The Influence of Environmental Factors and Landcover Change on the Distribution and Metacommunity Structure of Upper Montane (Shola) Forests in the Western Ghats

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Certificate

This is to certify that the thesis entitled "***The influence of environmental factors and landcover change on the distribution and metacommunity structure of upper montane (shola) forests in the Western Ghats***" submitted by Ms. Arundhati Das, for the award of Doctor of Philosophy for, Manipal University, Manipal, is a record of the research work carried out by her during the period of her study in this university under my guidance and supervision and the thesis has not formed the basis for the award of any degree, diploma or other similar titles.

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I Arundhati Das, hereby declare that this thesis "***The Influence of Environmental Factors and Landcover Change on the Distribution and Metacommunity Structure of Upper Montane (Shola) Forests in the Western Ghats***" has been compiled by me under the supervision of Dr. Kamaljit Singh Bawa, President, Ashoka Trust for Research in Ecology and the Environment (ATREE), Bangalore. This thesis has not been previously submitted for the award of any degree, diploma, associateship, fellowship or its equivalent to any other university or institution.

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Executive Summary

Tropical montane cloud forests are unique habitats with great ecological and hydrological significance. In the Western Ghats, these upper montane forests (also known as *sholas*) and associated grassland habitats form approximately 1% of the land area but harbour disproportionately high numbers of endemic taxa. Despite their great conservation significance, little is known about how patterns of tree and shrub species composition vary across space, how environmental factors such as soil, climate and topography affect tree and shrub community composition, and how widespread conversion of surrounding grasslands to tea and exotic tree plantations has affected *shola* forest communities.

The naturally fragmented nature of *shola* communities, which display patchiness at hierarchically nested scales, also makes them an ideal system in which to study metacommunity structure as species distributions, interactions and ecological processes, within and across fragments are likely to have equilibrated over many hundreds of generations (for trees). Hence the central underlying assumption of the species sorting perspective of the metacommunity framework, (i.e. that local community dynamics are at equilibrium) is more likely to be met in such a system. Further, recent conversion of the natural grassland matrix to exotic tree plantations and tea estates, is likely to have disrupted this equilibrium in complex and unpredictable ways, which can provide greater insights into mechanisms driving metacommunities dynamics in general and effects of landscape matrix conversion on plant communities in particular.

In this thesis I attempt to understand the patterns of distribution and plant community composition of *shola* forests and their drivers at different spatial scales. I investigate the topographic and bioclimatic determinants of vegetation pattern within *shola*-grassland mosaics across their distribution in the central and southern Western Ghats. I then focus on studying the distribution and metacommunity patterns of *shola* tree and shrub species at the landscape scale in the southern and western Upper Nilgiris Plateau. I identify important environmental gradients structuring tree and shrub metacommunities, and determine the extent to which the latter are influenced by abiotic factors such as climate, topography and soil versus biotic factors such as dispersal. I also examine effects of grassland conversion to tea and exotic tree plantations on the structure, composition and regeneration of *shola* forest fragments.

In order to fulfil these objectives, I use various analytic approaches including conditional inference classification trees, generalized linear models with an information theoretic framework, spatial eigenvectors and variation partitioning. I also develop a novel approach to modelling spatial connectivity created by dispersal processes in topographically heterogeneous terrain using a combination of spatial eigenvectors derived from a Circuit Theory approach.

I find that both vegetation pattern within *shola*-grassland mosaics in general, and the *shola* tree and shrub metacommunity in particular, are strongly structured by the elevation gradient. In particular, above approximately 2000m elevation, there appear to be shifts in both the distribution of forest and grassland within these mosaics, as well as large changes in community composition within *shola* fragments. The *shola* metacommunity in the Upper Nilgiris primarily exhibits a Clemenstian pattern of species distribution along an elevation gradient with high turnover and significant clumping of range boundaries. Spatially structured environmental variability, accounts for much of the explained variation in *shola* tree and shrub abundances, while dispersal limitation accounts for about 10% of explained variation. Approximately half of the variation in tree and shrub communities remains unexplained by the environmental, historical and spatial predictors considered. Finally, *sholas* located within a landscape matrix of grassland differ significantly in terms of structure, composition as well as regeneration levels from those located within an altered landscape matrix of tea plantations and wattle (*Acacia mearnsii*), indicating that landscape matrix conversion has affected the structure and dynamics of vegetation in *sholas*.

