental gradients, and then sort species into community types which is practical from an ecosystem restoration standpoint.

Mountain ecosystems are understudied relative to other environments despite their importance for biodiversity, ecosystem services and resources they provide, both in the mountains and lowlands (Price et al. 2000, Beniston 2003). Mountain ecosystems, particularly in the tropics, are more vulnerable to global change agents because of the high level of endemicity encountered here (Bruijnzeel and Hamilton 2000, Bubb et al. 2004). The effects of climate change will be most pervasive to mountain biota because of their inherent sensitivity to climate, and also because of the unique niches that these species cannot
find elsewhere (Foster 2001). Unfortunately, little information is available on the ecology of montane species to develop appropriate conservation strategies.

The montane grasslands 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). The Nilgiris is an important region in the Western Ghats, which is ranked among the top eight global biodiversity hotspots (Myers et al. 2000). The Nilgiris is also one of the earliest botanized ecoregions of the world and boasts of excellent floras (example: Wight and Walker-Arnot 1834, Hooker 1875, Fyson 1915, Gamble 1921).

Of the many ecological studies done here, some have identified grassland (or community) types based on visual classification (example: Shankaranarayan 1958, Gupte et al. 1967, Blasco 1970, Gurukula Botanical Sanctuary 2005). The Gurukula Botanical Sanctuary (2005) describe a range of grassland types, from the predominant and fairly continuous grasslands to the fringe types such as the rocky, shrubby and marshy grasslands. In the predominant grassland type, communities ranging from tall to short characterized by typical species associations were identified. A typical view of the landscape here encompasses nearly all of these grassland types. In montane grasslands, plant distribution is mainly determined by abiotic environmental factors which in turn are correlated to microtopography (Sebastiá 2004, Bennie et al. 2006). Different aspects experience different temperature and light regimes as a result of latitudinal position and direction of prevailing winds (Bennie et al. 2008). Shallow slopes tend to be correlated with deeper soils (Miller and Donahue 1990), and these sites tend to be more productive than those with steep slopes and shallow soils that have poorer nutrient conditions. Hence, these factors can have a strong bearing on plant distributions. In the Nilgiris, grassland patches occurring in close proximity but on contrasting aspects appear to support visually distinct communities. Further, within a given aspect communities differ based on slope inclination and position. Despite these obvious patterns, little is documented about the distribution of plant species and communities in relation to environmental factors.

A majority of the Nilgiris landscape, which was originally under natural grass cover, has been urbanized, farmed, submerged by massive reservoirs, or converted to commercial plantations of tea and exotic trees, viz., black wattle (Acacia mearnsii), blue gum (Eucalyptus globulus) and pine (Pinus patula), (Figure 1.1). The tree plantations have been abandoned for the last few decades (Gurukula Botanical Sanctuary 2005). The remaining grasslands are being encroached by natural expansion of these plantation species and other introduced woody exotic shrubs such as scotch broom (Cytisus scoparius) and gorse (Ulex europaeus) (Srinivasan et al. 2007, pers. obs.). The Nilgiris is an important watershed because the Bhavani River, which benefits a sizeable population of south India, originates from the shola-grasslands. Hence restoring the grasslands will reinstate ecosystem services.

Ongoing small scale restoration activities in the Nilgiris and in similar habitats in the adjoining Palani Hills do not attempt to accommodate the environmental preferences of species. Restoration that involves haphazard planting of ramets can do more harm than good, especially when ramets are unsustainably harvested from the wild. Thus, one of the objectives of my study is to describe species distributions and responses along easily measurable complex environmental gradients. Specifically, I tested whether the community composition was explained by multiple environmental gradients; I further examined how the abundances 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 neighbors. This is in the context of increasing evidence for facilitative associations in natural communities (Callaway 2007, Brooker et al. 2008). Thus, I used numerical classification to identify community types and assessed their environmental preferences. I use the phrase ‘community type’ to refer to a group of vegetation samples that are compositionally alike. Finally, I examine the role of environmental factors in driving vegetation characteristics other than community composition, viz., community structure (species richness, diversity) and ecosystem properties (biomass).
Methods

Study area

The Nilgiri Hills, an integral part of the Western Ghats mountains, is located between 11°10′-10°30′ N and 76°25′-77°00′ E (Figure 1.2a). 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 a second from the northeast monsoon between October and December. The western regions of the plateau receive about 2500 mm of rainfall and exceeds 5000 mm in certain areas (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-allophanic andisols (Caner et al. 2000).

Vegetation in the upper Nilgiris consists of patches of stunted tropical evergreen forests (locally called *shola*) surrounded by grasslands. According to recent vegetation nomenclature (Whitmore 1986, Ashton 2003), 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 disturbances (see Thomas and 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), long before humanization 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 and Palmer 2007).

Vegetation sampling

The vegetation was sampled in eighty-one 9m² plots in 27 grassland sites spread across an area of nearly 6 km² in the Lakkadi area of the Nilgiris South Division Reserve Forest (Figure 1.2b). All the sites were sampled 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. I defined a site as a visually homogenous grassy slope which was at least 30 m wide. The visual appearance of these grassy patches, lend themselves to colloquial naming of these patches as short, mixed, tall and lush communities, the very approach adopted by earlier authors. I identified sites along multiple 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. Within each site, three 9m² plots were randomly located. Besides the above criteria and accessibility, the sites were chosen in no particular pattern. At each plot, community composition was sampled in six-1m² 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 the quadrat. This generated a list of plants with their percent cover for each plot – a relevé. Plants were identified to the species level using a regional flora (Fyson 1915); the same can be used as a reference for botanical authorities and nomenclature.

Plant height was measured at 10 points uniformly distributed within each plot and averaged. The above-ground biomass at each plot was measured by clipping two-0.1 x1 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.

A series of environmental variables were recorded at each plot. Slope inclination was measured using a clinometer. Soil depth was measured at 10 random points and averaged in each plot, by gently pushing a 2 mm metal probe into the ground until no further easy penetration was possible. Elevation and aspect were also recorded.
Data analysis

I used Canonical Correspondence Analysis (CCA) to test the relationship between grassland plant community composition and the measured environmental variables. 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 each species or relevés or both. CANOCO v. 4.5 (ter Braak and Smilauer 2002) was used to run the CCA. Rare species were downweighted; otherwise I used the default settings. Monte Carlo permutation test with 499 permutations was used to test the significance of the species-environment relationship. The environmental variables were slope, soil depth, elevation, northness (cos(θ), where θ is the aspect in degrees) and eastness (sin(θ)). Biplots of species and environmental vectors were created to understand the environmental basis for the species, and triplots were used to define classified relevés in the species-environment space. To improve clarity, low frequency species were not shown in the diagram by adjusting the species weight range in CanoDraw 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 relevés that were compositionally alike into community types. In the TWINSPLAN software (WinTWINS, Hill and 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 my data. Species that had five or fewer occurrences were excluded from the analysis. Kruskal-Wallis ANOVA was used to test for differences in cover of the dominant grasses between the classified communities. The non-parametric test was used 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 plant height) and ecosystem (graminoid and forb biomass) parameters between community types. The data for the following variables were transformed to meet the assumptions of parametric statistics: plant height (log10), Shannon index (cubic), graminoid biomass (square root), forb biomass (log10 (forb biomass +1)).

Regression analysis was used to illustrate coenoclines of multiple species 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 important environmental factors. Slope is often thought to be negatively correlated to soil depth; here they were considered independently as they were not significantly correlated (r = -0.183, P = 0.102). The heat load index (equation 1), is a reasonable proxy for the effects of aspect. This rescales aspect to a scale of 0 to 1, corresponding to the coolest (northeast) and warmest (southwest) slopes in the northern hemisphere, respectively (McCune and Keon 2002). 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). I applied a correction to the heat load index by multiplying equation 1 by the sine of the slope angle $\phi$, producing the adjusted heat load index (equation 2). PROC REG (SAS v. 9.2) was used to determine the appropriate fit for each coenocline.

\[
\text{Heat load index} = \frac{1 - \cos(\theta - 45)}{2}, \text{ where } \theta \text{ is the aspect in degrees} ...
\]

\[
\text{Adjusted heat load index} = \sin(\phi) \times \frac{1 - \cos(\theta - 45)}{2} ...
\]

The adjusted heat load index, a synthetic variable, 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 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* was the only fern recorded. Vegetation sampling was restricted to relatively homogenous open grassland slopes, while rocky patches, stream and *shola* edges, and marshy habitats were not sampled. *Dichanthium polyptychum*, *Themeda tremula*, *Ischaemum indicum* and *Eulalia phaeothrix* were the most abundant grasses, and *Hypochaeris glabra*, *Anaphalis leptophylla* and *Swertia corymbosa* the most abundant forbs (in order of decreasing abundance for both groups). Of the 77 species recorded, 56 of these were forbs; however, they represented only 3.4% of the total plant biomass.

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 (Figure 1.3). 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 1.1). The intraset correlations are a measure of the strength of the association between community composition and environmental variables, when 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 (Figure 1.3). *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* was most abundant in sites with deeper soil and low slope, while the opposite conditions were more conducive to *Eleocharis congesta* and *I. indicum*. Species distributed near the origin (e.g. *Cymbopogon lividus*, *H. glabra*, *S. corymbosa*, *E. phaeothrix*) have less specific environmental affinities.

Coenoclines: species response to environmental gradients
Clear patterns of species distributions in response to environmental gradients were observed (Figures 1.4-1.6). 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* and the forb *H. glabra* responded positively (Table 1.2, Figure 1.4). The coenoclines 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* (Figure 1.4a). 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 (Figure 1.4 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* (Figure 1.5, Table 1.2). The same set of species exhibited opposite trends when their abundance was regressed with soil depth (Figure 1.6, Table 1.2).

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 1.2).

Interestingly, multiple grasses co-occurred in appreciable abundances in adverse conditions; for example, *T. tremula, I. indicum* and *A. purpurea* were found together 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 (Figures 1.3-1.6). These observations suggest the possibility of facilitative species associations in adverse environments; this remains to be experimentally tested.

**Classification of the community in relation to the environment**

TWINSPAN was used to delineate four communities from the 81 relevés of plant community data. The TWINSPAN assignment of the relevés to the four communities viz., *T. tremula-I. indicum, D. polyptychum-T. tremula, D. polyptychum-E. phaeothrix* and just *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. Upon qualitative inspection, 91% of the TWINSPAN classification of relevés matched with the field assignment of the relevés to the respective communities. Also, the number of relevés in TWINSPAN classification versus field classification was not significantly different ($\chi^2 = 0.909, df = 3, P = 0.8232$).

*T. tremula-I. indicum* communities were dominated by *T. tremula, I. indicum* and *A. purpurea* (Table 1.3). These species are short and are characterized by growth that hugs the surface; hence I refer to these as "short" communities. This was the least productive of all communities (see Table 1.4), but appears to better endure harsher environmental conditions such as the warmer southwestern aspects, steep slopes and shallow soils (Figure 1.7).

*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 1.3). This community had the highest species diversity (Table 1.4). "Mixed" communities were found in topographies that were comparable to short communities, except that these sites were not in the extreme southwestern aspects (Figure 1.7).

*D. polyptychum-E. phaeothrix* communities: The "tall" communities had appreciable cover of *D. polyptychum* and *E. phaeothrix* (Table 1.3). These species thrived on cooler and wetter northeast-facing, gentler slopes with deeper soils (Figure 1.7). 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 1.4).

*D. polyptychum* communities were distinguished by the luxuriant growth of *D. polyptychum* (Table 1.3); these were the most productive (hence I refer to them as "lush"), but also the least diverse communities (Table 1.4). 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 (Figure 1.7).

The Gurukula Botanical Sanctuary (2005) recognize the same set of species as the defining species of the grassland. The structural appearance of the communities described in their report concurs with my observations. This concurrence holds for the composition of lush communities as well. Unfortunately, the report did not describe the species composition of the short, mixed and tall 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 1.5). 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 explained by soil depth and slope. Similar effects of environmental variables were expected for both these variables as 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 remained unexplained (see results of the CCA). This could be attributed to unmeasured environmental variables such as slope position, soil chemistry, and other terrain characteristics that could influence 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 and 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 high abundance species. Aspect was the most important factor: the northern facing slopes were preferred by the dominant grass \textit{D. polyptychum} and southern aspects by the \textit{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 southwestern slopes (Perring 1960, Lakhani and Davis 1982). 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 1.2 and Figure 1.4a). Pemadasa and Mueller-Dombois (1979) found \textit{I. indium} and \textit{T. tremula} in drier sites of a similar landscape – \textit{Patanas} in the central highlands of southwestern Sri Lanka. Among the important species only \textit{I. indicum} was strongly related to increasing slope (Figures 1.3, 1.5a) suggesting an ability to tolerate lower soil nutrients and moisture characteristic of steeper slopes (Bennie et al. 2006). \textit{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 and Donahue 1990).

All this taken together suggests that \textit{D. polyptychum} thrives in fertile soils and is less heat tolerant, while \textit{T. tremula, I.indicum} and \textit{A. purpurea} are adapted for relatively unfertile and drier environments. Thus \textit{D. polyptychum} dominates the lush communities, and \textit{T. tremula} and \textit{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, are loose intergrading aggregations strewn along complex environmental gradients.

Trends in coenoclines

The compensatory interactive patterns of the coenoclines of \textit{D. polyptychum} and the \textit{T. tremula-I.indicum-A. purpurea} group highlights the complimentary 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. polyptichum* and *T. tremula* reached equal abundance (Figures 1.4a, 1.6a). A curious pattern that emerged from the coenoclines was that multiple species tracked one another: *I. indicum* and *A. purpurea*, and *C. lividus*, *H. glabara* and *S. corymbosa*. What could be the explanation for these observations? The species associations within a community type (Table 1.3, Figure 1.7) or at the ecosystem level (Figure 1.3) 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 coenoclines 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. However, the versatility of the individualistic continuum concept is limited by the plethora of empirical evidence for facilitation and indirect interactions (Callaway 2007). 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. Hence it can be argued that the association of *T. tremula, I. indicum and A. purpurea* is a product of mutual facilitation in relatively adverse conditions. Thus, facilitation and competition could be the principal mechanism that affects community assembly in adverse environments and benign environments, respectively (see Choler et al. 2001).

整体的环境和群落结构与生态系统特性

**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. polyptichum* 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 1.5) can be attributed to the displacement of many forbs by matrix forming grasses, mainly *D. polyptichum*, which thrive in deeper soils, rich in SOM and nutrients (Miller and Donahue 1990). *D. polyptichum* 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. polyptichum* with soil depth and flat terrain. Lush communities were virtually composed of *D. polyptichum*; these sites had the deepest soils and lowest species richness and diversity (Table 1.4). Based on observations in the field, lush communities often occurred at foot-slopes which had deeper soils due to poorer drainage (Figure 1.7). Patterns of decreasing graminoid (C4) biomass and increase in forb (C3) biomass with slope, as seen in this study, was also reported by Gong et al. (2008); soil water and macronutrients were thought to be the principle factors that limited the growth of C4 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 and Mueller-Dombois 1979) and mesic tropical locales of Afromontane archipelago (Meadows and Linder 1993). There was an overlap of five species when the eight most frequent species
in my 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*, a dominant grass in ENP (Karunakaran et al. 1998), did not occur in my site or elsewhere in the Nilgiris (Fyson 1915). However, *I. indicum* is common in the Nilgiris (based on my data and work by other authors, see: Gupte et al. 1967, Gurukula Botanical Sanctuary 2005, Anamalais (Karunakaran et al. 1998), *Patanas* (Pemadasa and Mueller-Dombois 1979) and presumably 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, my study can be compared to the other two studies only to a limited extent because (1) I measured complex environmental gradients (e.g. aspect) while other studies measured direct gradients (e.g. soil potassium), (2) my study focused on characterizing the predominant grassland type, hence, I did not sample the minor habitats such as marshes, stream sides, rocky grassland, etc. The other two studies included minor habitats which harbor a host of species that are exclusive to such conditions. In the Nilgiris I visited several *shola*-grassland sites 5 - 20 Km west of Lakkadi which receive higher annual precipitation (>500 mm) than Lakkadi. During casual surveys there I found that there was a near complete species overlap but stark differences in relative abundances. *E. phaeothrix* was more abundant and, there was a visibly higher frequency of forbs, even though the visit was made during the dry season. I also conducted informal field surveys in areas adjoining the ENP, and highly degraded grassland fragments in the Palni hills, both over 120 km from Lakkadi. In both of these locations, I was able to place several forbs to familiar genera from the Nilgiris, and recognize several grasses to be ecological or functional equivalents. 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.

**Management implications**

In the Nilgiris there are more than 200 species of plants in the grasslands, excluding the scores of tree species in the *sholas*. Twenty-two of these plants are endemic to the Nilgiris; further, the grasslands have the highest diversity of scapigerous *Impatiens*. Overall at least 38 species of *Impatiens* are found here, which is quite high for a given region (Gurukula Botanical Sanctuary 2005). Thus, it is indeed ironic that the grasslands until recently were considered wasteland, fit to be replaced by exotic commercial tree plantations. 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 unprotected grassland patches 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.

Restoration can either be passive or active. Passive restoration would involve clearing patches of plantations and maintaining such clearings by weeding them of plantation species. This would eventually allow colonization and expansion of native plants. Active restoration would require introduction of grassland plants through seeding and planting of ramets in accordance with the environmental preferences of species or species associations. Restoration activities should in no way damage wild populations, as nearly all the plants here are slow growing. The genus *Dichanthium* reproduces mainly via clonal growth (de Wet and Harlan 1970) and seldom flowers (personal observation). Extraction of ramets from the wild for restoration planting will be unsustainable in the long run. Hence it will be a worthwhile investment to initiate tissue culture programs in the existing network of government nurseries. It must be kept in mind that the previous occupants of the cleared space could have modified the soil conditions substantially (reviewed by Ehrenfeld 2003) thus affecting restoration success. Ideally,
Restoration experiments should be initiated in degraded grasslands rather than amidst extensive plantations. This would ensure species colonization from neighboring seed pools, and also incorporate the environmental preferences of dominant species and species associations from neighboring reference patches. As mentioned in the previous section, community composition can vary dramatically even over a spatial scale of a few kilometers when superimposed by a rainfall gradient. If vegetation inventories in nearby reference sites indicate affinities between multiple species, for instance the coenoclines of dominant species being 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 analyze 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.
Table 1.1. Intraset correlations of environmental variables with the first two axes of canonical correspondence analysis (CCA).

<table>
<thead>
<tr>
<th>Environmental variables</th>
<th>Correlation coefficients</th>
<th>Axis 1</th>
<th>Axis 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td></td>
<td>0.1096</td>
<td>0.1982</td>
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<tr>
<td>Soil depth</td>
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<tr>
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</tr>
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<td></td>
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<td>-0.4775</td>
</tr>
<tr>
<td>Slope</td>
<td></td>
<td>-0.4893</td>
<td>-0.7489</td>
</tr>
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</table>
Table 1.2. 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*.

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>R²</th>
<th>Relationship</th>
<th>Equation</th>
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</thead>
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<td><strong>Adjusted heat load index</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><em>Dic pol</em></td>
<td>1, 79</td>
<td>61.7</td>
<td>&lt;0.0001</td>
<td>0.4385</td>
<td>linear</td>
<td>$y = -9.4883x + 7.1304$</td>
</tr>
<tr>
<td><em>The tre</em></td>
<td>2, 78</td>
<td>32.18</td>
<td>&lt;0.0001</td>
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<td>$y = -20.796x^2 + 19.114x + 0.112$</td>
</tr>
<tr>
<td><em>Isc ind</em></td>
<td>3, 77</td>
<td>19.21</td>
<td>&lt;0.0001</td>
<td>0.428</td>
<td>cubic</td>
<td>$y = 163.82x^3 - 129.76x^2 + 32.14x - 0.0057$</td>
</tr>
<tr>
<td><em>Eul pha</em></td>
<td>1, 79</td>
<td>6.96</td>
<td>0.01</td>
<td>0.081</td>
<td>linear</td>
<td>$y = -1.1449x + 2.0868$</td>
</tr>
<tr>
<td><em>Cym liv</em></td>
<td>3, 77</td>
<td>3.01</td>
<td>0.0353</td>
<td>0.1049</td>
<td>cubic</td>
<td>$y = -39.235x^3 + 31.439x^2 - 5.5862x + 1.7598$</td>
</tr>
<tr>
<td><em>Aru pur</em></td>
<td>3, 77</td>
<td>20.41</td>
<td>&lt;0.0001</td>
<td>0.443</td>
<td>cubic</td>
<td>$y = 61.112x^3 - 54.308x^2 + 16.559x - 0.0269$</td>
</tr>
<tr>
<td><em>Hyp gla</em></td>
<td>3, 77</td>
<td>2.97</td>
<td>0.0368</td>
<td>0.1038</td>
<td>cubic</td>
<td>$y = -56.878x^3 + 43.907x^2 - 7.5096x + 1.59$</td>
</tr>
<tr>
<td><em>Ana lep</em></td>
<td>1, 79</td>
<td>38.64</td>
<td>&lt;0.0001</td>
<td>0.3284</td>
<td>linear</td>
<td>$y = -2.5775x + 1.9665$</td>
</tr>
<tr>
<td><em>Swe cor</em></td>
<td>3, 77</td>
<td>5.19</td>
<td>0.0026</td>
<td>0.1683</td>
<td>cubic</td>
<td>$y = -69.591x^3 + 58.554x^2 - 13.117x + 1.2505$</td>
</tr>
<tr>
<td><strong>Slope</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dic pol</em></td>
<td>1, 79</td>
<td>10.62</td>
<td>0.0017</td>
<td>0.1185</td>
<td>linear</td>
<td>$y = -0.146x + 8.4196$</td>
</tr>
<tr>
<td><em>The tre</em></td>
<td>1, 79</td>
<td>9.27</td>
<td>0.0032</td>
<td>0.105</td>
<td>linear</td>
<td>$y = 0.1368x - 0.5012$</td>
</tr>
<tr>
<td><em>Isc ind</em></td>
<td>1, 79</td>
<td>22.94</td>
<td>&lt;0.0001</td>
<td>0.225</td>
<td>linear</td>
<td>$y = 0.1484x - 1.4275$</td>
</tr>
<tr>
<td><em>Eul pha</em></td>
<td>1, 79</td>
<td>0.07</td>
<td>0.7971</td>
<td>0.0008</td>
<td>no relationship</td>
<td>$y = 0.0035x + 1.7459$</td>
</tr>
<tr>
<td><em>Cym liv</em></td>
<td>1, 79</td>
<td>0.71</td>
<td>0.4025</td>
<td>0.0089</td>
<td>no relationship</td>
<td>$y = 0.0091x + 1.5583$</td>
</tr>
<tr>
<td><em>Aru pur</em></td>
<td>1, 79</td>
<td>8.39</td>
<td>0.0049</td>
<td>0.096</td>
<td>linear</td>
<td>$y = 0.0592x - 0.101$</td>
</tr>
<tr>
<td><em>Hyp gla</em></td>
<td>1, 79</td>
<td>0.55</td>
<td>0.4591</td>
<td>0.007</td>
<td>no relationship</td>
<td>$y = -0.0106x + 1.8525$</td>
</tr>
<tr>
<td><em>Ana lep</em></td>
<td>1, 79</td>
<td>1.4</td>
<td>0.2409</td>
<td>0.0174</td>
<td>no relationship</td>
<td>$y = -0.0176x + 1.7957$</td>
</tr>
<tr>
<td><em>Swe cor</em></td>
<td>2, 78</td>
<td>3.45</td>
<td>0.0368</td>
<td>0.0812</td>
<td>quadratic</td>
<td>$y = -0.0032x^2 + 0.1202x - 0.1725$</td>
</tr>
</tbody>
</table>
Table 1.2 (continued)

<table>
<thead>
<tr>
<th>Species</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>$R^2$</th>
<th>Relationship</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Soil depth</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dic pol</td>
<td>1, 79</td>
<td>19.48</td>
<td>&lt;0.0001</td>
<td>0.1978</td>
<td>linear</td>
<td>$y = 0.2818x + 1.7983$</td>
</tr>
<tr>
<td>The tre</td>
<td>1, 79</td>
<td>12.02</td>
<td>0.0009</td>
<td>0.132</td>
<td>linear</td>
<td>$y = -0.2291x + 5.3081$</td>
</tr>
<tr>
<td>Isc ind</td>
<td>3, 77</td>
<td>5.43</td>
<td>0.0019</td>
<td>0.1746</td>
<td>cubic</td>
<td>$y = -0.008x^3 + 0.2851x^2 - 3.242x + 13.617$</td>
</tr>
<tr>
<td>Eul pha</td>
<td>1, 79</td>
<td>1.68</td>
<td>0.1991</td>
<td>0.0208</td>
<td>no relationship</td>
<td>$y = 0.0257x + 1.5377$</td>
</tr>
<tr>
<td>Cym liv</td>
<td>1, 79</td>
<td>1.68</td>
<td>0.1991</td>
<td>0.0081</td>
<td>no relationship</td>
<td>$y = -0.0129x + 1.9175$</td>
</tr>
<tr>
<td>Aru pur</td>
<td>1, 79</td>
<td>9.12</td>
<td>0.0034</td>
<td>0.1035</td>
<td>linear</td>
<td>$y = -0.0918x + 2.3301$</td>
</tr>
<tr>
<td>Hyp gla</td>
<td>1, 79</td>
<td>1.04</td>
<td>0.3119</td>
<td>0.0129</td>
<td>no relationship</td>
<td>$y = 0.0216x + 1.3579$</td>
</tr>
<tr>
<td>Ana lep</td>
<td>1, 79</td>
<td>1.96</td>
<td>0.1659</td>
<td>0.0242</td>
<td>no relationship</td>
<td>$y = 0.0309x + 1.0333$</td>
</tr>
<tr>
<td>Swe cor</td>
<td>1, 79</td>
<td>0.01</td>
<td>0.9405</td>
<td>0.0001</td>
<td>no relationship</td>
<td>$y = 0.0013x + 0.761$</td>
</tr>
</tbody>
</table>
Table 1.3. 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. Different superscript letters denote significant differences. 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Short, N = 18</th>
<th>Mixed, N = 22</th>
<th>Tall, N = 30</th>
<th>Lush, N = 11</th>
<th>Kruskal-Wallis H, P</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dic pol</em></td>
<td>2.15 ± 0.95&lt;sup&gt;a&lt;/sup&gt;</td>
<td>18.59 ± 4.54&lt;sup&gt;b&lt;/sup&gt;</td>
<td>47.16 ± 3.39&lt;sup&gt;c&lt;/sup&gt;</td>
<td>60.83 ± 5.95&lt;sup&gt;c&lt;/sup&gt;</td>
<td>68.31, &lt;0.0001</td>
</tr>
<tr>
<td><em>The tre</em></td>
<td>40.97 ± 6.64&lt;sup&gt;a&lt;/sup&gt;</td>
<td>14.8 ± 2.66&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.83 ± 1.07&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0&lt;sup&gt;d&lt;/sup&gt;</td>
<td>68.24, &lt;0.0001</td>
</tr>
<tr>
<td><em>Isc ind</em></td>
<td>15.65 ± 4.89&lt;sup&gt;a&lt;/sup&gt;</td>
<td>14.14 ± 3.62&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.21 ± 0.75&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.18 ± 0.24&lt;sup&gt;c&lt;/sup&gt;</td>
<td>51.69, &lt;0.0001</td>
</tr>
<tr>
<td><em>Eulpha</em></td>
<td>1.43 ± 0.54&lt;sup&gt;a,d&lt;/sup&gt;</td>
<td>4.07 ± 0.81&lt;sup&gt;b,c&lt;/sup&gt;</td>
<td>5.28 ± 0.74&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.46 ± 1.82&lt;sup&gt;c,d&lt;/sup&gt;</td>
<td>36.14, &lt;0.0001</td>
</tr>
<tr>
<td><em>Cym liv</em></td>
<td>4.39 ± 1.03&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.20 ± 0.75&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>3.63 ± 0.56&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>2.07 ± 1.18&lt;sup&gt;b&lt;/sup&gt;</td>
<td>9.64, 0.0219</td>
</tr>
<tr>
<td><em>Aru pur</em></td>
<td>7.56 ± 2.48&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.86 ± 1.11&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.68 ± 0.34&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0&lt;sup&gt;b&lt;/sup&gt;</td>
<td>60.22, &lt;0.0001</td>
</tr>
</tbody>
</table>
Table 1.4. 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. Different superscript letters denote significantly different means ($P < 0.05$). All variables except species richness have been back transformed for presentation.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Short, $N = 18$</th>
<th>Mixed, $N = 22$</th>
<th>Tall, $N = 30$</th>
<th>Lush, $N = 11$</th>
<th>ANOVA: $F$, $P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant height (cm)</td>
<td>22.43 ± 0.81$^a$</td>
<td>28.59 ± 1.49$^b$</td>
<td>42.19 ± 1.99$^c$</td>
<td>53.16 ± 3.31$^d$</td>
<td>43.28, &lt;0.0001</td>
</tr>
<tr>
<td>Species richness</td>
<td>19.39 ± 0.76$^a$</td>
<td>21.45 ± 0.73$^{a,b}$</td>
<td>22.77 ± 0.72$^b$</td>
<td>18.91 ± 0.67$^a$</td>
<td>5.32, 0.002</td>
</tr>
<tr>
<td>Shannon index</td>
<td>1.55 ± 0.07$^a$</td>
<td>2.09 ± 0.04$^b$</td>
<td>1.61 ± 0.05$^a$</td>
<td>1.16 ± 0.09$c$</td>
<td>50.42, &lt;0.0001</td>
</tr>
<tr>
<td>Graminoid biomass (g/m$^2$)</td>
<td>256.48 ± 15.32$^a$</td>
<td>323.52 ± 20.11$^{a,b}$</td>
<td>355.77 ± 24.12$^b$</td>
<td>477.18 ± 50.25$c$</td>
<td>8.17, &lt;0.0001</td>
</tr>
<tr>
<td>Forb biomass (g/m$^2$)</td>
<td>6.35 ± 2.01$^a$</td>
<td>9.80 ± 1.87$^{a,b}$</td>
<td>16.59 ± 3.19$^b$</td>
<td>13.55 ± 3.07$^{a,b}$</td>
<td>5.04, 0.003</td>
</tr>
</tbody>
</table>
Table 1.5. 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.

<table>
<thead>
<tr>
<th>Dependent Variable</th>
<th>df</th>
<th>F</th>
<th>model P</th>
<th>$R^2$</th>
<th>model</th>
<th>standardized coefficient (P value)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>soil depth</td>
</tr>
<tr>
<td>Species richness</td>
<td>2, 78</td>
<td>6.21</td>
<td>0.003</td>
<td>0.137</td>
<td>$\sqrt{\text{species richness}} = b_0 + b_1 \times \text{northness} + b_2 \times \text{soil-depth} + \text{error}$</td>
<td>-0.275 (0.018)</td>
</tr>
<tr>
<td>Diversity</td>
<td>2, 78</td>
<td>7.93</td>
<td>0.001</td>
<td>0.169</td>
<td>$\text{Shannon index}^3 = b_0 + b_1 \times \text{northness} + b_2 \times \text{slope} + \text{error}$</td>
<td>-</td>
</tr>
<tr>
<td>Biomass</td>
<td>2, 78</td>
<td>25.48</td>
<td>&lt;0.0001</td>
<td>0.395</td>
<td>$\log_{10}(\text{biomass}) = b_0 + b_1 \times \text{soil-depth} + b_2 \times \text{slope} + \text{error}$</td>
<td>0.525 (&lt;0.0001)</td>
</tr>
<tr>
<td>Graminoids biomass</td>
<td>2, 78</td>
<td>23.23</td>
<td>&lt;0.0001</td>
<td>0.373</td>
<td>$\log_{10}(\text{graminoids}) = b_0 + b_1 \times \text{soil-depth} + b_2 \times \text{slope} + \text{error}$</td>
<td>0.526 (&lt;0.0001)</td>
</tr>
<tr>
<td>Forbs biomass</td>
<td>2, 78</td>
<td>10.09</td>
<td>&lt;0.0001</td>
<td>0.206</td>
<td>$\log_{10}(\text{forb + 1}) = b_0 + b_1 \times \text{northness} + b_2 \times \text{slope} + \text{error}$</td>
<td>-</td>
</tr>
</tbody>
</table>
Figure 1.1a. Pristine shola-grasslands in Mukurthi National Park, the Nilgiris. Shola is the local word for stunted tropical montane forest.
Figure 1.1b. Invaded *shola*-grasslands in the foreground, dense plantation of black wattle and blue gum, reservoirs and intensively farmed slopes in the far ground.
Figure 1.2a. Shola-grassland sites in south India and similar landscapes called Patanas in Sri Lanka. All these sites share similar paleohistories and there is considerable overlap of plant taxa among these locations.
Figure 1.2b. Layout of sampled plots in the study area - Lakkadi, the Nilgiris.

Legend:

TWINSPLAN classified communities:

▲ *D. polyptychum* – *T. tremula* communities (mixed)  □ *T. tremula* – *I. indicum* communities (short)

○ *D. polyptychum* – *E. phaeothrix* communities (tall)  ● *D. polyptychum* communities (lush)

Contours are drawn at 10 m intervals
Figure 1.3. Distribution of 15 important plant species in the Nilgiris grasslands using CCA ordination biplot of species 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 gambeli*, *Swertia corymbosa*, *Themeda tremula*, *Tripogon bromoides*. 
**Figure 1.4.** 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 coenoclines for that environmental gradient. See Table 1.2 for the equations of the fitted lines and other relevant statistics. Species are represented by first three letters of the genus and species, see legend of Table 1.2 or Figure 1.3 for full botanical names of species.
**Figure 1.5.** 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 coenoclines for that environmental gradient. Lines for non-significant relationships are colored grey. See Table 1.2 for the equations of the fitted lines and other relevant statistics. Species are represented by first three letters of the genus and species, see legend of Table 1.2 or Figure 1.3 for full botanical names of species.
Figure 1.6. 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 coenoclines for that environmental gradient. Lines for non-significant relationships are colored grey. See Table 1.2 for the equations of the fitted lines and other relevant statistics. Species are represented by first three letters of the genus and species, see legend of Table 1.2 or Figure 1.3 for full botanical names of species.
Figure 1.7. CCA triplot showing the distribution of 15 important plant species and the 81 sampled plots in the Nilgiris grasslands along environmental gradients. The relevès are classified into the four communities viz., short (open squares), mixed (filled triangles), tall (open circles), and lush (filled circles). Species are represented by first three letters of the genus and species, see legend of Table 1.2 for full botanical names of species.

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CHAPTER TWO

Patterns of Scotch broom (*Cytisus scoparius*) invasion in high altitude grasslands of Nilgiris, south India.

Summary

I investigated age and size class structures of Scotch broom stands, and the effects of invasion on the native plant community, in the high altitude grasslands of the Nilgiris. Girth, height and age of Scotch broom stems were recorded in random plots. Native vegetation cover was assessed under broom and in surrounding grasslands. Age was positively correlated with girth and height of broom. Intermediate age classes were better represented than the younger classes in the sampled population. Although the recruitment appears to be briefly interrupted there was no evidence for a population decline. Species richness and diversity of native plants were negatively impacted by invasion intensity but not duration. But invasion also facilitated some shade-tolerant native plants.

Introduction

Grasslands and savannas worldwide are undergoing phenomenal transformations in structure, composition and ecosystem function due to expansion of woody invasive plants (Brown and Archer 1999, Levine et al. 2003). Changes in relative proportion of woody and herbaceous biomass bring about structural modifications, while displacement of original species or release of new species can alter the composition of the plant community (Hobbs and Huenneke 1992, Rose et al. 1995, McPherson 1997). Dramatic shifts in patterns of dominance and distribution in native plant communities can not only lead to the extinction of less common plant species (Morgan 1998), but can also impact the populations of native fauna, directly through availability of food resources and habitat, and indirectly through competitive interactions (reviewed in Levine et al. 2003). Establishment of exotic plants is often facilitated by the disturbances in the landscape (Hobbs and Huenneke 1992). As soon as a self-sustaining population is established most species modify existing disturbance regimes, or create new disturbances and transitional states, that affect ecosystem structure and function (Mack and D'Antonio 1998).

The grasslands of the upper Nilgiris are home to several endemic flora and fauna (Rawat et al. 2003). The grasslands are being fast closed in by various exotic species (Rawat et al. 2003, Zarri et al. 2006; personal observation). Invasion by *Chromolaena odorata*, *Cytisus scoparius* and *Ulex europaeus* was first reported in the late 1930s (Ranganathan 1938). Wattle (*Acacia mearnsii*), planted extensively in the latter half of the nineteenth century, has become naturalized and is now fast encroaching the grasslands (Rawat et al. 2003; personal observation). *C. scoparius* (Scotch broom or broom) appears to be dominating vast sections of the grasslands in the Nilgiris (Zarri et al. 2006; personal observation). Though concern over expansion of broom has initiated attempts to test the efficacy of various chemical and mechanical methods (Zarri et al. 2006), little has been done to understand the mechanism of invasion and its impact on the native flora.

The majority of weed control programs are discontinued after initial trials, as the potential threats posed by exotics are not well perceived; other reasons are the high costs of weed eradication, and the existence of doubts regarding the effectiveness of control methods (Pimentel et al. 2000). Scientific documentation of negative effects of exotic invasion is essential to provide impetus to any eradication program. Similarly, it is imperative to understand the population ecology, including factors responsible for establishment and persistence, not only to determine types and levels of control, but also to target the life-stage of the weed that might be most vulnerable to a given control method (Paynter et al. 2000a).

Age and size class structure are good indicators of the health of plant populations, specifically regeneration patterns (Agren and Zackrisson 1990). In stable populations, there is highest
representation of smaller and younger individuals, while the larger and older individuals are poorly represented. The age and size class distribution of such a population produces a characteristic reverse J-shaped curve (Agren and Zackrisson 1990), or an exponential decline. I hypothesized that the above described pattern will be seen in the broom population sampled in upper Nilgiris if they are stable, assuming age and girth are positively related.

Invasion of woody exotic plants is often associated with decline in species diversity and biomass of herbaceous native plants (Levine et al. 2003). So, I hypothesized that there will be a negative relationship between species diversity and biomass of native plants, and invasion intensity. Further, this pattern may also be influenced by the duration for which the infestation has been present at a particular site. A survey was carried out in sites invaded by broom in the high altitude shola-grasslands of Nilgiris to test the above hypotheses.

Methods

Study area

The Nilgiri Hills, an integral part of the Western Ghats complex, is located between 11°10’ and 10°30’ N, and 76°25’ and 77°00’ E, at the junction of the Eastern and Western Ghats. The altitude in the upper areas of the Nilgiris ranges from 1800 to 2500 m above msl. May is the warmest month with a mean maximum temperature of 25 °C, while January is the coolest month with a mean maximum temperature of 5 °C. The Nilgiris experiences two wet periods, the first receiving rain from the South West Monsoons between June and September, and a second post monsoon period between October and December. The western regions of the plateau receive rainfall in the range of 3000mm and exceed 5000mm in certain sites. The bedrock of the Nilgiris consists of Precambrian rocks, chiefly gneisses, charnockites and schist (Sukumar et al. 1993). The soils are classified as non-allophanic andisols (Caner et al. 2000). The natural vegetation of the upper regions is classified as Southern Montane Wet Temperate Forests and Montane Grasslands (Champion and Seth 1968). The montane vegetation consists of patches of stunted evergreen forests (locally referred to as ‘sholas’) surrounded by grasslands. There is a sharp ecotone between the sholas and grasslands, and this “dual climax” (Meher-Homji 1967) had been attributed to in the past, to a combination of factors--frost, fire and grazing (Ranganathan 1938, Meher-Homji 1967). 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 and Palmer 2007).

This study was restricted to the area around Upper Bhavani Reservoir, specifically the Lakkadi area (Nilgiris South Division), in the southwest corner of the Nilgiris plateau. This region fringes with the Mukurthi National Park, which is prime habitat of the endangered and endemic Nilgiri Tahr (Hemitragus hylocrius). These regions are well protected relative to other parts of the Nilgiris. However, invasion by the exotic shrubs Scotch broom (Cytisus scoparius) and grouse (Ulex europaeus) is prevalent here. Acacia plantations occur scattered throughout the landscape. A typical view of the hills in Lakkadi presents Acacia saplings climbing down the hills and Scotch broom climbing up, thereby sandwiching the grassy stretches.