I present a synthesis of the main results and conclusions with a discussion of potential climate change impacts on *shola* forests and further research priorities. The specific conservation and management implications emerging from this study are also highlighted.

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List of Abbreviations

AIC: Akaike information criteria

CT: Classification tree

GLMs: Generalized linear models

IVI: Importance value index

MEMs: Moran’s Eigenvector Maps

RDA: Redundancy analysis

SL: Sri Lanka

TMCF**:** Tropical montane cloud forests

TCI: Topographic convergence index

TPI: Topographic position index

WG: Western Ghats

Chapter 1
Introduction

Tropical montane cloud forests (*shola*) in the Western Ghats, India

Tropical montane cloud forests (TMCF) are defined as forests that are frequently immersed in mist (Hamilton et al. 1995). These ecologically unique and hydrologically important habitats (Bruijnzeel and Proctor 1995) are restricted to a mere 0.14% of earth's land surface (Scatena et al. 2010). Found between 30°N and 30°S latitudes, they predominantly occur between 1200-2800m in elevation with records as low as 400m and others as high as 3500m (Jarvis and Mulligan 2011). The largest existing area of TMCF is found in Asia, mainly in Indonesia and Papua New Guinea, followed by the Americas. In Asia TMCF constitutes only 5.9% of all tropical montane forests (Scatena et al. 2010).

The large variation in elevation and latitude within which cloud forests occur is attributed to differences in the interaction between climate and topography, specifically height of the mountain range and its distance from the coast, which affects the incidence and frequency of ground level mist (Jarvis and Mulligan 2011). Mist provides these forests with an additional source of water through horizontal precipitation. Bruijnzeel and Proctor (1995) found that typically, horizontal precipitation inputs in these forests average 5-20% of rainfall. Recent ecophysiological studies from the Neotropics have shown that cloud forest tree species have the capacity to absorb water and nutrients directly through their leaves and are known to be very susceptible to drought (Goldsmith et al. 2013, Oliveira et al. 2014). This could explain why TMCF occur closer to the coast in topographically complex regions with higher rainfall and lower seasonality of precipitation than other tropical montane forest types (Jarvis and Mulligan 2011).

Apart from providing hydrological services such as increased throughfall and dry season streamflow (Bruijnzeel et al. 2010), this intriguing and heterogeneous biophysical context creates conditions for high levels of beta diversity and endemism across several taxa (Hamilton et al. 1995, Nair et al. 2001, Bruijnzeel et al. 2010), with many new species still being discovered from these habitats (Narayanan et al. 2013, Verma et al. 2013, Kumar et al. 2014). Recent international conservation initiatives (Bubb et al. 2004) have highlighted the ongoing threat to these rare and biologically rich habitats, which include conversion to agriculture and grazing, increased levels of invasion by exotics and increased frequency of fire (Scatena et al. 2010). Changing temperature and precipitation patterns have potentially serious implications for these mountain-top habitats (Sukumar et al. 1995, Foster 2010). However additional meteorological data of higher spatio-temporal resolution are needed to understand temporal and spatial variation in climate and address the questions of climate change impacts on these forests (Foster 2010).

Current knowledge gaps for conservation and management include: lack of information on the spatial variation in species composition and richness at multiple scales, nutrient dynamics and carbon cycling, impacts of land use conversion on species and ecosystems and lack of information on conservation status and restoration potential (Scatena et al. 2010). In particular, researchers have identified a need for further studies on the above from Asia and Africa. Very few studies on TMCF in these continents exist and the current knowledge arises from only a few locations within these vast continents (Bruijnzeel et al. 2010).