Study plant

Scotch broom is a polycarpic perennial plant, native to parts of central and western Europe (Rees and Paynter 1997). This leguminous shrub grows to nearly 3 m tall in the study site. Plants exhibit plastic traits; in the Nilgiris, it is seen in a range of habitats ranging from open high altitude grasslands (c.a. 2200 m) to Eucalyptus plantations at slightly lower elevations, and leaves are broader in plants growing under tree cover than in open grasslands. Scotch broom seeds and seedlings germinate and survive better in disturbed sites (Paynter et al. 1998); seeds remain viable in seed banks for decades (Smith and Harlen 1991, Bossard 1993). Plants were in flowering and fruiting condition during the study period from May to August 2005. The earliest published reports of broom invasion in the Nilgiris date back to 1938; it
Vegetation sampling

The study was carried out between June and July 2005, and plots were set up in the Lakkadi grasslands, large areas of which were occupied by broom thickets. Eighteen 25 m² (5 m x 5 m) plots were setup in or around broom thickets of similar topographic position, such that the centre of the plot roughly coincided with the centre of the thicket. The girth at base of all the broom shrubs in the plot was measured. Subplots (1 m x 1 m) were placed at three randomly selected points by casting a 1 m x 1 m frame over the shoulder while standing at the corners of the plot. Broom individuals encountered within the 1 m x 1 m subplots were cut at the base to count the growth rings to determine the age, girth at the base, and height from the base to the tip of the longest branch, which was measured prior to harvest of the these individuals. Small seedlings (< 0.5 cm) were not enumerated as the majority of the young seedlings are not likely to survive (Downey and Smith 2000) and also because they were too numerous to count under monsoonal weather conditions. The cover of native grasses and forbs was assessed within each of these subplots by estimating the relative contribution to cover of each species. Estimates were made by placing a 1 m x 1 m frame (divided into 10 grids of equal size) on the ground over the herbaceous vegetation. If species 'X' covered half the area of one grid (10cm x 10cm) it's cover was estimated at 5%; the percent cover for various species was averaged among the 3 subplots to arrive at an estimate for the 25 m² plots in which they were nested. Biomass of the native herbaceous plants was measured by harvesting 0.1 m² of biomass by clipping at ground level from the centre of each subplot. Biomass samples were returned to the field station oven dried at 80 °C until constant mass and their weights were recorded. Similarly, eight 5 m x 5 m plots were set up in uninvaded grassland patches adjacent to broom stands. Measurements of species richness, species cover and biomass were made in these plots. I was unable to sample more plots due to time constraints.

Data analysis

Histograms of age and size of broom were constructed to discern patterns in population structure and regeneration dynamics of broom stands. Correlations were used to examine the strength of the relationships between age and girth, and age and height of broom plants; also, regression analyses were performed to examine the nature of these relationships. Basal area of broom within a 25 m² plot was considered as a measure of the invasion intensity. This was regressed against species richness, diversity and biomass of native plant species to understand the nature of the change in native plant structure and community in relation to broom invasion. Average age of broom within each plot was regressed against native species parameters to test if duration of infestation at each plot influenced community structure of native species. Diversity was calculated using the Shannon index as $H' = -\sum p_i \ln(p_i)$ (Magurran 1988), where $p_i$ represents the mean (averaged among the 3 subplots) proportional contribution of the $i$th species to the canopy.

Mann-Whitney U-tests were used to test for significant differences in species richness, diversity, and biomass of native plant species between the uninvaded grassland plots (N = 8) and broom sites (N = 18). Native species were classified into two functional groups namely graminoids and forbs to examine the response of each of these groups to broom invasion.

SAS 8.2 (SAS 2008) was used for the statistical analyses.

Results

Age and size structure

Age of the broom plants ranged from less than a year to a maximum of 13 years (mean ± SD = 4.8 ± 0.23, N = 157). Age was positively correlated with girth ($r = 0.69, P < 0.001$) and height ($r = 0.64, P <$
0.001) linearly (Figure 2.1). Age explained 44% of the variance in girth and 35% in height. The trends from the regression suggest that girth could be a better indicator of the age of a plant rather than the height. The characteristic reverse J-shaped curve was not observed in the age and size class structures of the broom plants in the study area (Figure 2.2). The regeneration appears to have been interrupted recently as suggested by the low numbers of seedlings and individuals aged less than 3 years encountered during the surveys. Similar patterns of fewer numbers of smaller individuals were observed in the height structure distribution of the population.

**Effect of broom invasion on native plants**

Mean species richness (grassland = 13.75, broom = 8.0, \( P = 0.013 \)) and biomass (grassland = 13.34 g 0.1 m\(^2\), broom = 6.18 g 0.1 m\(^2\), \( P = 0.045 \)) of native vegetation were significantly different in scotch broom stands and adjacent uninvaded grasslands. However diversity did not significantly decrease due to the presence of broom (grassland = 1.52, broom = 1.15, \( P = 0.217 \)). But within the broom stands, a significant quadratic fit was observed for species richness (\( R^2 = 0.25, P = 0.12 \)) and diversity (\( R^2 = 0.46, P = 0.001 \)) with invasion intensity as measured by basal area of broom in the 25 m\(^2\) plots (Figure 2.3). Species richness and diversity of native plants were least at intermediate intensities of invasion compared to low and high levels of invasion. However there was no significant relationship between herbaceous native biomass and invasion intensity. The average residence time of broom, in other words, the mean duration for which broom stands were present in the 25 m\(^2\) plots, did not influence any of the native plant community parameters mentioned above.

Though over 60% of the native plant species encountered were forbs, they accounted for only 11% of the total cover across all the plots sampled, while grasses and sedges constituted 88% of the total native plant cover. Among the graminoids, *Isachne kunthiana* was dominant under broom stands, while *Dicanthium polyptychum* and *Chrysopogon zeylanicum* dominated the grassland sites (Figure 2.4a). Among forbs, *Hypochaeris glabra* was found in comparable numbers in both broom and grassland plots. Certain species such as *Justicia latispica* and *Fragaria nilgerrensis* were found only under broom stands, while *Curculigo orchiodes* and *Leucas suffruticosa* were more common in grasslands than in broom plots (Figure 2.4b). However, most of these differences were not statistically significant. Percentage cover of *Leucas suffruticosa* and *Isachne kunthiana* were significantly different (at the \( P = 0.05 \) level) between grassland sites and under broom stands. Some of the graminoids and forbs that were recorded under broom and not in the sampled grassland plots appeared to be common in the grassland in general, suggesting that the grassland was under-sampled.

**Discussion**

Strong correlations between age, girth and height of broom plants as reported from this site, have been well documented in New Zealand, Australia and France (Paynter et al. 2003). These trends can be interpreted as the growth of broom being uniform over time. Paynter et al. (2003) found that age explained 88% of variance in stem diameter, and 66% of variance in height. I found that age explained only 44% and 35% of variance in girth and height respectively, and these were statistically significant. The aforementioned age structure studies were conducted in temperate regions where there are stark differences between summer and winter temperatures relative to the Nilgiris. The low difference between summer and winter temperatures possibly resulted in growth ring patterns that are not as discrete as might be seen in temperate regions. The indistinct patterns may have lead to the subjective estimation of age in some cases, which in turn reduced the explanatory power of my model. Additionally, *sambar* (deer) browsing of broom (Zarri et al. 2006; personal observation), which is common in the region, would have affected the model. Thus, girth was considered to be a better predictor of age than height.
Out of the nine sites surveyed by Paynter et al. (2003), only five exhibited appreciable number of individuals in the lower age classes, yet they failed to see the characteristic reverse J-shaped curve in most of the sites. However, open sites had a slight tendency to exhibit this exponential decline. I found similar patterns as encountered in the open sites surveyed by Paynter et al. (2003). Parker (2000) has observed in the prairies of western United States, progressively higher numbers of individuals with increasing adult size. Though this may appear to be the feature of a declining population, she asserts that despite these trends, models predict that the species can maintain self-sustaining populations for indefinite periods, owing to persistent seedbanks of broom. Year round flowering and fruiting of broom, except during the monsoons, was reported by Zarri et al. (2006) in the Nilgiris grasslands, but I observed flowering and fruiting in the monsoon season as well. The recruitment decline observed in my site, as evidenced by the relatively lower numbers of young individuals, could be speculated as an undocumented increase in seed predation or seedling mortality, or conditions inhibiting germination of seeds, for example, lack of dormancy breaking factors. Also, it must be kept in mind that my sampling discounted numerous small seedlings.

It was interesting to observe that sites with intermediate levels of broom invasion showed the maximum loss in native species richness and diversity. This is contrary to the Intermediate Disturbance Hypothesis (Connell 1978), according to which intermediate levels of disturbance support higher diversities primarily due to the fact that heterogeneity would allow the full range of species traits to coexist and lead to maximal species diversity (Tilman 1999). I believe the following process might explain the low diversity at intermediate invasion intensities seen in my study: the herbaceous plant community in the shola-grasslands consists of light demanding grassland species, and shade specialist _shola_ species. As broom invades the grasslands, light demanding species are steadily eliminated; however as the thickets increase in density, shade specialist species, dispersed from the adjacent sholas, establish themselves and predominate. Average age of the broom stands was not correlated with the density of the stand, and did not control species richness, diversity and biomass of native plants. It would be worth testing whether different trends emerge when sampled across a larger landscape.

Despite disparity in the number of plots sampled in grasslands (N = 8) versus broom stands (N = 18), significant differences emerged in species richness and biomass of herbaceous vegetation. Though the species richness and biomass of native plants do not show a clear decline with broom densities, presence of broom itself affected the plant community parameters. Although the species diversity values were not very different (P = 0.145) between broom stands and grassland plots, the composition of native plants differed in patterns of dominance, suggestive of species replacement rather than loss. _Isachne kunthiana_, a broad leaved, shade tolerant grass, contributed to much of the biomass under broom stands, while _Dicanthium polyptychum_ and _Chrysopogon zeylanicum_, which are among the dominant species in these grasslands, were almost completely eliminated under broom. Paynter et al. (1998) and Sheppard et al. (2002) found that reducing the effects of competition by native vegetation can favor the survival and early flowering of broom. Dramatic loss in native species richness and cover has been reported in a recent study in a subalpine habitat in Australia (Wearne and Morgan 2004). Exotic plants are often implicated in modifying soil properties that might affect the success of native plants (Cannon et al. 1995, Evans et al. 2001). Other mechanisms of displacement of native plants by exotics include allelopathy and shading effects, competition for resources, and alteration of disturbance regimes among others (Lippincott 2000). Wearne and Morgan (2004) have attributed reduced light levels and accumulation of a thick litter layer under broom as barrier for germination of native forbs. The mechanisms by which broom displaces native vegetation might be various depending on the affected species, at least in the Nilgiris.
Implications for control

The age structure data suggests that recruitment of broom had been interrupted in the past two or three years. This species however has been known to be extremely successful in grassland ecosystems (Parker 2000) - seeds in the seed bank may not germinate for years (Smith and Harlen 1991, Bossard 1993) - and it may be premature to assume a declining trend in the population.

More research needs to be directed towards understanding the factors controlling establishment of broom in the Nilgiris. Researchers have listed several factors for the same, such as life history strategies of the species, in conjunction with dispersal, disturbances and competing vegetation (Parker 2000, Sheppard et al. 2002). These factors need to be examined in the Nilgiris context. Initial evidence of species loss and alterations in community composition and structure by broom increases the importance for extensive examination of patterns in species or community shifts.

Parker (1996) has reported that disturbances such as fire reduced seedling establishment of broom. Since fire has been a part of this landscape for several centuries, it may be considered as an efficient and inexpensive management tool in the Nilgiris. It might be worthwhile to experiment the use of fire. Some researchers (Rees and Paynter 1997, Syrett et al. 1999) have achieved reasonable success in broom removal with biocontrol agents. However such trials must be adopted with great caution in ecologically sensitive regions such as the Nilgiris. Chemical control has been tried in the Nilgiris (Zarri et al. 2006) and elsewhere (Gilchrist 1980, McCavish 1980), and the success of this might be evaluated to base future decisions on. Mechanical removal has been attempted in this site (Zarri et al. 2006; personal communication, A. C. Soundarajan); additional removal and monitoring of succession in eradicated sites will provide useful insights into the regeneration potential of native plants.
Figure 2.1. Relationship between (a) stem girth at base and (b) height, and age (years) of broom plants in the population.
Figure 2.2. (a) Age class and (b) girth class structures of the sampled plants in the broom population.
Figure 2.3. Regression of (a) species richness and (b) diversity, expressed as a Shannon-Wiener index, with basal area of broom as a measure of invasion intensity within the 25m² plots.
Figure 2.4. Comparison of cover of common species of (a) graminoids and (b) forbs in broom and grassland plots. Forbs from left to right: Hypochaeris glabra, Justicia latispica, Curculigo orchiodes, Fragaria nilgerrensis, Anaphalis leptophylla, Oxalis corniculata, Leucas suffruticosa. Graminoids from left to right: Isachne kunthiana, Dicanthium polyptychum, Carex brunnea, Eragrostis nigra, Elaeocharis congesta, Chrysopogon zeylanicum, Ischaemum indicum, Eulalia phaeothrix, Cymbopogon lividus. Means ± SE are shown. Significant differences (P < 0.05) between broom and grassland are marked with an asterisk (*).
CHAPTER THREE

Seedling germination success and survival of the invasive shrub Scotch broom (Cytisus scoparius) in response to fire and simulated grazing in the montane grasslands of the Nilgiris, south India

Summary
The spread of the exotic shrub Scotch broom in the montane grasslands of the Nilgiris is one of the major threats to biodiversity and ecosystem function there. It is likely that fire suppression over the past few decades is the proximate cause of expansion of broom populations. Biomass removal by graziers is relevant in the context of invasion as it can alter fire fuel and competitive environments. This study capitalizes on a wildfire event to examine fire effects on mature broom populations and soil seedbanks. Fire resulted in widespread elimination of mature broom stands but also stimulated broom soil seedbanks. However, this initial difference in seedling densities in burned and unburned plots was lost over time due to continuous recruitment in unburned plots. The effects of fire, simulated grazing and their interaction on seed germination were studied in a seed addition experiment. Plots in which fire fuel was reduced by clipping showed higher germination success, possibly because fire temperature was moderated by biomass removal. In another experiment non-dormant broom seeds were added after the wildfire to plots receiving clipping treatments. There were no differences in survival of broom seedlings in clipped versus unclipped plots. Burning of broom patches can be effective in eliminating mature stands and subsurface soil seedbanks. Seeds that are stimulated but not killed by the fire can be eliminated using repeated prescribed burns coinciding with the maturing of recruits. In the absence of repeated burning, grazing could interact with fire to pose an invasion risk if grazers severely reduced fire fuel in open grassland with large broom seedbanks.

Introduction
Extensive research has focused on the causes, consequences and control of exotic invasive species, and there is a substantial understanding of the complexities related to these topics (Drake et al. 1989, Hobbs and Huenneke 1992, Lodge 1993, Hobbs and Humphries 1995, Maron and Vilà 2001, Ehrenfeld 2003, Levine et al. 2003). However, this is still inadequate to effectively manage invasions; exotic species have the propensity to invade sites of varying conditions, and multiple species with widely differing traits can invade the same site, so the underlying principles related to invasion mechanisms and control are not always universally applicable. Invasion by both native and exotic woody plants is a common problem in grasslands, and the pervasive effects of invasive woody plants on native communities and ecosystem is well documented (Jackson et al. 2002, Grice 2004, Wearne and Morgan 2004).

The montane grasslands of the Nilgiris, south India, have shrunk due to naturally expanding exotic tree plantations and shrubs, besides other unsustainable land use practices. The invasion of the grasslands by the exotic shrub Cytisus scoparius (Scotch broom, hereafter broom), though not as dramatic in extent and expansion rate as Eucalyptus and Black wattle (Acacia mearnsii) plantations, is by no means a problem to ignore (see Figure 3.1). Literature dating back to the early 1900's (Ranganathan 1938, Meher-Homji 1967, Zarri et al. 2006, Srinivasan et al. 2007) cautioned about the spread of broom in the Nilgiris; recent studies highlighted the healthy population structure of broom in the Nilgiris grassland and its adverse effects on native plant communities and ecosystem function (Srinivasan et al. 2007; chapter 4). Broom invasion in grasslands is also a serious problem in other parts of the world, including Australia, New Zealand, South Africa, Canada (Hosking et al. 1998, Smith et al. 2000) and the Pacific Northwest (Bossard 2000).

The common methods employed in the attempts to control and eradicate broom in these habitats include the use of herbicides, mechanical removal, managing seed vectors, biological control and prescribed burning (Andres et al. 1967, Bossard 2000, Rice 2004). Although burning broom stands
appears to be an effective approach, the potential unintended consequences associated with burning, particularly widespread seedbank stimulation, stand regeneration, and unrecoverable fire damage to native vegetation, make its use highly debated (see Mobley 1954, DiTomaso et al. 2006). However, there have also been success stories (Agee 1996, DiTomaso et al. 2006). There is more evidence of fire deterring, rather than promoting, woody invasions in grasslands compared to other ecosystems (van Auken 2000, Roques et al. 2001). In the Nilgiris, indigenous pastoralists, the Todas have been systematically burning the grasslands for several centuries. However, reserve managers have suppressed fire in the past few decades. Whether the reason for preventing fires stems from the fact that fire is not essential to maintain this ecosystem, or that it may attract unfavorable public opinion, remains a conundrum. Nevertheless, reports (Kumar 1993, Srivastava 2002) and personal interviews consistently indicate that the woody exotics have greatly expanded since fire suppression.

Grazing is another important grassland disturbance that has been shown to directly and indirectly affect woody plant invasion in grasslands. This is mediated through seed dispersal, reduction of competition from the resident community, and by affecting fire frequency and intensity through alteration of fire fuel (Brown and Archer 1989, Hobbs and Huenneke 1992, van Auken 2000). The influence that grazers can have on broom regeneration in the Nilgiris grasslands is unknown, as is the interaction of fire with grazing.

The primary goal of this study was to assess the effectiveness of fire as a tool to deplete and possibly eliminate broom in the montane grasslands of the Nilgiris. This is a worthwhile exercise because other data show that fire does not negatively affect the native grassland community (see chapter 4). Additionally, I studied how fire interacts with grazing to influence broom seedling survival in the context of fire fuel conditions and competitor release. First, I examined the efficacy of fire in killing mature broom stands. I was specifically interested in determining whether fire selectively killed younger stems as opposed to thicker stems. Since fire stimulates seedbanks of broom by breaking dormancy, I examined whether the seedling density in burned broom stands was greater than that in unburned stands. Further, I followed a subset of these broom stands over time to test if seedling survival was influenced by burning. Since grazers, prominently sambar deer (Cervus unicolor), disperse broom seeds into open grasslands (Zarri et al. 2006), I assessed the effect of fire on seed germination and seedling survival in the open grasslands as well. Seed germination in burned areas may be greater than unburned areas, and the seedlings may have higher survival over the long-term due to reduced native competitors immediately after the burn. Grazing moderates fire temperature (Zimmerman and Neuenschwander 1984, Hobbs et al. 1991), therefore it is relevant to know if broom can recruit better in burned grazed sites; hence I compared recruitment in high and low fuel treatments. Higher density of seedlings in burned areas can conflict with the objective of using fire to control broom. Finally, I tested if clipping of native plants can promote broom seedling survival, because grazing can alter the competitive environment of the seedlings.

**Methods**

**Study area**

The Nilgiri Hills, an integral part of the Western Ghats mountains, is located between 11°10’-10°30’ N and 76°25’-77°00’ E. 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 a second from the northeast monsoon between October and December. The western regions of the plateau receive about 2500 mm of rainfall and exceeds 5000 mm in certain areas (see Caner et al. 2007 for detailed meteorological information). The soils are classified as
The natural vegetation in the upper Nilgiris consists of patches of stunted tropical evergreen forests (locally called *shola*) surrounded by 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 disturbances (see Thomas and Palmer 2007), but recent evidence has shown that the grasslands were present in the Nilgiris for at least 40,000 years BP (Caner et al. 2007), long before humanization of this landscape. The current accepted view is that the strong monsoon winds and frost during winter preclude expansion of the native tropical trees into the open slopes (see Caner et al. 2007, Thomas and Palmer 2007).

**Broom invasion in the study site**

Scotch broom is a polycarpic perennial shrub, native to parts of central and southwestern Europe (Rees and Paynter 1997). This leguminous shrub grows to nearly 3 m in height in my study site. Broom plants exhibit plasticity in traits: in the Nilgiris, it is seen in a range of habitats from open high-altitude grasslands (> 2300 m) to *Eucalyptus* plantations at slightly lower elevations, and the leaves are broader in plants growing under tree cover than in the open grasslands. In the Nilgiris, broom plants usually start flowering in the fourth year, flowering peaks from March to May. A single plant can produce several thousand seeds each year (Bossard 1990). Broom seeds germinate and seedlings survive better in disturbed sites (Smith and Harlen 1991) and seeds can remain viable in the seedbanks for decades (Bossard 1993, Paynter et al. 2003). Broom seeds exhibit physical dormancy and germination can be achieved by scarification of the seed coat by fire or other means (Abdallah et al. 1989). Scotch broom is believed to have been introduced into the Nilgiris by the British in the early 1900's (Ranganathan 1938). It was introduced as an ornamental for its bright yellow blooms.

The current study was conducted in a site called Lakkadi in the Upper Bhavani reservoir area located in the southwestern corner of the Nilgiris plateau. A typical view of Lakkadi presents a mosaic of various vegetation classes: wattle plantations on the hilltops and distinct patches of broom amidst patches of remnant grasslands (Figure 3.1a). The broom invasion tends to be thicker along the reservoir’s shoreline and among the ruins of makeshift houses that are scattered throughout the region. This pattern suggests that localized sites of soil disturbance may have been the stronghold of the invasion earlier on and it later spread to adjoining areas. The *sambar* deer which heavily use broom patches are suspected to be important dispersers in the Nilgiris (Zarri et al. 2006). Population structure patterns and the impact of broom stands on native plants in Lakkadi can be gleaned from Srinivasan et al (2007).

**Field methods**

A series of opportunistic experiments and surveys were employed to ascertain the impact of a wildfire event, which occurred at the end of March 2007, on mature broom stands (Figure 3.1b), and on soil seedbanks in broom invaded and uninvaded grasslands. An experiment was also conducted to test how removal of native competitors would affect broom survival.

**Surveys in broom stands**

A survey was carried out in October 2007 in burned broom stands to assess the impact of the wildfire on mature broom. The centers of thirty-three 5 x 5 m plots were located by walking distances in the range of 100 to 200 footsteps in compass directions selected at random. In each plot the basal area of all the stems were measured. Plants were examined closely and stems were broken to determine if they were alive. A total of 1629 stems were censused in 33 plots. The estimate may be slightly biased towards dead stems as some of the stems thought to have been killed by the fire were probably dead prior to the fire. However, it was usually possible to identify and eliminate previously dead stems, as these were charred completely, while the stems killed by the fire appeared cooked.

A onetime seedling survey was conducted in October 2007 to compare seedling densities in burned and unburned broom stands. The burned and unburned patches were in the same general areas and
were separated by a road that acted as a fire barrier. Broom seedlings were counted in 82 and 88 (1 x 1 m) burned and unburned plots respectively; plots were located in broom stands as described above. A seedling was defined as a broom plant measuring < 10 cm in height and < 5 mm in basal diameter, as this seemed to be the general size of seedlings aged less than one year.

In a subset (21 in unburned broom and 20 in burned broom) of the plots used for the above survey, seedlings enumerated during the initial survey were marked with a plastic tag and these plots were monitored for seedling germination and recruitment over an additional 12 month period. Seedling densities were measured in February 2008 in the dry season and after the initial census and finally in October 2008. New recruits were tagged during each sampling event.

Surveys and experiments in open grasslands

A survey similar to the monitoring of seedlings in broom invaded sites was conducted in the open grasslands as well. Twenty-one plots were located in the unburned grasslands close to (5 to 10 m) unburned broom plots of the previous survey and, similarly, 20 plots were located in burned grasslands. All these plots were monitored over a 12 month period similar to the survey of seedlings in the broom stands.

The wildfire also burned through an existing experiment in the open uninvaded grassland that involved broom seed addition to clipped plots. This allowed documentation of the effect of fire fuel conditions on seed viability. Fifty-four (1 x 1 m) subplots each located in a 5 x 5 m plot were studied. These larger plots were laid in a randomized complete block design; there were 54 plots total (18 plots in each of the 3 blocks). The vegetation in half of these plots (9 per block) was clipped to a height of 10 cm to simulate extremely intense grazing by sambar deer in this site (personal observation) and in other mountain grasslands in southern India (Sankaran 2005), while the rest were left unclipped. The clipped biomass was removed from the plots. Following the setup of the experimental plots the wildfire swept through all three blocks. Because each of the above subplots were seeded with 50 broom seeds prior to the fire, it allowed for assessing the effects of fire fuel on seed viability. The seeding procedure involved making a tiny scratch on the soil surface (where the soil was hard and dry) so that the seed could be inserted a few millimeters into the soil to prevent it from being washed away. Since the amount of biomass was substantially greater in the unclipped plots than in the clipped plots just prior to the wildfire, it is reasonable to expect that on average the fire temperature may have been hotter in the unclipped plots. Thus, the clipped plots are referred to as the low fire fuel treatment, while the plots that were not clipped prior to the fire are referred to as the high fire fuel treatment. Germinated seedlings were first marked with plastic tags in October 2007 and these subplots were sampled again in December 2007 to capture any subsequent germination.

To study the effect of clipping on seedling survival another set of 36 (1 x 1) subplots were each seeded with 50 non-dormant broom seeds two weeks after the fire, and a new clipping treatment was applied after the fire. The treatment levels included clipping to a height of 10 cm or no clipping. Physical dormancy was broken by repeatedly immersing the seeds in boiling water and liquid nitrogen (Abdallah et al. 1989). Twenty-seven of these subplots were located in the high fire fuel treatment plots of the experiment described above, and 9 subplots were located in 3 additional plots that were laid in each block. The additional plots had not been clipped prior to the fire and hence were similar in conditions to the 27 high fire fuel plots. Half the plots in each block were randomly assigned to be clipped, while the other half were left unclipped. Plots were first clipped in October 2007; the treatment was repeated in February 2008. Germinated seedlings were first marked with plastic tags in October 2007, the seedling subplots were monitored until late January 2009.

Data analysis

Descriptive statistics are reported for the number of broom stems that were dead and alive per plot, the basal area of dead and alive stems, and the density and total basal area of plots that had live stems.
Box and whisker plots were used to illustrate the distribution of basal areas of live and dead stems. A two sample\textit{t}-test for unequal sample variances was used to test for significant differences in mean seedling densities in burned and unburned broom stands. To understand broom recruitment over time in burned and unburned broom stands and grassland, repeated measures ANOVAs were run separately for the number of seedlings at each time point in broom stands and grasslands. Data were transformed to meet assumptions of ANOVAs. Proc GLM (SAS 2008) with a repeated statement was used to analyze the data. Terrain characteristics such as aspect - (northness and eastness) measures, slope, elevation, curvature and compound terrain index (also known as wetness index), were extracted from the ASTER Global digital elevation model (EOSDIS 2009) using ArcGIS ver. 9.2 (ESRI 1999-2006). The terrain variables were input as covariates in the ANOVA, and a stepwise backwards elimination procedure was used to eliminate non-significant covariates to arrive at the final model. The data from the fire fuel and the clipping experiment were both analyzed using repeated measures ANOVA as a randomized complete block design (Proc Mixed, SAS 2008).

Results

\textit{Fire effects on mature boom stands}

On average, fire killed 98.7\% of the broom stems surveyed in the 33 plots; of all the sampled plots only four had live stems. This is significant given that these stands were thriving before the fire. The mean number of dead and living stems per plot was 48.94 (± 11.9 95\% CI) and 0.61 (± 0.7), respectively. Individual plants were killed regardless of their girth (basal area) as indicated by the overlap in the range of basal areas between the two groups (mean basal area of stems: dead = 8 cm\textsuperscript{2}, range = 0.08 - 60.4 cm\textsuperscript{2}, live = 1.93 cm\textsuperscript{2}, range = 0.08 - 6.6 cm\textsuperscript{2}; see Figure 3.2). However, live stems were consistently found in plots that had low broom density (mean ± 95\% CI: 16 ± 9.63 vs. 54.07 ± 12.3) and low total basal area (76.06 ± 70.31 vs. 440.24 ± 72.06 cm\textsuperscript{2}). This suggests that the girth of the stems is not a factor in preventing top kill from fire, and higher girth does not ensure better survival.

\textit{Seedlings density in burned and unburned broom and grassland}

The mean number of seedlings in the burned broom stand was threefold higher than in the unburned stands when surveyed once 6 months after the wildfire (burned: 30 ± 3.14, N = 82; unburned: 9.01 ± 1.13, N = 88; t = 6.306, df = 101.75, P = <0.0001; Figure 3.3).

However, there were no overall differences in mean seedling densities between burned and unburned broom stands when the plots were followed over a period of 12 months. There was a significant interaction between treatment and time (\(F_{2,78} = 4.23, P = 0.0181\)). The initial significant difference seen in October 2007 (Figure 3.4; \(t = 2.34, df = 74.1, P = 0.0221\)) disappeared in February and October of the following year. The seedling densities increased significantly (via germination) over time in the unburned broom plots (Oct '07 to Feb '08: \(t = -4.38, df = 78, P = < 0.0001\); Oct '07 to Dec '08: \(t = -4.31, df = 78, P = <0.0001\)) but not in the burned broom plots.

Similarly, in the grasslands the mean seedling densities were higher in the burned plots compared to unburned plots 6 months post-fire in October 2007 (Figure 3.5; \(t = 1.82, df = 76.3, P = 0.073\)). But this difference was not maintained over time, as there was a significant rise in seedling densities in the unburned grasslands due to further recruitment from the seedbank (Oct '07 to Feb '08: \(t = -2.99, df = 78, P = 0.0038\); Oct '07 to Dec '08: \(t = -3.00, df = 78, P = 0.0036\)).

\textit{Effect of fire fuel and clipping on broom seedlings recruitment}

For the seeds planted prior to the fire, the overall broom seedling germination was significantly lower under high fire fuel conditions (\(F_{1,102} = 8.96, P = 0.0035\)) at both time points (Oct '07: \(t = 1.89, df = 102, P = 0.06\); Dec '08: \(t = 2.35, df = 102, P = 0.02\)) and further recruitment in both treatments was negligible.
For the non-dormant seeds planted after the fire, the clipping treatment failed to have an overall significant effect on the broom seedling germination or survival. But seedling densities decreased steadily (Figure 3.7; \( F_{3,134} = 9.40, P < 0.0001 \)) under both clipped and unclipped treatments, starting from December ’08.

**Discussion**

Since broom does not resprout, the overwhelming top killing of broom stands without girth discrimination suggests that fire is extremely effective in killing mature broom stands. Only four of the 33 sampled plots had live stems; these plots did not have different topographies which could potentially affect fire dynamics. Since live stems were consistently found in plots that had low broom density and total basal area, this suggests that the fire temperature in the low density plots may not have reached the critical threshold required to kill broom stems. All else being equal, fire temperatures increase with the amount of available fuel; Bailey and Anderson (1980) found that the hottest fire temperatures were recorded where shrub densities were the highest.

Extensive stimulation of broom seedbank in burned broom relative to unburned stands seen in the current study (Figure 3.3, Results) is also well documented elsewhere (Agee 1996, Bossard 2000). Fire breaks physical dormancy in broom by scarifying the seedcoat (Bossard 1993). Fire temperatures in the mature broom stands under dry conditions can be hot enough to annihilate a large proportion of broom seeds on the soil surface and in the organic horizon; Bossard (1993) has shown that heating broom seeds in soil to a modest temperature of 150 °C for 60 seconds can render them nonviable. However, the presence of a large persistent seedbank on the surface and buried in the soil (which can escape lethal temperatures) ensures widespread regeneration. According to Downey (2002 ), broom seedbanks can grow to over 60000 seeds per square meter. Hence, prescribed burning has often been advocated as a means to flush and deplete broom seedbanks which otherwise remain viable for decades (Agee 1996, Bossard 2000).

Monitoring burned and unburned plots both in broom invaded and open grasslands revealed that there was little or no further recruitment in burned plots while there was a significant increase in recruitment in both unburned broom and grassland plots. Perhaps this recruitment occurred during the interim months from October 2007 till the end of the second wet period in December 2007. The seedbank was probably exhausted in the burned sites but seeds in the unburned sites continued to continuously recruit from the seedbank. It is puzzling why the upward trend in seed recruitment was not maintained until October 2008 (Figure 3.4), because the first wet period for the calendar year is from June to August. One of the factors could be that the southwest monsoon in 2008 was unusually weak; but it is likely that there could be several other reasons, such as seedling predation. I observed a small green unidentified caterpillar feeding on several seedlings in October 2008; this was not seen in the previous year. Downey and Smith (2000) have reported that the majority of the broom seedlings experience chronic browsing until they are 50 cm tall and so there is high mortality in the first 3 years. Based on dung density data from the same site, Zarri et al. (2006) have reported that sambar deer preferentially use broom invaded habitats more than any other natural or semi-natural habitat.

According to these authors sambar deer prefer to browse on mature bushes over palatable native grasses. Also, the majority of sambar sightings were in broom invaded patches (personal observation). It is very likely that seedlings are being culled as a result of sambar foraging in the Nilgiris but I do not have data on how great these proportions are. In the United Kingdom, Paynter et al. (2000b) found that rabbits foraged heavily on broom seedlings and juveniles and significantly reduced survival and fecundity; but such effects were not seen with sheep grazing in Australia (Sheppard et al. 2002). While I agree with Zarri et al. (2006) that there is widespread browsing of shrubs, the majority of foraging in the broom habitats appears to be directed towards the secondary herbaceous native communities encountered under broom (personal observation).
The reduction in fine fuel achieved (by clipping the vegetation down to a height of 10 cm) seemed to exceed levels of biomass removal by herbivores even in the heavily grazed sites. The results suggest that heavy grazing can significantly increase germination by moderating fire temperatures. The proportion of germination success in open grasslands in December 2008 was 0.05 and 0.02 for low and high fire fuel treatments, respectively; this proportion was calculated based on the 50 seeds that were added to each experimental unit. The fire in open grasslands would be similar to that in my high fuel fire treatment. According to Parker (2001), a fecund broom shrub that produces 17000 seeds can broadcast 50 seeds to a 1 m² area roughly 4 m away; this estimate is based on her study populations in the glacial outwash prairie in Washington State. Since open grasslands are likely to have smaller seedbank sizes and lower germination success following burning, one could expect that the stimulation of meager seed pools in the grassland by burning is unlikely to pose a significant invasion risk.

Seedling survival was unaffected by clipping; the decline in survival in both treatments over time could be attributed to other stress factors or predation. In a study conducted in a similar grassland community consisting of perennial tussock grasses in New Zealand, the removal of tussocks reduced broom survival by exposing them to sheep grazing (Bellingham and Coomes 2003). Thus broom invasion in grasslands may be influenced by the role of grazers as seed dispersers rather than grazers as regulators of competition. Perhaps eliminating aboveground competition would be a critical factor in rangelands that are dominated by turf and fodder grasses where their rhizomatous network forms a mat-like growth that can potentially suppress young shrub seedlings through intense belowground competition. In an Australian grassland, Sheppard et al. (2000, 2002) found that sheep grazing increased broom seedling survival by possibly mitigating competition from native grasses.

Future directions and recommendations
The standard methods of weed control viz., mechanical, chemical and biological, have been sufficiently discussed for broom and related species (Swezy and Odion 1997). The advantage and disadvantage of each method varies with context. Herbicides such as 2, 4-D, and glyphosate are undoubtedly effective in killing broom and have successfully been used to kill a variety of noxious invasives (Bossard 2000), but these are also notorious for killing non-target native species. In the Nilgiris, Zarri et al. (2006) used these herbicides on broom stands and reported that the application killed several species of native plants. Thus, the use of broadcast herbicides is not an option for an eco-sensitive, biodiversity rich region such as the Nilgiris. Painting individual cut stems with glyphosate (LeBlanc 2001) may be safer, but this must be exercised with extreme caution and discipline. Mechanical methods of control, mainly uprooting shrubs, are effective in managing adults. But both use of herbicides and mechanical removal fall short of depleting the persistent seedbank. In the Pacific Northwest and California grassland managers and researchers have advocated using fire to control and eradicate broom, often in conjunction with standard methods (DiTomaso and Johnson 2006). For example, slashing the growth in the regenerating stands and allowing it to dry in place before burning, or supplementation with additional biomass where needed, is recommended (Bossard 2000). However, there is some hesitation to burn broom in France as fire causes considerable damage to the ground flora (Paynter et al. 1998). This may not be a serious concern in the Nilgiris because, until a few decades ago, these grasslands were systematically burned for several centuries. These historical fires are said to have been conducted at intervals of 2 to 3 years. Hence the native plant community may have undergone continuous selection for fire tolerance. A simultaneous study (Srinivasan, unpublished) that compared plant composition in burned and unburned areas, both under broom and grassland, found that the recovered communities in the burned areas were almost indistinguishable compared to their corresponding unburned treatments just 18 months post-fire. As seen in the Nilgiris, grassland studies elsewhere have demonstrated the resilience of plant communities to burning (Jacobs and Schloeder 2002, Sankaran 2005). Fire effects on grassland fauna are seldom generalizable. A review (Swengel 2001) of fire effects on insect communities and population in
open habitats found that broadly, insect communities were quick to recover from fires, unless the events were frequent. Nonetheless, the burns must strictly target only broom stands and must be contained within them. Uncontrollable fires will be disastrous to the rich grassland fauna of the region, besides accelerating the rate of soil erosion by several folds as seen elsewhere (Johansen et al. 2001). Repeated burning of broom stands has been advocated as an effective control method (DiTomaso and Johnson 2006). An initial fire will kill mature stands, stimulate the seedbanks and deplete them to a large extent; the follow-up burns will be effective in eliminating recruits. I recommend landscape scale future experiments to test a similar strategy in the Nilgiris to manage the broom invasion problem here. According to Zarri et al. (2006) broom starts reproducing after four years in the Nilgiris. Hence the follow-up burn must be done just before the recruits start reproducing and augmenting the seedbanks. This time interval will also allow for the growth and accumulation of the biomass of weedy grasses that will provide the fine-fuel needed to sustain the spread of fire within the stands, as availability of ample fire fuel is often cited as a major obstacle for exercises involving prescribed burning (Bossard 2000). I also recommend that detailed studies on the impact of fire on native biota and ecosystem process and services be undertaken within the framework of the proposed fire experiments before the implementation of repeated fire as a management practice in the Nilgiris to control and eradicate broom.
Figure 3.1a. Scotch broom invasion in Lakkadi grasslands—mature stands in the foreground and in the valley beyond; black wattle plantations on the hill tops.
Figure 3.1b. Burned broom stands in the foreground, and unburned grasslands in the far ground.
Figure 3.2. Box-whisker plots showing the data spread of the basal area of individual live and dead stems. The box represents the data ranging from the first to the third quartile, and the horizontal line within the box marks the median. The lower whisker is the minimum data range while the upper whisker marks the inner fence (i.e. 1.5 x inter-quartile range). Extreme outliers lie outside the outer fence (i.e. 3 x inter-quartile range)
Figure 3.3. One time seedling density under burned (N = 82) and unburned (N = 88) broom stands. (a) Mean ± se of seedlings show with the data swarm for each group. (b) Box-whisker plots showing the spread of data points among the two groups. To interpret the boxes and whiskers, see caption of figure 3.2.
Figure 3.4. Seedling survival and recruitment in burned and unburned broom plots over a period of 18 months post-fire; the wildfire occurred in March 2007. Means ± SE are shown. Treatment data points at each time point were offset to enhance clarity and avoid overlap.
Figure 3.5. Seedling survival and recruitment in burned and unburned grasslands over a period of 18 months post-fire; the wildfire occurred in March 2007. Means ± SE are shown. Treatment data points at each time point were offset to enhance clarity and avoid overlap.
Figure 3.6. Effect of fire fuel conditions on broom germination success in the grassland, measured at the end of each wet season in that year. Means ± SE are shown. Treatment data points at each time point were offset to enhance clarity and avoid overlap.
Figure 3.7. Effect of experimental clipping of grassland vegetation on the survival of broom seedlings. Means ± SE are shown. Treatment data points at each time point were offset to enhance clarity and avoid overlap.
Exotic shrub invasion in a montane grassland: the role of fire as a potential restoration tool

Summary
In recent years, invasion of native grasslands by exotic woody plants has been recognized as a global problem with multiple adverse ecological and socio-economic consequences. Reasons for such expansions are numerous, including fire suppression. An important example of this problem is the native montane grassland in the Nilgiris of the Western Ghats in India, a biodiversity hotspot threatened by invasion of multiple woody species. In this study, the impacts of the highly invasive, nitrogen fixing exotic shrub Cytisus scoparius (Scotch broom) on the grassland community and ecosystem function have been quantified and the role of fire as a potential management tool evaluated. I established paired plots in uninvaded and broom-invaded grasslands that were either unburned or burned by an unplanned wildfire event. Invasion negatively impacted the grassland community structure and composition, favoring shade tolerant and weedy native plants, but did not greatly alter ecosystem function. Eighteen months after the fire, there were no notable fire-effects on the grassland communities or ecosystem properties. However, fire did decrease soil moisture and nitrogen levels in former broom patches. Taken together, the results suggest that fire might be an effective tool for broom control, as other research has shown that fire can kill broom stems. At the end of the study period burned-broom communities did not become more similar to uninvaded-grasslands; presumably the recovery process may be slow without additional management intervention.