The cloud forests of the Western Ghats, also known as *sholas*, represent hotspots within a globally recognized biodiversity hotspot (Myers 2003) and have the potential to provide important ecological, evolutionary and management insights towards international efforts to conserve TMCF. The ecologically apt term *shola,* derived from the Tamil word '*Cholai*' or '*Chola*' in Malayalam, refers to a shaded, wet grove and directly associates this vegetation type with a water source (Nair and Khanduri 2001). Some authors estimate that up to 50% of *shola* forests have been lost in the last century and a half (Sukumar et al. 1995). Unfortunately previous syntheses of work on TMCF (Hamilton et al. 1995, Bruijnzeel et al. 2010) have not sufficiently represented the existing information on *shola* forests of the Western Ghats (Bunyan et al. 2012).

Status of research on plant communities of *shola* forests

Recent reviews of literature on the *shola* ecosystem (Bunyan et al. 2012, Robin and Nandini 2012) conclude that despite high levels of endemism and anthropogenic threat, this habitat and the complex mosaic that it forms with natural grasslands, has received relatively little research attention. The highest proportion (39%) of the 279 studies reviewed were focussed on describing phytosociology and diversity of flora (Robin and Nandini 2012). Bunyan et al. (2012) found that these studies varied greatly in their estimates of alpha diversity and endemism (19.5 % to 83.3%). A possible reason for this is that most studies are fairly restricted in spatial extent of sampling and inference, and apart from a few (Nair and Baburaj 2001, Nair and Menon 2001, Davidar et al. 2007a, Bunyan 2009, Mohandass and Davidar 2010), generally do not attempt comparisons across different regions or within larger landscapes. Even fewer studies have attempted to explore patterns of species abundance and turnover within this upper montane ecosystem at larger spatial scales (e.g. hundreds of square km) and how they relate to abiotic influences such as climate, topography, soil and biotic factors such as dispersal (but see Nair and Baburaj 2001, Swarupanandan et al. 2001, Joseph et al. 2012). There is however, plenty of evidence for the distribution of mid-elevation evergreen species in the Western Ghats being strongly influenced by both elevation and precipitation gradients at very large (ecoregional) spatial scales (Ramesh and Pascal 1997, Gimaret-Carpentier et al. 2003, Davidar et al. 2005, 2007b, Ramesh et al. 2010). Owing to the lack of large scale studies in the upper montane region, elevation boundaries for the occurrence of *shola* forest in the Western Ghats are yet to be rationalized. Several different lower elevation limits for *shola* have been suggested in the literature, ranging from 1400-1800m (Nair et al. 2001, Bunyan et al. 2012, Joseph et al. 2012, Robin and Nandini 2012). Most are based on observations of structure and physiognomy of the forest stands, rather than correlations with bioclimate and elevation. Similarly, transitional zones along elevation and rainfall gradients between different types of *shola* communities need to be identified in order to better understand, monitor and manage this rare habitat.

Finally, the impact of the extensive transformation over the last century and a half of natural grasslands to tea and exotic tree plantations on *shola* communities is largely unknown. For instance, the occurrence and spread of exotic invasives, recognized as a serious threat to the grasslands (Srivastava 2001, Seshan 2005, Zarri et al. 2006, Thomas and Palmer 2007), might well be aggravated by the interaction between land cover conversion and climate change.

Study area and landscape history

The primary study area is located in the Upper Nilgiri Plateau in the Western Ghats. A detailed description of this landscape can be found in chapters 3 and 4. The western and southern parts of the Upper Nilgiris Plateau still hold large areas of natural *shola* grassland mosaic, which dates back to at least 40,000 years ago (Caner et al. 2007). Other predominant land cover types in the region have come into being relatively recently.

Nomadic pastoralism, hunting, gathering and shifting agriculture were the predominant forms of subsistence on the plateau from about 2,000 years ago until the 15th century AD. The Badaga community settled in the northern and eastern parts of the Nilgiris plateau in the 15th century A.D. and converted large areas to permanent agriculture. Even more extensive land use change came much later with the advent of the British (1813-1818) who first envisioned the area as a potential location to set up a European colony (Prabhakar 1994). They encouraged the settlement and development of the plateau, introduced major infrastructural and development projects and market-based agriculture (Prabhakar 1994). Several exotic plants from temperate regions were also introduced into the area (Prabhakar 1994). This period was marked by an increasing exploitation of *shola* forests, especially around Ootacamund, primarily for fuelwood. In 1841, concerned about the felling of *sholas*, the British introduced a timber conservancy system, under which contracts were issued to bidders to fell wood from certain *shola* patches (Siddiqi 2005).