Introduction
Rapid depletion of biodiversity and disruption of ecosystem function as a result of exotic plant invasion has been well studied from an ecological, environmental and economic perspective (Drake et al. 1989, Jackson et al. 2002, Pimentel 2008). Uncontrolled plant invasions in terrestrial environments, if allowed sufficient time, have the potential to transform the earth's landscape to a scale only second to anthropogenic habitat destruction (Vitousek et al. 1997, Mooney and Hobbs 2000).

Over the past century, invasion by exotic woody plants in grass dominated ecosystems has become a worldwide phenomenon (Brown and Carter 1998, Roques et al. 2001, Briggs et al. 2005), with adverse ecological and socio-economic consequences (Archer et al. 2000, Jackson et al. 2002). The displacement of herbaceous flora along with potential compositional changes in the native communities that accompany woody plant invasions often leads to trophic cascades (reviewed in Levine et al. 2003). A range of direct and indirect mechanisms including allelopathy, resource competition, shading and physical displacement, and modification of disturbance regimes contribute to the negative effects on native ecosystems (Levine et al. 2003, Wearne and Morgan 2004, Gooden et al. 2009). Once woody invaders are introduced into grasslands, their further establishment and spread are often promoted by disturbances such as fire, grazing and soil disturbances, though in some cases their absence can also lead to invasion (reviewed in Hobbs and Huenneke 1992, van Auken 2000). There are several examples of fire suppression promoting woody encroachments in grasslands (South Africa: Cowling et al. 1986, mesic grasslands of North America: reviewed in Briggs et al. 2005). Grazers rarely deter woody invaders in grasslands; in fact, they promote invasion by dispersing seeds, and creating safe sites for the establishment of invaders by reducing competition and disturbing soil (Brown and Carter 1998, Brown and Archer 1999, Drewa et al. 2001). Diversity and density of the herbaceous resident community, at best, has a minor role in resisting woody invasions due to niche separation between the two growth forms (Brown and Archer 1989, Bellingham and Coomes 2003, Sankaran et al. 2004).

The shrub Cytisus scoparius (Scotch broom, henceforth broom) is a nitrogen fixing, noxious invader of grasslands in many parts of the world (Hosking et al. 1998, Bossard 2000, Smith et al. 2000), and...
poses a significant threat to native biota. This shrub has made significant in-roads into the montane grasslands of the Nilgiris, an important region in the Western Ghats, which is ranked among the top eight global biodiversity hotspots (Myers et al. 2000). According to Zarri et al. (2006) the overall population of the endemic grassland bird Nilgiri pipit has dwindled due to broom invasion; they reported a fivefold decline in pipit densities in broom invaded grasslands. A small scale survey showed that herbaceous species diversity was negatively related to broom invasion intensity, in addition to compositional changes in the native community (Srinivasan et al. 2007). This is a major concern because the montane grasslands of the Nilgiris are known for their high degree of diversity and endemcity across plant and animal taxa (Gurukula Botanical Sanctuary 2005). Besides scotch broom, other woody exotics, coffee, tea and tree plantations of *Eucalyptus spp.*, *Acacia spp.* and *Pinus spp.* have covered large proportions of the montane grasslands in the Nilgiris. In general, there is greater appeal and potential for the Indian Forest Department to direct management efforts to control broom, rather than the exotic plantations that have long been nurtured by them. However, detailed documentation is needed to strengthen the cause for conservation action.

In the Nilgiris, indigenous pastoralists, the Todas, have systematically burned the grasslands for several centuries. Although reserve managers have suppressed fire in the past few decades, occasional wildfires do occur. Reports (Kumar 1993, Srivastava 2002) and personal interviews consistently indicate that the woody exotics have greatly expanded since the adoption of fire suppression practices. A recent wildfire that swept through some parts of the Nilgiris grasslands resulted in widespread death of mature broom stands. Further, there was no appreciable recruitment of broom associated with burning (chapter 3). Thus fire could serve as a potential tool to manage woody invasions in the Nilgiris. In addition, it would be advantageous if fire could reverse the effects of invasion by fostering the recovery of native plants and ecosystem function, and initiating a positive feedback loop between these two processes. For instance, topkill of mature broom can negate the common adverse effects of exotic shrubs viz., shading and alteration of soil chemistry (Archer et al. 2000). The simultaneous burning of the herbaceous secondary communities that characterize invaded sites may provide an establishment opportunity for shade-intolerant grassland specialists. The potential amelioration of site conditions over time in favor of native grassland species should make burned-invaded sites resemble uninvaded sites. This would imply that, following a realistic recovery period, for any measured community or ecosystem variable, burned-invaded sites should be similar to burned-uninvaded or even unburned-uninvaded sites, while the unburned-invaded sites should be distinct from the above three treatments. This is contingent upon the fire having little to no effects on the grassland community, assuming centuries of periodic burning has selected for fire tolerance. The perennial species, which are the predominant plants here, should resprout following burning.

The objectives of the current study are first, to quantify the extent to which broom invasion affects the plant community and ecosystem function in this landscape. Given the evidence for the negative impacts of shrub invasion on grasslands, (Parker et al. 1997, Wearne and Morgan 2004, Srinivasan et al. 2007), I predict that invasion will decrease native species richness and diversity and increase dominance. The herbaceous community composition in the broom invaded sites will be different from uninvaded grasslands. Ecosystem properties, in particular herbaceous biomass and soil properties, will be altered in invaded sites, as reported by other authors from grassland studies elsewhere (Lett et al. 2004, Knapp et al. 2008). Second, since these grasslands have historically experienced regular burning, I expect that this ecosystem will be resilient to burning; burned-grassland will resemble unburned-grasslands over a relatively short recovery period, with respect to the measured responses. Third, I examined the effectiveness of fire in dampening the negative effects of invasion. I predicted that the effects of fire will be stronger in invaded sites; their community and ecosystem properties will become more similar to uninvaded treatments over time. There will be a significant interaction between fire and invasion if the
above predictions are true for a measured response. The direction and the strength of the interaction will indicate the effectiveness of fire as a restoration agent.

Methods

Study area

The Nilgiri Hills, an integral part of the Western Ghats mountains, is located between 11°10′-10°30′ N and 76°25′-77°00′ E (Figure 4.1). 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 a second post-monsoon period between October and December. The western regions of the plateau receive about 2500 mm of rainfall and exceeds 5000 mm in certain areas (see Caner et al. 2007 for detailed meteorological information). The soils are classified as non-allophanic andisols (Caner et al. 2000). The natural vegetation in the upper Nilgiris consists of patches of stunted tropical evergreen forests (locally called shola) surrounded by 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 disturbances (see Thomas and Palmer 2007), but recent evidence has shown that the grasslands were present in the Nilgiris for at least 40,000 years BP (Caner et al. 2007), long before humanization 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 and Palmer 2007).

Broom invasion in the study site

Scotch broom is a polycarpic perennial shrub, native to parts of central and southwestern Europe (Rees and Paynter 1997). This leguminous shrub grows to nearly 3 m in height in our study site. Broom plants exhibit plasticity in traits: in the Nilgiris, it is seen in a range of habitats from open high-altitude grasslands (> 2300 m) to Eucalyptus plantations at slightly lower elevations, and the leaves are broader in plants growing under tree cover than in the open grasslands. In the Nilgiris, broom plants usually start flowering in their fourth year, flowering peaks from March to May. A single plant can produce several thousand seeds each year (Bossard 1990). Broom seeds germinate and seedlings survive better in disturbed sites (Smith and Harlen 1991) and seeds can remain viable in the seedbanks for decades (Bossard 1993, Paynter et al. 2003). Broom seeds exhibit physical dormancy and germination can be achieved by scarification of seed coat by fire or other means (Abdallah et al. 1989). Scotch broom is believed to be introduced into the Nilgiris by the British in the early 1900's (Ranganathan 1938). It was introduced as an ornamental for its bright yellow blooms.

The current study was conducted in a site called Lakkadi in the Upper Bhavani reservoir area located in the southwestern corner of the Nilgiris plateau. A typical view of Lakkadi presents a mosaic of various vegetation classes: wattle plantations on the hilltops and distinct patches of broom amidst patches of remnant grasslands (Figure 4.2). The broom invasion tends to be thicker along the reservoir’s shoreline and among the ruins of makeshift houses that are scattered throughout the region. This pattern suggests that localized sites of soil disturbance may have been the stronghold of the invasion earlier on and it later spread to adjoining areas. The sambar deer, which heavily use broom patches, are suspected to be important dispersers in the Nilgiris (Zarri et al. 2006). Population structure patterns and the impact of broom stands on native plants in Lakkadi can be gleaned from Srinivasan et al. (2007).

Field methods

A wildfire, which occurred in the end of March 2007, swept through a large part of the landscape; several hectares of grasslands, both invaded and unin invaded, were burned, but the presence of barriers
such as roads and water bodies prevented the fire from spreading to other potential sites. The patchy distribution of broom in the landscape allowed comparison of paired invaded and uninvaded sites within larger burned and unburned watersheds (Figures 4.1, 4.2).

A total of eighty-two 3 m² plots were located in the Lakkadi grasslands over an area of 3 Km² in October 2007. Pairs of plots were located such that one of the plots was in a broom thicket (about 10 m across); the other was located roughly 5 m away from the edge of the thicket in the open grasslands. Presumably this distance was close enough to minimize the site differences between plots, and at the same time far enough to avoid the effect of broom thicket on the adjacent plot. Thus the difference between the plots in each pair was assumed to be the presence and absence of invasion alone; care was also taken to avoid other obvious irregularities, such as the presence of rocky outcrops, when locating plots. Twenty such paired plots were located randomly in burned areas, and similarly, 21 pairs of plots were located in unburned areas. In burned patches the fire resulted in widespread death of adult plants that were reduced to dead stumps, while in the unburned broom stands, only a few mature stems were dead. Each plot was ‘L’ shaped and subdivided into three 1 x 1 m² subplots. One of the subplots was reserved solely for plant community sampling and care was taken not to disturb it. The other two subplots were used to measure ecosystem variables; this involved coring for soil samples and clipping for biomass. Plant community and ecosystem parameters were first measured in October - November 2007 in all the plots after the monsoons. Subsequent re-sampling of the plots was carried out in October 2008.

Vegetation sampling

The cover of native grasses and forbs was measured within each of these plots by estimating the relative contribution to cover of each species. Relative abundance estimates of plant species were made by placing a 1x1 m² grid of equal size) on the ground over the herbaceous vegetation. This generated a list of plants with their percent cover for each plot. Estimates of above ground biomass were made by clipping vegetation at ground level in a 0.1 x 1 m² strip. A different strip of vegetation was clipped during each sampling session and a 20 cm buffer was maintained between clipped strips. Clipped biomass was sorted into graminoids and forbs and weighed after oven drying at 60 °C for 72 hours.

Soil sampling

Plant available soil nitrogen (N: NH₄⁺-N and NO₃⁻-N) was measured during every sampling session; 2 soil cores (2.5 cm diameter x 10 cm length) from each plot were composited in the field and placed in Ziploc bags. These samples were stored over ice until they were brought back to the field station. Each composited sample was sieved using a 2 mm mesh. A known weight of a fraction of the soil was oven dried at 100 °C for 48 hours to estimate gravimetric water. Ten grams of the sieved sample was shaken with 50 ml of 1 N KCl for 2 hours to extract available soil nitrogen in the form of nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N). The agitated extracts were filtered using No. 2 Whatman filter paper after letting it stand overnight. Filtered extracts were collected in 20 ml scintillation vials and frozen for laboratory analysis at a later date. The concentration of N (NH₄⁺-N and NO₃⁻-N) was determined colorimetrically using a Bran Luebbe Continuous Flow Auto Analyzer II (Bran + Luebbe Inc., Delavan, WI, USA).

Data analysis

The plant community structure (species richness, diversity and dominance) and descriptors of ecosystem function (percent plant cover, graminoid and forb biomass, percent soil moisture and soil NH₄⁺-N; NO₃⁻-N data was excluded from the analysis as it was not detectable in the vast majority of the samples at both time points) were analyzed as a full factorial repeated measures ANCOVA (analysis of covariance) in a split-plot design. The paired invaded and uninvaded subplots together constituted a whole-plot, where whole-plots had received either burned or unburned treatments. In the analysis, the
subplots were treated as subjects and the random factor was defined by nesting paired subplots in whole-plots. The response variables were appropriately transformed where needed to meet the ANOVA assumptions. Six terrain characteristics (see below) measured at the subplot level were included as covariates in the model. The covariates were added as main effects only and no interaction terms involving covariates were included. Input terrain variables included elevation, slope (inclination), aspect (northness and eastness), curvature, compound topographic index (also known as wetness index), all extracted from the ASTER Global digital elevation model (EOSDIS 2009) using ArcGIS ver. 9.2 (ESRI 1999-2006). These variables encompass complex-composite gradients; for example, aspect encompasses other influences like insolation, the direction of monsoonal winds, and so forth. PROC MIXED (SAS 2008) was used for the analyses.

To detect changes in community composition among treatments and to quantify variation in species distribution explained by each treatment factor and their interaction a partial Canonical Correspondence Analysis (pCCA) was implemented in CANOCO v. 4.5 (ter Braak and Smilauer 2002). Separate analyses were conducted for data from 2007 and 2008. Species abundances were square-root transformed, and rare species were down-weighted. To test whether the inertia explained by each treatment was significantly stronger than expected by chance, I used a Monte Carlo Permutation Test with 9999 permutations. Variation (inertia) explained purely by fire was calculated by partialling out the effects of invasion by including it as a covariate; similarly fire was partialled out to calculate variance explained purely by invasion. The CCA was run as a split-plot design: while testing for the effects fire, the permutation test was run by randomizing only between whole-plots, and while testing for the effects of invasion, randomization was restricted within whole-plots. To measure the variance explained by the interaction of fire and invasion, the interaction term was included as the main effect while pure fire and pure invasion were partialled out. To remove the effect of the location of the plots from the species-environment matrix, the same terrain variables explained previously were used as additional covariates in all the above models. To construct the CCA diagram, data from both years were used in order to depict which treatment combinations converged over time in the species-environment space. To plot the centroids of treatment combinations, dummy variables for each combination were input as supplementary variables in CanoDraw v. 4.0 (Smilauer 1999-2002). To improve clarity, a few rare species were not shown in the diagram by adjusting the species weight range in CanoDraw.

The differences in the responses of common plants to fire and invasion were tested using non-parametric Kruskal-Wallis ANOVA. For this, species cover data was used only from the final sampling session. Common species were defined as those occurring in at least one-third of all the sampled plots. The species cover was standardized across treatments by dividing each cover value by the maximum cover value for that species.

Results

Species richness, diversity and dominance

There was an appreciable decline in species richness associated with broom invasion (Figure 4.3a-b, Table 4.1), both at six and eighteen months after the fire. Overall, fire did not affect species richness significantly (Table 4.1); there were no significant differences in species richness between burned and unburned grassland plots, and burned and unburned broom plots. Also, the interaction between fire and invasion was non-significant (Table 4.1), indicating that burning the broom plots did not increase species richness at either of the sampling points or over time. Trends in species diversity were identical to trends in species richness (Figure 4.3c-d, Table 4.1). Variance in both species richness and diversity were also partially explained by slope. Broom plots had higher dominance (as measured by the Simpsons' index) when compared to grassland plots regardless of fire treatment at both time points (Table 4.1). This difference between broom and grassland was more marked in the unburned pairs than
the burned (Figure 4.3e-f). However, there was no evidence to suggest that fire could decrease species dominance in invaded sites, as a significant interaction between fire and invasion was absent. Possible compositional changes were examined in further analysis.

**Community composition: CCA, partial CCA and variation partitioning**

The percent variation in species data explained jointly by fire and invasion at 6 months (14.12%) and 18 months (14.97%) post-fire was very similar. At both time points the variation explained by invasion was much greater than that explained by fire (Table 4.2). There was a marginal decrease in variation explained by fire at the second time point suggesting a slight reduction in fire-effects over time. The interaction between fire and invasion, though small, remained significant at both time points indicating that burning caused a change in community composition in invaded plots (also see Figure 4.4).

In the CCA analysis of combined community data from both time points, the overall ordination significantly explained 17.6% of the variation in species data (Monte Carlo test: F = 6.678, \( P = 0.0001 \)). The first CCA axis explained 12.8% of the above variation and was correlated with the presence or absence of invasion (see Table 4.3). The second CCA axis explained an additional 2.3% of variation and was related to fire. Besides being depauperate in species richness and diversity, the herbaceous plant community in broom invaded sites was distinct from uninvaded sites (Figure 4.4, 4.5). Albeit in low frequencies, several characteristic grassland species managed to survive in broom invaded areas. However, broom invaded sites were characterized by shade-tolerant graminoids (e.g. *Isachne kunthiana*, *Agrostis pilosula*, *Digitaria sp.*.) and a ruderal grass—*Eragrostis nigra*, and forbs (e.g. *Justicia latispica*, *Hypochoeris glabra*, *Erigeron mucronatus*, *Fragaria nelgerrensis*); except *E. mucronatus* all the other plants are native. Among the species listed above *I. kunthiana*, *Digitaria sp.*, *J. latispica* and *E. mucronatus* are particularly weedy. These species are not usually encountered in the open grasslands but are common along road sites, under tree plantations, near human habitation and also occur in special natural habitats such as the *shola*-grassland ecotone and minor riparian zones in the grasslands that invariably have a few *shola* trees. The effects of burning were most apparent in the broom-invaded sites earlier in the recovery process, six months post-fire; these sites had low species richness and also very low abundances. Thus, the group centroid of the burned-broom sites (in 2007) appeared in the area of the CCA graph that was devoid of species. Eighteen months post-fire, the plant community composition in burned-broom plots was transformed by an increase in frequency of the shade-tolerant grasses and forbs, and was not clearly distinguishable from unburned broom-invaded plots. The composition of burned grassland was distinct from unburned grassland sites six months after the fire, but these sites became more similar to one another over time. Also minor changes in community composition between the sampled years was seen for the unburned broom and grassland sites (see displacement between UB'07-UB'08 and UG'07-UG'08, Figure 4.4), suggesting there were general compositional changes in the community between the years. Taken together, the results show that fire effects on plant community composition in grassland sites are quite small; the changes in composition are more noticeable in invaded plots, and these showed a propensity to resemble unburned broom sites rather than the grassland sites.

**Species-specific responses**

Twelve species of native plants including grasses, sedges and forbs were common to one-third of the sampled plots. Of the six species of grasses four were particularly abundant or common in the uninvaded grassland (species in Figure 4.5b-e) while two (species in Figure 4.5a, f) were somewhat abundant in invaded patches. The former (characteristic grassland species) were severely impacted by invasion but clearly recovered from the fire over the 18 months; the latter grasses, which were facilitated by invasion, also recovered from fire. Particularly, *E. nigra* responded positively to fire in broom-invaded patches and attained levels of abundances higher than in unburned broom. Among the sedges, *Carex brunnea* was unaffected either by fire or invasion, while *Carex sp1* responded positively to
fire regardless of invasion. Of the four species of forbs that were evaluated *J. latispica* was promoted by invasion while *H. glabra* was significantly reduced in cover despite being present in most of the invaded plots. Both *H. glabra* and *J. latispica* were negatively affected by the fire, while the cover *Anaphalis leptophylla* increased in burned areas. Among the moderate to high frequency species, *Carex sp1* and *A. leptophylla*, both characteristic grassland plants, colonized burned broom patches. Overall, invasion had a strong negative impact on nine of the twelve species, regardless of the functional group they belonged to, whereas fire adversely affected only one forb—*H. glabra*.

**Cover and aboveground biomass**

There was a significant decline in plant cover with burning both in broom invaded and uninvaded sites (Figure 4.6a-b, Table 4.4); the reduction in cover was most dramatic during the first sampling period when the burned-broom plots were compared to their corresponding unburned treatment. The decrease in cover in the uninvaded-grassland plots, though statistically significant, was not as dramatic. Overall, cover was significantly reduced by invasion and the interaction of fire and invasion (Table 4.4). Plant percent cover in unburned-broom was not different from unburned-grassland treatment; this was consistent in both years. But plant cover was significantly lower in burned-broom when compared to burned-grassland in both years. Thus burning caused a disproportionate reduction in cover in broom invaded sites when compared to the grassland sites. The effect of time was significant due to a congruent increase in plant cover in all the treatments, from 2007 to 2008 (Table 4.4). However, the patterns and trends in the treatments and their interactions remained unchanged over time.

Graminoid biomass was comparable among the unburned treatments across both sampling time points (Figure 4.6c-d). Burning resulted in a significant decrease in graminoid biomass both in invaded and uninvaded plots, initially in 2007, but there was a notable increase in biomass over time in the same plots (see significant Fire x Time interaction in Table 4.4). Despite the statistically significant difference between burned-broom and burned-grassland, these treatments were mutually comparable and similar to levels seen in unburned grasslands in 2008. In addition to the treatment effects, variance in graminoid biomass was positively explained by ground curvature; downwardly concave slopes had greater biomass than convex slopes.

There were no statistically significant differences in forb biomass either between invaded and uninvaded sites or burned and unburned sites. Overall trends suggested that invasion seemed to depress forb biomass, and forbs seemed to have recovered slightly better in burned-broom sites compared to burned-grassland. (Figure 4.6e-f). Overall, there was an increase in forb biomass under all treatments in 2008 (Table 4.4). Patterns in forb biomass were also partially driven by (positively correlated) northness.

It appears that the recovery of biomass in the burned grassland sites is biased towards graminoids, and possibly towards the recovery of forbs in the burned broom sites (see Figures 4.6d, 4.3f).

**Soil moisture and nitrogen**

Unburned invaded sites had significantly higher levels of soil moisture than unburned-grassland in both years (Figure 4.7a-b), whereas burning always resulted in the convergence of soil moisture levels in broom and grassland plots. Variation in soil moisture was also explained by the covariates eastness (positive correlation), slope (negative correlation) and CTI (positive correlation) (Table 4.5).

Soil NH$_4^+$ levels in unburned broom and grassland sites were similar in both years (Figure 4.7c-d). Burning reduced N levels in broom plots and this pattern was consistent over time. Overall, the effect of time was significant because there was a corresponding decrease in soil N in 2008 with reference to 2007 levels (Table 4.5). Further, changes in soil N were partially associated with eastness (positive correlation), curvature (positive correlation) and slope (negative correlation) (Table 4.5).
Discussion

Community structure and composition

Invasion had a strong and significant negative effect on grassland community structure and composition. The effects of fire on the plant community were transient, and the grassland clearly recovered from burning in a relatively short period of time. Although the evidence for recolonization of characteristic grassland species in burned broom plots is scanty, the definitive recovery of native shade-tolerant plants is reassuring, as the presence of the vegetation can restore certain vital functions. For example, the soil is no longer completely exposed to erosion. Importantly, burning killed the mature broom stands and depleted broom seedbanks (see chapter 3).

The decline in species richness and diversity and the corresponding increase in species dominance, coupled with dramatic shifts in the community composition, in the presence of invasion are characteristic of shrub invasions in general (south-eastern Australia: Costello et al. 2000, Central Prairies: Briggs et al. 2005, Lett and Knapp 2005). Such patterns are no exception for Scotch broom invasion in grasslands (Parker et al. 1997, Sheppard et al. 2000, Wearne and Morgan 2004). All the dominant grasses characteristic of the open grasslands in the Nilgiris were almost completely eliminated by the invading broom stands. The presence of thick broom litter is usually the principal mechanism responsible for the decline of light demanding grassland species (Parker et al. 1997, Wearne and Morgan 2004). In a greenhouse experiment, Wearne and Morgan (2004) demonstrated that broom litter and shade severely depressed germination and growth of a dominant grassland forb. The shade-tolerant species in the present study were exclusive to, and abundant, in the invaded sites; nearly all of these are native species common in wooded areas in the upper Nilgiris (Srinivasan et al. 2007). Similarly, Lett and Knapp (2005) reported ten shade-tolerant forbs found only under clonal stands of the shrub Cornus drummondii which has invaded the Central Prairies in the United States; these forbs were otherwise found in nearby woodlands. This implies that reduction in light availability under broom could be an important driver of community shifts in the Nilgiris as well. Other mechanisms of broom impact on native ecosystems besides shading have been reported. Haubensak et al. (2004) was able to demonstrate the allelopathic effects of broom: Achillea sp. (family: asteraceae) grew only to one-third of its normal size when it was grown in soil collected from under broom. Yet another path by which native plants could be suppressed is by depletion of resources other than light, such as soil moisture and nutrients. It is suggested that the extent of suppression of native species could be positively correlated with broom density (Haubensak et al. 2004); presumably resource acquisition is proportional to stand density. Others have proposed that the duration of invasion could also be an important factor (Sheppard et al. 2002). In the Nilgiris, the density of broom stems is the main factor responsible for native species displacement rather than duration of invasion (Srinivasan et al. 2007).

The compositional dissimilarity between burned and unburned grasslands six months post-fire was more apparent than at 18-months post-fire: there was a considerable recovery in the burned grassland sites over time. Minor compositional differences persisted between burned and unburned grasslands at the end of the 18 month recovery period. However, it must be noted that the burned-grassland sites from 2008, though not quite as similar as unburned grassland sites from the same year, were almost indistinguishable from unburned-grassland sites from 2007 (Figure 4.4). The compositional differences between the burned and unburned grassland pairs 18 months post-fire could be attributed to a combination of two important factors. First, an inadequate recovery period: perhaps 18 months is too short a period for a predominantly C4 grassland community to recover, considering the year-round cold temperatures in these high elevation sites. Second, there were location differences between burned and unburned plots. It must also be noted that there were compositional changes between the years for the same treatment plots, probably because 2008 was an unusually dry year. Examining the results under these circumstances supports the conclusion that the community is at little to no risk of sustaining
damaging effects from a wildfire. Grassland communities differ in their resilience to fire events. The state of a recovered community is determined to a large extent by fire frequency and intensity (Anderson and Bailey 1980, Adams et al. 1982, Abrams and Hulbert 1987, Copeland et al. 2002, Jacobs and Schloeder 2002, Sankaran 2005). Jacobs and Schloeder (2002) and Sankaran (2005) found that burned sites were indistinguishable from unburned sites over a recovery period of two years.

To a large extent the herbaceous community under broom was resilient to burning both structurally and compositionally. This observation mirrors reports of alien grasses recolonizing invaded sites following fire events in many parts of the world (reviewed in D’Antonio and Vitousek 1992); here I consider the shade-tolerant colonizers under broom to be analogous to the alien grasses. In retrospect, the regrowth of the shade-tolerant species is no surprise as they are all native perennials which were historically restricted to disturbed, shaded environments such as the shola edges and riparian patches in this landscape. Though success stories are too few in the restoration case studies involving more passive methods of restoration, they do happen: Lett and Knapp (2005) reported that richness and diversity recovered to grassland values within two years since C. drummondii stands were removed from the Central Prairies. Although there were no signs of rapid colonization of characteristic grassland species in the Nilgiris over the observed time frame, it is likely to happen in the future in the absence of allelopathic, competitive and shading effects of broom.

Ecosystem function

The effects of invasion on ecosystem function were small where present. For most of the measured variables, the effects of fire were stronger in broom invaded sites than in the open grasslands. Plant cover was reduced by fire; this effect was stronger in broom sites than in grassland sites. The trends suggest that maximum cover can be attained in the burned-grassland sites sooner than in the burned-broom sites. Fire also reduced soil N, but only in the broom plots. However, there was no effect of fire on soil moisture, though the effects of invasion were significant.

Several studies have reported a loss in herbaceous cover due to woody invasion (van Vegten 1984, Braithwaite et al. 1989, Wearne and Morgan 2004). In the Nilgiris, the loss of shade-intolerant grassland species was compensated by the colonization of shade-tolerant weedy species. The plant cover in the burned-invaded treatment was much lower than the burned-grassland site and this difference was most dramatic six months post-fire. This is mainly because the characteristic grassland species, predominantly tussock grasses, have been replaced by shade-intolerant herbaceous plants in the invaded sites. The tussock grasses have substantial belowground investment while the shade-tolerant species lack these reserves. Further, much of the sub-surface rhizomes of the weedy grasses were burned away; hence there is a lag in the turnover of aboveground biomass under broom relative to the grassland sites. The same pattern was also reflected in the graminoid biomass. In another study, Lett and Knapp (2003) found that over two growing seasons following the removal of C. drummondii-shrubs the cover and biomass of graminoids fully recovered to levels comparable to open grasslands at the ecotone between the grasslands and the now cut shrub islands. They explain that the surviving graminoid rhizomes in this zone were able to exploit the pulse of light and nutrients during the recovery process.

There was a slight trend of increasing forb biomass with burning in broom sites and a decrease in grassland sites; though this was not statistically significant, it may be biologically meaningful. Several less abundant species of native forbs (e.g. Gentiana quadrifaria, Swertia corymbosa, Polygonum sphaerocephalum, Serpicula brevipes) which were virtually eliminated because of broom invasion appeared to recolonize burned-broom patches. In general, grassland forbs are less tolerant to fire and take a longer time to recover (Abrams and Hulbert 1987), while results from the present study suggest that the forbs in the invaded sites appear to respond better to disturbance. Lett and Knapp (2005) found that the biomass of forbs was twice as high in sites where C. drummondii was removed compared to open grasslands. A major fraction of this biomass was comprised of ruderal forbs; however, graminoid
production was not restored to reference levels over the two year period the authors monitored their plots.

Some of the covariates significantly explained the change in plant cover and graminoid and forb biomass in addition to the treatment effects. The covariate CTI, also referred to as the wetness index, is correlated with several soil attributes such as horizon depth, organic matter content and phosphorus (Moore et al. 1993). Hence plant cover should increase with CTI as it is a metric of resource availability. Since upwardly concave surfaces would collect more soil moisture, curvature can play a role in promoting the growth of dominant grasses; hence we see the relationship between graminoid biomass and curvature. As seen in a previous study (chapter 1), the forb biomass was negatively related to northness. This aspect favors dominant graminoids that suppress the abundance of forbs.

The higher soil moisture under unburned-broom compared to its grassland counterpart can be explained by the following mechanisms. It is possible that the shading and the thick broom litter could prevent moisture loss. It is also possible that hydraulic lift is operating under the broom stands: the water drawn from the deeper strata of soil by the deep broom roots during the day is released by the shallow roots at night, increasing the soil moisture in the upper strata (Caldwell and Richards 1989, Caldwell et al. 1998). We see a slight trend of decreasing soil moisture under burned broom; perhaps the loss of cover coupled with the absence of hydraulic lift makes the soil more prone to drying here. Soil moisture was explained by the covariates slope, eastness and CTI in decreasing order. Steeper slopes tend to be better drained than shallower slopes. Soil on the west-facing slopes, which has already been warmed by the morning sun is further dried by the afternoon sun (Perring 1960); hence the relationship with aspect. CTI is a wetness index which is derived from slope and drainage patterns in the landscape.

Overall, the soil N was lower in 2008 compared to 2007, possibly due to the low rainfall in 2008. Although the relationship between the amount of precipitation and N availability is complex and difficult to generalize, some authors have reported a positive correlation between soil moisture and N availability (Robertson et al. 1988, Dividson et al. 1990, Cain et al. 1999). The relationship of soil N with eastness, curvature and slope could be driven by moisture patterns as well. The levels of soil N in unburned broom and grassland sites were similar for both years. Since Scotch broom is a legume, higher levels of available N are expected in invaded sites due to N fixation. According to Haubensak and colleagues (2004) N mineralization rates were three times higher in broom invaded sites compared to control sites in Washington state. But studies have also reported that the N availability under N-fixing legumes is not considerably high because the plant uses a substantial amount of the N it fixes (Watt et al. 2003, Caldwell 2006). Also, the weedy vegetation under broom are resource-demanding (Grime 1977) and could be using up the available nitrogen.

Usually, a pulse of N is seen in grasslands after burning because N is converted from organic to inorganic forms primarily due to microbial release of immobilized nitrogen (Raison 1979). But over time, N levels decrease because there is a net loss of N from the ecosystem owing to volatalization from aboveground biomass and litter during the process of burning (Blair et al. 1998, Wan et al. 2001). I did not find an appreciable decrease in available soil N in the uninvaded-grassland after burning. However, burning did result in a significant decline in N levels in broom sites. Apart from volatile losses, and more importantly the loss of the N fixer itself, the weedy vegetation under broom sites may have assimilated the now reduced N budget, hence reducing the availability in soil. The reduction in soil moisture in invaded plots following burning could also be responsible for reduction in N levels for the reasons discussed earlier.

Conclusions and management recommendations

In the Nilgiris, broom invasion has proved to be catastrophic to the ecosystem. Although the effects on ecosystem function are not that pressing, the effects on community structure and composition have
been quite detrimental. This highlights the vulnerability of the Nilgiris grassland community to invasion by woody exotics. In contrast, the effects of fire were not severe in this ecosystem. The fire effects, as measured by community structure, composition and the ecosystem function, almost disappeared over a period of 18 months; this is a relatively short recovery period, considering that this perennial grassland experiences a relatively cold climate (for a tropical ecosystem), and excessive nutrient loss due to high rainfall. For the entire duration of the study, there were no interactive effects of the fire with invasion, suggesting fire by itself cannot be an agent of recovery of invaded sites in the short term. But importantly, fire has been shown to cause widespread death of mature stands and depletion of seedbanks here (see chapter 3) and elsewhere (Haubensak et al. 2004, DiTomaso and Johnson 2006). The removal of the broom canopy causes higher light incidence on the ground, while burning of litter returns nutrients to the soil, stimulating productivity (Knapp and Seastedt 1986). Although the flux of nutrients probably benefited the aggressive colonizers, mainly *I. kunthiana* and *E. nigra* in this case, these grasses are native and hence are bound to be limited by natural enemies and competitors. Further, these grasses will provide the environment for succession by the mainstream grassland species in the absence of light limiting broom thickets. Since reproduction of most of the tussock grasses is by clonal growth, it can be expected that the edges of the burned-broom patches will be colonized first. As discussed earlier, graminoids recovered fully in the shrub island-grassland edge in the central prairies (Lett and Knapp 2003). Incidentally, I sampled invaded patches in the core of the broom stands; sampling the edges may have better captured this colonization. A longer monitoring period will present a better understanding of the spatio-temporal patterns of the colonization process.

Since the results of this study do not overwhelmingly indicate that burning had engendered rapid colonization of characteristic grassland plants, the use of fire in the Nilgiris may not be readily justifiable to critics of burning the grasslands. But, the status quo, which is to ignore the existing problem and expect the natural demise of broom, can be potentially disastrous. It must be kept in mind that 18 months is a relatively short time period to expect dramatic community changes in burned-broom plots; however, it must be emphasized that the uninvaded grassland recovered from fire over this short-time span. Thus, it might be worthwhile to use fire to eliminate mature broom, which would otherwise be sources of propagules that would further spread invasion. Ideally, broom stands must be cut at the ground level as this usually kills the plant; cut stems must be allowed to dry in place, and this should be followed by localized burning. This would also ensure the depletion of seedbanks partly by killing seeds and partly by breaking dormancy. Prior research has shown that the broom seedbanks can be substantial and burning can be an effective method to diminish it (Haubensak et al. 2004; chapter 3). A subsequent burn may be required to kill the recruits prior to the advent of reproduction. This technique might be more pragmatic than other methods such as aerial broadcast of herbicides (Swezy and Odion 1997) or introduction of biocontrol agents (discussed in Downey and Smith 2000); the former is dangerous and can be particularly damaging to the native community in general, while the latter, apart from being a threat to non-target species, has been shown to be ineffective. Burning alone may not be effective to initiate the recovery of the gamut of mainstream grassland plants; perhaps supplemental seeding of mixed species or planting plugs of competitively dominant grasses will greatly enhance grassland recovery. In a pilot experiment, I found that nearly all the plugs of the dominant grass *D. polyptychum* planted in burned broom patches survived and showed appreciable growth over a period of nine months. Further, Haubensak et al. (2004) have recommended addition of sawdust to immobilize the soil N to encourage colonization of stress tolerant grassland species over resource-demanding ruderals. Considering the ubiquity and pervasiveness of shrub invasions in grasslands, studies that document or attempt to document the recovery of these ecosystems after removal of the invasives are disproportionately few. Such research is vital to generate an impetus for conservation actions. I believe that it would be a valuable exercise to monitor the recovery of native
species in burned-broom thickets in grasslands invaded by broom. This knowledge must be integrated into invasive shrub management strategies in grasslands worldwide.
Table 4.1. Results of factorial ANCOVA on the community structure responses to fire and invasion over time.

<table>
<thead>
<tr>
<th>Treatment effect</th>
<th>Species richness</th>
<th></th>
<th>Diversity, Shannon Index</th>
<th></th>
<th>Dominance, Simpson's D</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Fire</td>
<td>1,72</td>
<td>0.04</td>
<td>0.8426</td>
<td>1,72</td>
<td>0.14</td>
<td>0.7076</td>
</tr>
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<td>Invasion</td>
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<td>94.04</td>
<td>&lt;0.0001</td>
<td>1,72</td>
<td>29.98</td>
<td>&lt;0.0001</td>
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<tr>
<td>Time</td>
<td>1,78</td>
<td>0.53</td>
<td>0.4688</td>
<td>1,78</td>
<td>0.03</td>
<td>0.8574</td>
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<td>Fire*Invasion</td>
<td>1,72</td>
<td>0.75</td>
<td>0.3891</td>
<td>1,72</td>
<td>0.22</td>
<td>0.6428</td>
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<td>Fire*Time</td>
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<td>1,78</td>
<td>1.18</td>
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<td>Invasion*Time</td>
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<td>0.7095</td>
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<td>0.69</td>
<td>0.4087</td>
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<td>1,78</td>
<td>0.09</td>
<td>0.7693</td>
<td>1,78</td>
<td>1.26</td>
<td>0.2656</td>
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<tr>
<td>Covariates</td>
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<td></td>
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<tr>
<td>Elevation</td>
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<td>0.8751</td>
<td>1,72</td>
<td>0.01</td>
<td>0.9096</td>
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<td>0.8339</td>
<td>1,72</td>
<td>0.06</td>
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<td>0.5422</td>
<td>1,72</td>
<td>0.08</td>
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<td>Curvature</td>
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<td>0.7921</td>
<td>1,72</td>
<td>0.00</td>
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<td>0.0983</td>
<td>1,72</td>
<td>0.78</td>
<td>0.3795</td>
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Table 4.2. Results of the partial CCA showing percent variation in community matrix explained by the treatments 6 months and 18 months post-fire.

<table>
<thead>
<tr>
<th>model</th>
<th>Percent variation explained by treatment</th>
<th>covariates + terrain</th>
<th>unexplained</th>
<th>model significance (Monte-Carlo P)</th>
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<tr>
<td><strong>6 months post-fire</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fire</td>
<td>2.51</td>
<td>23.98</td>
<td>73.51</td>
<td>0.0009</td>
</tr>
<tr>
<td>Invasion</td>
<td>11.57</td>
<td>14.88</td>
<td>73.54</td>
<td>0.0001</td>
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<tr>
<td>Interaction (fire x invasion)</td>
<td>2.17</td>
<td>26.49</td>
<td>71.34</td>
<td>0.0001</td>
</tr>
<tr>
<td><strong>18 months post-fire</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Fire</td>
<td>2.11</td>
<td>23.70</td>
<td>74.19</td>
<td>0.0189</td>
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<td>Invasion</td>
<td>12.86</td>
<td>12.98</td>
<td>74.15</td>
<td>0.0001</td>
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<tr>
<td>Interaction (fire x invasion)</td>
<td>1.87</td>
<td>25.81</td>
<td>72.32</td>
<td>0.0009</td>
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</tbody>
</table>
Table 4.3. Results of the CCA of combined community data, both 6 and 18 months post-fire. Intraset correlations of the natural treatments with the first two CCA axes.