By 1860, an increasing emphasis on linkage with the market economy of the plains, resulted in a net flow of resources out of the area, increased immigration of people, disruption of traditional cropping patterns and greater dependence on the market-based economy for livelihood (Prabhakar 1994). *Shola* grassland mosaics in the central and northern plateau were converted to commercial agriculture. The area under commercial vegetable cropping in the Nilgiris increased over 100-fold between 1847 and 1950 (Prabhakar 1994). Under the Waste Land Rules (1863), large transfers of land (~350 ha) to European cultivators were undertaken. *Shola* forests were cleared to make way for tea, coffee and cinchona plantations (Prabhakar 1994). By 1900 tea and coffee plantations occupied about 50% of the cultivated lands in the plateau, mostly in the central and eastern parts of the plateau (Prabhakar 1994).

In 1883, the passage of the Madras Forest Act, enabled the British to assume control of forest lands, declaring them to be Reserve Forests and abolishing local rights (Prabhakar 1994). While this limited conversion of natural forest and grassland to agriculture, it allowed the Forest Department to execute another major conversion of this ecosystem. Exotic tree plantations were introduced during the mid-1800's on an experimental basis to meet fuelwood and timber needs. Australian wattles (*Acacia* sp.) were introduced first (1832), followed by *Eucalyptus* sp. (1847). By 1910, there were 635 ha of exotic tree plantations under the Forest Department and an additional 400 ha of private plantations to meet fuelwood demands (Prabhakar 1994). *Acacia dealbata* was planted in the Kundahs in 10-15 acre plots in order to fill the grasslands which were considered to be "wastelands" (Ranganathan 1938 Working Plan cited by Siddiqi 2005).

Post-independence, the commercial exploitation of forest and water resources in the Nilgiris intensified tremendously, this time by the Indian State. *Acacia mearnsii* De Wild. (black wattle) had been recognized as a weedy invasive as early as 1856 and in the mid-1860's *Eucalyptus globulus* was favoured over *Acacia* sp. as a plantation tree (Siddiqi 2005). However, with the cessation of trade relations with South Africa in 1940, *A. mearnsii* was cultivated over large areas of grassland for extraction of tannin from its bark. In 1953, *Acacia* plantations occupied 995 ha of the plateau (Prabhakar 1994). T. Jayadev's Working Plan (1954-1964) was the first of a series of five-year plans that established large-scale plantations in the southern and western parts of the plateau (Jayadeva 1954 and Thyagarajan 1964 Working Plans for the Nilgiris Division cited by Sandilya 2005). By 1963, the area under *A. mearnsii* was reported to be 12,140.59 ha. Therefore much of the wattle was introduced in the last 50 - 70 years. This species is an aggressive invasive that poses a major threat to the remaining grasslands of the plateau (Thomas and Palmer 2007). Ironically, following a growing realization of the conservation value of the grasslands, the Forest Department has been engaged in large-scale clearing of the wattle plantations in and around Mukurthi National Park over the last decade (Srivastava 2001).

The radical transformation of the Upper Nilgiris over the past 200 years from rolling grasslands with pockets of *shola* forest in folds and swamps in valley bottoms to an intensively used patchwork of agriculture, commercial plantation, monoculture tree stands and settlements will have had a profound impact on the ecology of *sholas* that is yet to be uncovered. The need to understand the impacts of landscape transformation on *shola* communities is urgent given climate change. Eventually, the ability of species in tropical montane forests to adapt and persist will depend largely on the quality and intensity of human land use in the surrounding matrix (Kupfer et al. 2006). In order to effectively maintain diversity and connectivity across *shola* forests in this landscape, it is imperative that conservation efforts first focus on understanding drivers of current patterns of species distributions at both local and landscape scales.