<table>
<thead>
<tr>
<th>Natural treatments</th>
<th></th>
<th>Correlation coefficients</th>
<th></th>
<th></th>
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<tbody>
<tr>
<td></td>
<td>6 months post-fire</td>
<td>18 months post-fire</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Axis 1</td>
<td>Axis 2</td>
<td>Axis 1</td>
<td>Axis 2</td>
<td>Axis 1</td>
</tr>
<tr>
<td>Burned</td>
<td>0.0786</td>
<td>0.7661</td>
<td>-0.0198</td>
<td>0.0737</td>
<td></td>
</tr>
<tr>
<td>Unburned</td>
<td>-0.0459</td>
<td>-0.1988</td>
<td>-0.0061</td>
<td>-0.5529</td>
<td></td>
</tr>
<tr>
<td>Invaded</td>
<td>-0.5500</td>
<td>0.2507</td>
<td>-0.6484</td>
<td>-0.2010</td>
<td></td>
</tr>
<tr>
<td>Uninvaded</td>
<td>0.5071</td>
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<td>0.5726</td>
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</table>
Table 4.4. Results of factorial ANCOVA on plant cover and above biomass responses to fire and invasion over time.

<table>
<thead>
<tr>
<th>Treatment effect</th>
<th>Plant cover</th>
<th>Graminoid biomass</th>
<th>Forb biomass</th>
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<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Fire</td>
<td>1, 72</td>
<td>58.08</td>
<td>&lt;0.0001</td>
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<tr>
<td>Invasion</td>
<td>1, 72</td>
<td>5.84</td>
<td>0.0182</td>
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<tr>
<td>Time</td>
<td>1, 78</td>
<td>60.86</td>
<td>&lt;0.0001</td>
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<tr>
<td>Fire*Invasion</td>
<td>1, 72</td>
<td>11.48</td>
<td>0.0011</td>
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<tr>
<td>Fire*Time</td>
<td>1, 78</td>
<td>0.83</td>
<td>0.3655</td>
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<tr>
<td>Invasion*Time</td>
<td>1, 78</td>
<td>1.14</td>
<td>0.2883</td>
</tr>
<tr>
<td>Fire<em>Invasion</em>Time</td>
<td>1, 78</td>
<td>2.34</td>
<td>0.1298</td>
</tr>
<tr>
<td>Covariates</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>1, 72</td>
<td>0.74</td>
<td>0.3933</td>
</tr>
<tr>
<td>Northness</td>
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<td>Curvature</td>
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<td>Slope</td>
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<td>CTI</td>
<td>1, 72</td>
<td>6.04</td>
<td>0.0164</td>
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Table 4.5. Results of factorial ANCOVA on soil moisture and available soil nitrogen responses to fire and invasion over time.

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<thead>
<tr>
<th>Treatment effect</th>
<th>Soil moisture</th>
<th>Soil N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Fire</td>
<td>1, 71.6</td>
<td>0.13</td>
</tr>
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<td>Invasion</td>
<td>1, 71.5</td>
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<tr>
<td>Time</td>
<td>1, 74.7</td>
<td>0.70</td>
</tr>
<tr>
<td>Fire*Invasion</td>
<td>1, 71.5</td>
<td>1.52</td>
</tr>
<tr>
<td>Fire*Time</td>
<td>1, 74.7</td>
<td>0.00</td>
</tr>
<tr>
<td>Invasion*Time</td>
<td>1, 74.7</td>
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</tr>
<tr>
<td>Fire<em>Invasion</em>Time</td>
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<td>0.32</td>
</tr>
<tr>
<td>Covariates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Elevation</td>
<td>1, 71.5</td>
<td>0.64</td>
</tr>
<tr>
<td>Northness</td>
<td>1, 71.7</td>
<td>0.05</td>
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<td>Eastness</td>
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<td>Slope</td>
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<td>CTI</td>
<td>1, 71.5</td>
<td>4.57</td>
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Figure 4.1. Layout of the treatment plots in the study site. The inset shows the rough extent of the Nilgiris in south India. Contours are drawn at 10m intervals.
Figure 4.2. A degraded montane grassland site in the Nilgiris (study area) showing different vegetation classes: Scotch broom, *Acacia* plantations in a grassland matrix.
Figure 4.3. Mean (± 1 SE) species richness (a, b), diversity (c, d), and dominance (e, f) in plots under fire and invasion treatments in 2007 and 2008. P-values for pairwise differences (Tukey post-hoc test) between relevant treatment combinations are tabulated in each graph. The treatment combinations are labeled as follows: the first letter is B for "burned" or U for "unburned", followed by the letter B for "broom" or G for "grassland".
Figure 4.4. CCA biplot showing species distributions with respect to the fire x invasion treatment combinations. The centroids of each treatment combination is plotted separately for 2007 and 2008: triangles represent burned-broom (BB) plots, diamonds represent unburned-broom (UB) plots, squares represent burned-grassland (BG) plots, circles represent unburned grassland (UG) plots. The year 2007 ('07) or 2008 ('08) follows each treatment combination; open symbols represent the year 2007 and closed symbols represent the year 2008. Species are represented by the first three letters of the genus and species: *Agrostis pilosula*, *Anaphalis leptophylla*, *Anaphalis subdecurrens*, *Arundinella purpurea*, *Carex brunnea*, *Carex sp1*, *Chrysopogon zeylanicus*, *Curculigo orchioides*, *Cymbopogon lividus*, *Dichanthium polyptychum*, *Dichrocephala chrysanthemifolia*, *Digitaria sp.*, *Eragrostis nigra*, *Erigeron mucronatus*, *Eulalia phaeothrix*, *Fragaria nelgerrensis*, *Gentiana quadrifaria*, *Hypochaeris glabra*, *Impatiens inconspicua*, *Isachne kunthiana*, *Ischaemum indicum*, *Justicia latispica*, *Leucas suffruticosa*, *Osbeckia brachystemon*, *Oxalis corniculata*, *Poa sp.*, *Polygonum sphaerocephalum*, *Rungia sp.*, *Serpicula brevipes*, *Swertia corymbosa*, *Themeda tremula*, *Tripogon bromoides*. To improve clarity, a few rare species are not shown in the diagram.
Figure 4.5. Mean percent cover (standardized proportion) of moderate to high frequency species across treatments. The treatments on the x-axis are coded as: unburned-broom (UB), unburned grassland (UG), burned-broom (BB), burned-grassland (BG). The $P$ value included in the graphs is based in the Kruskal-Wallis test statistics. Error bars are 95% confidence intervals. Treatment means with different lower case letters are significantly different at $P < 0.05$. 
Figure 4.6. Mean (± 1 SE) plant cover (a, b), graminoid biomass (c, d), and forb biomass (e, f) in plots under fire and invasion treatments in 2007 and 2008. P-values for pairwise differences (Tukey post-hoc test) between relevant treatment combinations are tabulated in each graph. The treatment combinations are labeled as before.
Figure 4.7. Mean (± 1 SE) percent soil moisture (a, b), and NH₄⁻N (c, d) in plots under fire and invasion treatments in 2007 and 2008. *P*-values for pairwise differences (Tukey post-hoc test) between relevant treatment combinations are tabulated in each graph. The treatment combinations are labeled as before.
CHAPTER FIVE

Immediate impacts of elevated nitrogen deposition on a montane grassland ecosystem in a biodiversity hotspot

Summary
Elevated anthropogenic nitrogen (N) deposition is considered to be one of the leading causes of biodiversity decline and disruption of ecosystem function and services. Current deposition levels have exceeded critical thresholds for species loss in some European ecosystems; studies are needed from understudied ecoregions such as the Western Ghats, to determine critical loads for these ecosystems. The Western Ghats has the highest deposition rate among the 34 world biodiversity hotspots, which is projected to increase in the coming years. I studied plant community and ecosystem responses to experimental N addition (ambient, 2 and 8 g N m\(^{-2}\) yr\(^{-1}\)) and reduction (500 g sucrose m\(^{-2}\) yr\(^{-1}\)) in the montane grasslands of the Nilgiris, Western Ghats. Throughout the study period (14 months), soil N availability and leaf N concentration increased significantly with increasing N addition. Plant cover and biomass responded positively to N addition, whereas soil moisture decreased in N addition plots. N enrichment had a positive effect on species richness and diversity, though the cover of one important native grass was significantly reduced by the higher N level. The study site was burned six months prior to the N treatment; hence the generally positive effects of N fertilization on diversity may be short-lived. The dominant matrix-forming grasses may benefit from N fertilization in the long term, suppressing subdominant species and potentially reducing species diversity. Periodic disturbances might reset the suppressive effects of dominant grasses thereby buffering the negative effects of N loading on community structure.

Introduction
The role of biodiversity in maintaining ecosystem function and stability in natural and semi-natural systems has been exemplified by numerous theoretical and empirical studies (Hector et al. 1999, Loreau 2000, Cardinale et al. 2006, Tilman et al. 2006). Anthropogenic nitrogen (N) deposition is one of the main causes of global biodiversity loss, only next to habitat destruction and climate change (Sala et al. 2000). In recent years, clear and considerable evidence for biodiversity loss caused by increased deposition of reactive N (Nr) has emerged from a range of terrestrial (temperate grasslands: Dise and Stevens 2005, Clark and Tilman 2008, forests: reviewed in Gilliam 2006, alpine grasslands: Bassin et al. 2007, coastal dunes: Remke et al. 2009, Mediterranean ecosystems: Ochoa-Hueso et al. 2011) and aquatic ecosystems (reviewed in Bobbink et al. 1998). In terrestrial environments the well recognized mechanisms of the impacts of elevated labile N compounds on plants as reviewed by Bobbink et al. (2010) are: (1) direct toxicity to species due to exposure to elevated levels or novel forms, (2) changes in plant species interactions due to opportunistic accumulation by a few species, (3) soil acidification mainly leading to loss of base cations and accumulation of toxic metals, (4) physiological changes such as increased tissue N that can make plants more susceptible to pests and pathogens. Currently, the global nitrogen budget has been tremendously altered relative to pre-industrialization times due to inputs of Nr from the burning of fossil fuels and production of fertilizers that involves conversion of the seemingly inert N\(_2\) to Nr (Galloway et al. 1995). According to Galloway and Cowling (2002) the annual rate of production of anthropogenic Nr in the year 2000 had increased to 165 Tg, an increase of 1100% compared to 1860 levels. Global models predict that some parts of the world are likely to see a five-fold increase in the N deposition rates by the year 2030 compared to the present (Dentener et al. 2006).

Nitrogen is a limiting nutrient in the majority of natural ecosystems. Limitation of N predominantly, and other macronutrients, is thought to be the main reason for rich biodiversity of many grasslands (Vitousek and Howarth 1991). Experiments and surveys in grasslands varying in climate and geology
have demonstrated that the principal mechanism for loss of diversity in grasslands is the disproportionate expansion of nitrophyllic, often competitively dominant grasses that out-compete low frequency forbs (temperate: Dise and Stevens 2005, Clark and Tilman 2008, arid: Báez et al. 2007, alpine: Bassin et al. 2007, Bowman et al. 2006, Mediterranean: Harpole et al. 2007, Eurasian steppe: Bai et al. 2010). The above compositional and assemblage changes can result in ecosystem feedbacks that can impact processes like primary production (Stevens et al. 2004), soil carbon storage (Wedin and Tilman 1996, Manning et al. 2006), microbial activity (Keeler et al. 2009), rates of decomposition (Knorr et al. 2005, Manning et al. 2008), N mineralization and retention (Matson et al. 2002), and tissue chemistry (Henry et al. 2006, Knops et al. 2007). Trophic interactions can also be destabilized by triggering an initially positive feedback between Nr deposition, productivity, herbivory and species loss (Jefferies and Maron 1997). All these can ultimately lead to disruption of ecosystem function and services.

Although the negative impacts of acute and chronic low levels of N deposition have been demonstrated in several ecosystems, the impacts may vary depending on local communities, ecosystem process and management and disturbance regimes. For example, Bai and colleagues (2010) reported that species declines with N addition were sharper in mature montane steppes in Mongolia compared to nearby degraded communities, whereas the productivity increases were greater in the latter due to N amendment. Ecosystem sensitivities to N vary greatly and, correspondingly, critical load thresholds for Nr deposition also vary. Critical load thresholds have been useful to governments to regulate N loading in sensitive ecosystems. Hence, more mechanistic studies of ecosystem responses to N loading are needed from areas of high conservation value. In fact, for the newly identified 34 global biodiversity hotspots, using global chemistry transport models, Phoenix and colleagues (2006) estimated that in the mid 1990s the average deposition rates across all the hotspots was 5.3 Kg N ha⁻¹yr⁻¹, 50% higher than the global terrestrial average of 3.5 Kg N ha⁻¹yr⁻¹. They projected that by 2050 the deposition rates could be more than double the current levels across these areas. Of all the hotspots, the Western Ghats and Sri Lanka had the highest average N deposition rate 13.0 Kg N ha⁻¹yr⁻¹ and the rate is predicted to be 33 Kg N ha⁻¹yr⁻¹ in 2050.

Here, I report the results of a short-term field experiment that examined the effects of N deposition on grassland plant composition and ecosystem function. I used two levels of N additions that were environmentally relevant and one level of reduction. Including the reduction dose helps to understand the grassland responses to varying rates of N deposition; further, this reduced level also represent pre-industrial and pre-agricultural levels of terrestrial N. The study was conducted in the montane grasslands in the Nilgiris mountains, an integral part of the Western Ghats. To my knowledge this is the first effort to study the effects of N loading in a natural ecosystem in India. In the upper Nilgiris more than 50% of land is under the cultivation of agricultural, horticultural and plantation crops (Kumar 1993) and these lands are intensively managed with very high levels of fertilizer input (Sebastian et al. 2007). About 20% of the remainder is occupied by tree plantations of the nitrogen fixing legume Acacia mearnsii (Kumar 1993). Because of the magnified local N dynamics in the Nilgiris, purportedly due to intensive cropping pattern that demands heavy fertilizer inputs over the last several decades, and potentially high nitrogen fixation in the plantations, it is likely that the Nilgiris is currently experiencing N deposition levels much greater than the average deposition rate for the Western Ghats estimated by Phoenix and others (2006). I tested the following questions: (1) does N amendment impact the grassland plant community and ecosystem properties? Specifically, which of the following will change in response to varying N levels: species richness, diversity, community composition, aboveground biomass, soil moisture, N mineralization and plant tissue chemistry? (2) Do N treatments alter the relationship between diversity and ecosystem function? Specifically, is the slope of the relationship between species richness and aboveground biomass significantly different between treatments?
Methods

Study area
The Nilgiri hills are located between 11°10′-10°30′ N and 76°25′-77°00′ E. 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 a second from the northwest monsoon between October and December. The western regions of the plateau receive about 2500 mm of rainfall, which exceeds 5000 mm in certain areas (see Caner et al. 2007 for detailed meteorological information). The soils are classified as non-allophanic andisols (Caner et al. 2000). The natural vegetation in the upper Nilgiris consists of patches of stunted tropical evergreen forests (locally called shola) surrounded by 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 disturbances (see Thomas and Palmer 2007), however, recent evidence has shown that the grasslands were present in the Nilgiris for at least 40,000 years BP (Caner et al. 2007), long before humanization 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 and Palmer 2007).

Experimental design
I employed a nested design consisting of seventy two—4 m² experimental plots. Groups of 4 plots were nested within 18 whole-plots; each plot within a whole-plot was randomly assigned to one of four treatments described below. Treatment plots were nested within the whole-plots to account for the micro scale variation in community composition and topography. Further, the whole-plots were distributed among three locations (blocks) to account for the landscape scale variation. There were six whole-plots in each of the three blocks; blocks were at least 300 m apart. Each plot was separated by a 1m buffer strip from the other plots, and the spatial separation between whole-plots in each block ranged from two to several meters. All experimental plots were located in a site that was burned due to an accidental anthropogenic fire 6 months prior to the start of the experiment.

The treatments included N reduction (500 g sucrose m⁻¹ yr⁻¹, NR) to simulate pre-industrial levels, ambient levels (0 g N m⁻¹ yr⁻¹, NA), a low dose (2 g N m⁻¹ yr⁻¹, NL) and a high dose (8 g N m⁻¹ yr⁻¹, NH) of N addition. Addition of sucrose and other sources of labile carbon (C) serves as a substrate for soil microbes, increasing microbial activity and subsequently microbial biomass, and in the process also increases microbial N uptake, thereby immobilizing the plant available soil N (Baer et al. 2003, Perry et al. 2010). Nitrogen was added as laboratory grade NH₄NO₃. Amorphous NH₄NO₃ was mixed with a small amount of fine sand collected from nearby stream banks to add bulk to the treatment mixture to facilitate uniform distribution of the inorganic N within the plots. Ambient plots received an equal amount of sand during each treatment interval. A partial dose of the treatments was first applied in October 2007 to all the plots, and subsequent partial doses were added at 4 month intervals to simulate continuous N loading, such that at the end of 12 months, the plots had received the full dose of the treatments: 500 g of sucrose per m² for the N reduction treatment, 2 g and 8 g of N m⁻² for the low and high dose N addition treatments, respectively. Compared to the ambient levels, the treatments altered soil N levels in the following manner: sucrose reduced NO₃⁻-N by 32% and NH₄⁺-N by 2%, the low dose increased NO₃⁻-N by 76% and NH₄⁺-N by 38%, the high dose increased NO₃⁻-N by 247% and NH₄⁺-N by 133% (also see the Results section).

Vegetation and soil were sampled at two time points, 5 months (February 2008) and 14 months (December 2008) after treatment addition began; the second sampling session was 2 months after the complete dose of treatments were added.
Vegetation sampling

The cover of each plant species was measured in a 1 m² quadrat in each plot dedicated to quantifying community composition. A 1 x 1 m gridded frame (divided into 100 units of equal size) was placed on the ground over the herbaceous vegetation to estimate relative abundance of species within the plot. This generated a list of plant species with their percent cover for each plot. Estimates of above ground biomass were made by clipping vegetation at ground level in two randomly selected 0.1 x 1 m² strips. A different strip of vegetation was clipped during each sampling session and a 20 cm buffer was maintained between clipped strips. Clipped biomass was sorted into graminoids and forbs and weighed after oven drying at 60 °C for 72 hours.

To quantify the treatment effects on plant chemistry, leaf tissue samples of similarly aged leaves were collected from the dominant grass Dicenthamium polyptuchum from multiple tussocks in each plot. Leaf samples were oven dried and ground with a Wiley mill through a number 20 mesh. Percent carbon (C) and N in the leaf tissue was determined by analyzing the samples with an Elementar Vario MAX CN analyzer (Elementar Analysysteme GmbH, Hanau, Germany).

Soil sampling

Plant available soil nitrogen (N) was measured during both sampling sessions. Two soil cores (2.5 cm diameter x 10 cm length) from each plot were composited in the field and stored in Ziploc bags. The samples were placed over ice until they were brought back to the field station. Each composited sample was sieved using a 2 mm mesh. A known weight of a fraction of the soil was oven dried at 100 °C for 48 hours to estimate gravimetric water. Ten grams of the sieved sample was agitated with 50 ml of 1 N KCl for 2 hours to extract available soil nitrogen in the form of nitrate (NO₃⁻-N) and ammonium (NH₄⁺-N). The agitated extracts were filtered using No. 2 Whatman filter paper after letting it stand overnight. Filtered extracts were collected in 20 ml scintillation vials and frozen at -20 °C for laboratory analysis at a later date. The concentration of N (NH₄⁺-N and NO₃⁻-N) was determined colorimetrically using a Bran Luebbe Continuous Flow Auto Analyzer II (Bran + Luebbe Inc., Delavan, WI, USA).

To estimate N availability, integrated though time, I installed a set of two nylon mesh bags, one containing 3 g of anion resin (Ionac ASB-1P, Sybron Chemicals, Birmingham, NJ, USA) and the other containing 3 g of cation resin (USF C-211, USFilter Corporation, Rockford, IL, USA), about 10 cm below the soil surface. The resins absorb the ions leaching through the soil profile. The resin bags were installed by creating a pocket in the soil in the following manner: a flat long and curving strip of metal was pounded in the soil at an angle, and the upper layer of soil was slightly heaved to insert the resin bag. The metal strip was carefully removed once the bag was in place. This method ensured minimal damage to the soil profile. In November 2008, two sets of resin were installed at two well-separated points in each plot; the resin bags were retrieved after a 30 day incubation period in December 2008. Incubated resin bags were air dried and refrigerated until laboratory extraction. Each pair of resin was extracted with 50 ml of 1 N KCl solution; the concentration of NH₄⁺-N and NO₃⁻-N in the extracts was determined as described earlier. Both NH₄⁺-N and NO₃⁻-N concentrations were expressed in mg L⁻¹ of KCl.

Data analysis

All response variables were transformed appropriately where needed to meet assumptions of parametric ANOVA. To test for treatment effects on grassland community structure (species richness and Shannon diversity) and ecosystem function (aboveground biomass, plant cover, soil moisture, soil N; February 2008 NO₃⁻-N data was excluded from the analysis as it was not detectable in the vast majority of the samples) I used mixed model ANOVAs (PROC MIXED) in the Statistical Analysis System (SAS version 9.2, SAS 2008). The response variables were analyzed independently for each sampling session. The random effects specified in each model (plot nested within whole-plot, whole-plot nested within block, and block) depended on what improved the model fit as determined by AIC statistics.
Occasionally, inclusion of a covariate (Shannon index in case of biomass as the response variable) improved the fit of the model; in such cases the covariate was maintained as a fixed effect in the final model. The Tukey-Kramer post-hoc test was used to identify significantly different treatments at the $P < 0.05$ level.

An ANCOVA was performed with the MIXED procedure (SAS 2008) to test if there were significant differences between the slopes of each treatment in the relationship between biodiversity and ecosystem function in the second sampling session. PROC MIXED was run with aboveground biomass as the response variable; fixed effects included treatment, overall species richness (mean centered within treatment) and the interaction of the two. Similarly, mixed models were analyzed with graminoid and forb biomass as the response variables and their respective fixed effects being graminoid species richness and forbs species richness, besides treatment.

Canonical Correspondence Analysis (CCA) was used to quantify the variation in species distribution explained by the treatments, and to test if the N treatments had significantly changed the grassland community composition. CCA was performed using CANOCO v. 4.5 (ter Braak and Smilauer 2002); rare species were down-weighted, while the rest of the options were left at default settings. To test whether the inertia explained by each treatment was significantly stronger than expected by chance, I used a Monte Carlo Permutation Test with 499 permutations. Plots were permuted completely at random within each of the three blocks.

Non-parametric Kruskal-Wallis ANOVA was used to test whether the treatments affected the frequency of the common plants (19 species, present in at least 25% of the samples). The non-parametric test was used due to the large number of zeros in the case of certain species as a result of their absence from some samples. Wherever a significant effect of treatment was found, pairwise comparisons were made using the non-parametric ranked sums Tukey test to identify which pairs were statistically different.

Results

Soil nitrogen

Nitrogen availability was reflective of the fertilization rates. The N inputs significantly increased extractable soil NH$_4$+-N in both sampling periods (Feb: $F_{3,66} = 7.30$, $P = 0.0031$; Dec: $F_{3,67} = 61.21$, $P < 0.0001$; Figure 5.1a), and the increase was particularly high for N$_H$ treatment in December (N$_H$ vs. N$_R$, $P < 0.0001$; N$_H$ vs. N$_A$, $P < 0.0001$). N$_L$ treatments increased soil NH$_4$+-N significantly in December compared to N$_R$ ($P = 0.0002$). Available soil NO$_3$--N levels were negligible in February 2008, and hence these data were omitted from analysis; in December 2008, only N$_H$ had significantly higher levels among all the treatments ($F_{3,51} = 28.74$, $P < 0.0001$; Figure 5.1b).

Cumulative soil N availability, as measured by the ion-exchange resin bags were significantly influenced by the treatments (NH$_4$+-N: $F_{3,66} = 12.42$, $P < 0.0001$; Figure 5.1d; NO$_3$--N: $F_{3,67} = 19.74$, $P < 0.0001$; Figure 5.1d). Compared to the N$_R$ treatment, the N$_L$ and N$_H$ treatments resulted in an appreciable increases for both NH$_4$+-N (N$_L$ vs. N$_R$, $P = 0.0222$; N$_H$ vs. N$_R$, $P < 0.0001$) and NO$_3$--N (N$_L$ vs. N$_R$, $P = 0.0011$; N$_H$ vs. N$_R$, $P < 0.0001$). The N$_H$ treatment also significantly increased soil NH$_4$+-N and NO$_3$--N compared to the N$_A$ treatment (both, $P < 0.0001$).

Ecosystem properties

Aboveground biomass was also considerably lower in February (Overall LS mean ± SE square-root transformed biomass: Feb = 11.58 ± 0.53 g m$^{-2}$, December = 17.28 ± 0.53 g m$^{-2}$; $F_{1,134} = 169.29$, $P < 0.0001$; Figure 5.2a). Treatment effects were not present in February ($F_{3,68} = 0.42$, $P = 0.7401$), but the N$_R$ and N$_L$ treatments were significantly different in December ($F_{3,67} = 3.13$, $P = 0.0313$) and there was a trend ($P = 0.07$) for the difference between N$_R$ and N$_H$ treatments.
As with aboveground biomass, plant cover across treatments was much lower in February compared to December that year (Overall LS mean ± SE cover: Feb = 38.38 ± 1.71 %, December = 67.07 ± 1.71 %; \( F_{1, 68} = 1029.29, P < 0.0001 \); Figure 5.2b), as the community was recovering from the fire. Treatments did not significantly influence plant cover for the first five months (\( F_{3, 51} = 0.92, P = 0.4383 \)), but had a significant effect after 14 months (\( F_{3, 51} = 3.89, P = 0.0128 \)). Sucrose addition (\( N_R \)) significantly depressed cover compared to \( N_A \) (\( P = 0.0139 \)) and \( N_N \) (\( P = 0.0365 \)), but not when compared to \( N_H \). There were no differences in cover between the ambient and \( N \) fertilization treatments.

Soil moisture levels were significantly lower in December compared to February (Overall LS mean ± SE soil moisture: Feb = 53.29 ± 2.04 %, December = 45.12 ± 2.04 %; \( F_{1, 119} = 78.86, P < 0.0001 \); Figure 5.2c). There was no effect of treatments on soil moisture in February (\( F_{3, 51} = 0.58, P = 0.6278 \)), but the sucrose addition plots had significantly higher moisture than all the other treatments in December (\( F_{3, 51} = 7.01, P = 0.0005 \)).

Treatments significantly impacted plant tissue chemistry. Foliar N percent increased significantly with fertilization both in February (\( F_{3, 51} = 7.42, P = 0.0003 \); Figure 5.3a) and December (\( F_{3, 50.4} = 9.43, P < 0.0001 \); Figure 5.3a). Percent foliar N was significantly and consistently higher under the \( N_H \) treatment compared to ambient levels by 13% in February (\( P = 0.0077 \)) and 24% in December (\( P < 0.0001 \)). In December there were trends for increases in foliar N with increasing input through treatments (\( N_A \) vs. \( N_N \); \( P = 0.0721 \)). Leaf C:N ratio was significantly affected by N treatments at both time points (Feb: \( F_{3, 51} = 6.72, P = 0.0007 \); Dec: \( F_{3, 50.4} = 9.76, P < 0.0001 \); Figure 5.3b). The leaf C:N ratio under \( N_H \) was significantly lower than both \( N_A \) and \( N_N \) treatments for February (\( N_H \) vs. \( N_A \), \( P = 0.0008 \); \( N_H \) vs. \( N_N \), \( P < 0.0001 \)). However, there was a trend for difference between \( N_N \) and \( N_A \) in February (\( P = 0.0777 \)), and a trend for a difference between \( N_L \) and \( N_A \) in December (\( P = 0.0801 \)).

Community structure and composition

The nitrogen amendment significantly influenced species richness during both the sampling sessions (Feb: \( F_{3, 66} = 2.83, P = 0.0453 \); Dec: \( F_{3, 66} = 3.40, P = 0.0228 \); Figure 5.4a). The \( N_H \) treatment had significantly higher species richness than the \( N_A \) treatment in February (\( P = 0.0250 \)), and both levels of N addition treatments had higher species richness than the \( N_R \) treatment in December (\( N_H \) vs. \( N_R \), \( P = 0.0084 \); \( N_N \) vs. \( N_R \), \( P = 0.0003 \); \( N_H \) vs. \( N_N \), \( P < 0.0001 \)). However, these did not differ significantly from the ambient treatment. There was a trend for treatments to influence species diversity, expressed as Shannon index, in February (\( F_{3, 51} = 2.61, P = 0.0613 \); Figure 5.4b), while this pattern was significant in December (\( F_{3, 51} = 3.50, P = 0.0218 \); Figure 5.4b). \( N_H \) increased diversity relative to \( N_R \) at both time points (Feb, \( P = 0.0422 \); Dec, \( P = 0.0116 \)).

In the CCA ordination, treatments failed to significantly explain the inertia in the species matrix at both sampling periods (Monte Carlo test: February, \( F = 0.967, P = 0.5660 \); December, \( F = 1.065, P = 0.3420 \)). Comparisons for the frequencies of common species failed to show any treatment effects except in the case of Eulalia phaeothrix (Kruskal-Wallis \( H = 7.76, P = 0.05 \); Fig. 5.5a) and Tripogon bromoides (Kruskal-Wallis \( H = 8.7, P = 0.03 \); Fig. 5.5b). \( N_H \) significantly depressed the abundance of E. phaeothrix compared to \( N_A \) treatment (\( P = 0.048 \)). On the other hand, \( N_A \) had a positive effect on the abundance of T. bromoides compared to the \( N_R \) treatment (\( P = 0.038 \)).

N treatments and the relationship between biodiversity and ecosystem function

N treatments did not significantly influence the slope of the relationship between biomass and overall species richness (\( F_{3, 64} = 0.33, P = 0.8052 \)). N treatments did not affect similar relationships for forbs (\( F_{3, 56.5} = 0.95, P = 0.4220 \)) and graminoids (\( F_{3, 64} = 0.18, P = 0.9099 \)) as well.
Discussion

Nitrogen treatments resulted in corresponding changes in soil N availability, both as snapshot and temporally integrated measures, suggesting that N deposition even in the short-term can result in significant increases in soil N availability in the Nilgiris grasslands. Soil responses to N loading can vary depending on various biotic and abiotic factors, such as the plant and microbial communities, temperature, moisture, soil chemistry, and so forth. In most cases, N enrichment results in increases in soil N pools and N cycling (Morecroft et al. 1994, Bowman and Steltzer 1998). Occasionally, a lack of response to moderate levels of N addition has been seen (example, grasslands of Rocky Mountain: Bowman et al. 2006, alpine heathlands in Scotland: Britton et al. 2008, inner Mongolian grasslands: Bai et al. 2010). Bai et al. (2010) found significant increases in soil N availability only at rates exceeding 17 g N m\(^{-2}\) yr\(^{-1}\) after 4 years of treatment. Likewise, in Rocky Mountain National Park, even after four years of continuous N addition at rates comparable to the current study, soil ammonium levels failed to increase, and nitrate levels increased only after two years (Bowman et al. 2006). Chronic deposition of N can saturate soil inorganic N pools leading to acidification and depletion of base cations, consequently disrupting nutrient exchange capacity and causing toxic buildup of non-base cations such as aluminum, iron and manganese (Horswill et al. 2008).

The lag in the aboveground plant biomass and cover between February and December could be partly due to an inadequate response time in February; the community in the Nilgiris has a relatively slow growth rate owing to year round low to moderate temperatures, and the recent fire may have further depressed the already slow growth rates via various direct and indirect mechanism. Also, over the nine month period between the two sampling sessions, the soil N availability may have been maintained at levels high enough to elicit a response; however, this cannot be confirmed as I did not measure in situ cumulative N availability using resin bags in February. In general, increases in biomass with N addition become apparent within the first few years of treatment (Tilman 1987, Bassin et al. 2007, Bai et al. 2010). The lack of a significant difference in aboveground biomass between ambient and N addition treatments, but significant differences between the N addition and the N reduction treatments suggests that the N limitation in this site has been alleviated to some degree by N inputs from the atmosphere. It must be noted that the Nilgiris is currently suspected to receive the highest N deposition rates among all biodiversity hotspots (Phoenix et al. 2006). In such a situation, a longer treatment period may be needed to see effects. According to LeBauer and Treseder (2008), a majority of the terrestrial biomes of the world, prominently grasslands, are considered N limited, but the degree of N limitation may be greatly reduced now and in the years to come due to substantial deposition rates. In lieu of this, it may be more informative to compare responses to N reduction with responses to N addition and ambient levels to understand the effects of N loading on the ecosystem.

Soil moisture levels in the N enrichment and ambient treatments were significantly lower than in the N reduction treatment in December, and the former treatment plots had lower moisture than all the treatments in February. Decline in soil moisture content with increasing N amendment is consistent with other grassland studies (Harpole et al. 2007, St Clair et al. 2009, Bai et al. 2010). Elevated soil N concomitantly increases foliar N leading to higher photosynthetic rates (St Clair et al. 2009). Increased water uptake because of higher rates of photosynthesis may have led to depletion of soil moisture levels under the N treatments. Increases in foliar N seen here mirror observations from other studies (Knops et al. 2007, Britton et al. 2008), and have implications to various ecosystem properties such as increased plant growth, changes in litter quality and decomposition rates (Reich et al. 2001, Knorr et al. 2005, Keeler et al. 2009), and altered microbial community and biomass (Egerton-Warburton and Allen 2000, Epstein et al. 2002). All these changes can have strong feedbacks to plant community composition. The increase in foliar N seen here was disproportionate to the changes in soil N availability in response to fertilization treatments. The lack of a sizable increase in production following N amendments suggests that the potential of this ecosystem to retain N in the form of organic matter is limited (Vitousek et al. 2006).
These grasslands may be highly prone to N saturation, and may be experiencing N losses through excessive leaching into streams because of the high rainfall. This could compromise ecosystem functioning with disastrous consequences to downstream ecosystems (Clark et al. 2009).

Numerous experiments and observational studies have reported a decline in species diversity associated with N fertilization (Tilman 1987, Zavaleta et al. 2003, Stevens et al. 2006, Zeng et al. 2010). In contrast, I found a slight but significant positive effect of fertilization on species richness and diversity. A qualitative assessment of the number of occurrences of each species under the different treatments in December revealed that there was an overall increase in occurrence for nearly half of the plants in the community with N enrichment (40-51% of species, depending on treatment comparison). Further, some species (graminoids: Arundinella purpurea, Cymbopogon lividus, Tripogon bromoides, Ischaemum indicum, Carex sp1; forbs: Curculigo orchiodes, Osbeckia brachystemon) responded consistently and positively to N addition (17-39% increase in occurrence); three forbs responded positively only to the higher dose of N. It is likely that many wild plant species are able to tolerate or benefit from moderate levels of N fertilization in the short term. This may not be apparent in many studies because of the longer duration of most similar experiments. The principal mechanism of species loss following N addition is the expansion of C4 grasses or other dominant species that outcompete subdominant species (Clark and Tilman 2008, Kleijn et al. 2008). It is possible that deprivation of light and nutrients caused by the aggressive dominant species outweighs the potential benefits of N fertilization. Toxic effects can also occur at high N concentrations both through direct (Pearson and Stewart 1993) and indirect mechanisms (Horswill et al. 2008). In this study, because of the physical space created by the recent wildfire, dominant species were able to expand without suppressing delicate forbs. Hence, the positive effects on species diversity seen here may be transient. The effects of elevated N on biodiversity may become apparent once the maximum coverage is attained. This ecosystem is prone to periodic disturbance events; this highlights the need to study the interaction of global change and disturbances on biodiversity here. Though the study period was rather short to see definite community-wide compositional changes, two common species showed a significant response to the treatments. Of particular interest is the inhibitory effect of the high N dose on the growth of E. phaeothrix, a common C4 grass; this grass is the predominant dietary species of the highly endangered and endemic mountain goat, Nilgiri tahr (Sumithran 1997). Possibly, a longer study period will bring out clearer effects as in the case of the low levels of chronic N exposure in grass-dominated landscapes of the American mid-West (Clark and Tilman 2008).

It is interesting that the Nilgiris grasslands responded to environmentally relevant doses of N deposition in a relatively short study period. This indicates that the system is N-sensitive, though not necessarily N-limited, and current deposition rates may have already had a significant impact on community and ecosystem properties. The N reduction treatment allows us to make this inference, and also predict how the ecosystem might respond if the region were to experience a cessation of atmospheric N deposition. To my knowledge, there are no published studies on the effects of N loading in natural terrestrial ecosystems in India. Given the immense industrial and agricultural growth expected in India and China, global N deposition models predict heightened N deposition in these regions in the years to come (Dentener et al. 2006). Hence, more studies are needed in conjunction with prevailing local disturbances across different ecosystems in this part of the world to understand critical thresholds of the ecosystems and species therein. This is especially crucial for endangered ecosystems.
Figure 5.1. Soil N in response to treatments. (a) extractable NH$_4$$^+$-N in February and December 2008; (b) extractable NO$_3$$^-$-N g$^{-1}$ soil in December 2008, February 2008 data is not shown as it was undetectable in the vast majority of the samples; (c) resin bag NH$_4$$^+$-N in December 2008; (d) resin bag NO$_3$$^-$-N in December 2008. N treatments: reduction (500 g sucrose m$^{-1}$yr$^{-1}$, NR); ambient (0 g N m$^{-1}$yr$^{-1}$, NA); low dose (2 g N m$^{-1}$yr$^{-1}$, NL); high dose (8 g N m$^{-1}$yr$^{-1}$, NH). Significantly different groups ($P < 0.05$, Tukey's post-hoc test) are denoted by different lowercase letters. Means ± SE are shown.
Figure 5.2. Ecosystem function: response of (a) aboveground biomass, (b) percent plant cover, (c) gravimetric soil water by treatment. N treatments: reduction (500 g sucrose m⁻¹yr⁻¹, Nᵣ); ambient (0 g N m⁻¹yr⁻¹, Nₐ); low dose (2 g N m⁻¹yr⁻¹, Nᵢ); high dose (8 g N m⁻¹yr⁻¹, Nᵦ). Significantly different groups (P < 0.05, Tukey’s post-hoc test) are denoted by different lowercase letters. Means ± SE are shown.
Figure 5.3. Tissue chemistry: response of (a) percent leaf N, (b) leaf C:N ratio by treatment. N treatments: reduction (500 g sucrose m\(^{-2}\) yr\(^{-1}\), N\(_R\)); ambient (0 g N m\(^{-2}\) yr\(^{-1}\), N\(_A\)); low dose (2 g N m\(^{-2}\) yr\(^{-1}\), N\(_L\)); high dose (8 g N m\(^{-2}\) yr\(^{-1}\), N\(_H\)). Significantly different groups (\(P < 0.05\), Tukey’s post-hoc test) are denoted by different lowercase letters. Means ± SE are shown.
Figure 5.4. Community structure: response of (a) species richness, (b) Shannon diversity index, by treatment. N treatments: reduction (500 g sucrose m$^{-1}$ yr$^{-1}$, NR); ambient (0 g N m$^{-1}$ yr$^{-1}$, NA); low dose (2 g N m$^{-1}$ yr$^{-1}$, NL); high dose (8 g N m$^{-1}$ yr$^{-1}$, NH). Significantly different groups ($P < 0.05$, Tukey’s post-hoc test) are denoted by different lowercase letters. Means ± SE are shown.
Figure 5.5. Percent cover of two common species (a) *Eulalia phaeothrix*, (b) *Tripogon bromoides* that were influenced by N treatments. N treatments: reduction (500 g sucrose m⁻¹ yr⁻¹, NR); ambient (0 g N m⁻¹ yr⁻¹, NA); low dose (2 g N m⁻¹ yr⁻¹, NL); high dose (8 g N m⁻¹ yr⁻¹, NH). Significantly different groups (*P* < 0.05, Tukey’s rank-sum post-hoc test) are denoted by different lowercase letters. Means ± CI are shown.
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