The metacommunity framework and its relevance to *shola* forests

Metacommunity theory and analysis provides an appropriate framework for understanding the structure of *shola* communities. A metacommunity is defined as a "*set of local communities that are linked by dispersal of multiple potentially interacting species*" (Leibold et al. 2004, p.602) The study of spatial patterns in species distributions over local and regional scales is therefore inherently important to such a framework (Holyoak et al. 2005). Understanding metacommunity structure at different spatial scales can give us insight into the relative importance of processes affecting community assembly such as dispersal, competition and niche-based species sorting (Holyoak et al. 2005). This is important both from an academic perspective as well as a more applied management perspective.The hierarchical framework suggested by metacommunity theory, which considers local and regional scales of organization is well suited to the *shola* grassland ecosystem as it is a naturally fragmented system which displays patchiness at hierarchically nested scales (Robin and Nandini 2012). Discrete forest patches occur in the midst of a matrix of grassland. Local communities are therefore easily defined and are linked to other local communities (or patches) by dispersal processes (Somasundaram and Vijayan 2010). At the landscape and then regional scales, groups of forest patches are separated from one another by increasingly impassable topographic barriers.

In addition to this, naturally fragmented forest systems such as the *sholas* offer a unique opportunity to study the effects of anthropogenic matrix conversion on metacommunities in a context in which it is far less confounded by other aspects of anthropogenic fragmentation such as habitat loss or partitioning (Fahrig 2003, Ewers and Didham 2006). Here discrete patches of forest habitat are surrounded by a relatively homogenous and structurally distinct matrix of grasslands. Species distributions, interactions and ecological processes are likely to have equilibrated within and across fragments in these systems over many hundreds of generations (for trees) (Núñez-Ávila et al. 2013). Hence a central underlying assumption of the species sorting perspective of the metacommunity framework (Leibold et al. 2004, Holyoak et al. 2005), (i.e. that local community dynamics are at an equilibrium condition) is more likely to be met in such a system. Further, recent conversion of the natural grassland matrix to exotic tree plantations and tea estates, is very likely to have disrupted this equilibrium in complex and unpredictable ways (Driscoll et al. 2013), which can now be studied to better understand mechanisms of metacommunities dynamics in general.

Objectives of the study

This study attempts to understand the patterns of distribution and community composition of *shola* forests at different spatial scales. In the second chapter I identify topographic and bioclimatic factors that predict occurrence of forest and grassland patches within tropical montane forest-grassland mosaics in central and southern regions of the Western Ghats. I further investigate whether interactions between topography and bioclimate are important in determining vegetation pattern at this ecoregional scale, and assess the role of measurement scale in determining the relative importance of specific topographic features. Finally, I examine whether the relative importance of these diverse explanatory factors changes with elevation across the latitudinal range of these mosaics. I assess prediction accuracy, predictor importance and potential interactions between predictors using two different analytic approaches: Random forests built on conditional inference classification trees (Hothorn et al. 2006), and generalized linear models (GLMs).

In the third chapter, I examine species richness, diversity, composition and stand structure of the *shola* woody communities in the Upper Nilgiris (covering a study area of approximately 600 km^2) and compare the result on floristics to similar studies from other *shola* forests in the Western Ghats. Using species presence-absence data, I compare observed metacommunity pattern to idealized theoretical patterns of vegetation distribution, such as the Clementsian, Gleasonian, neutral, and random (Leibold and Mikkelson 2002). I then assess the correlation of the observed metacommunity pattern to elevation and precipitation gradients in the study area. I also use species abundance data to examine community similarity among plots and the relationship with elevation. Finally, I attempt to identify a transition zone between lower and upper montane *sholas* by investigating the nature of floristic change along the elevation gradient at the Family and species- level and compare the results to existing knowledge of montane forest zonation in tropical Asia (Ohsawa 1991, Ashton 2003).

The fourth chapter assesses the relative influence of abiotic factors (i.e. climate, topography, soil and habitat) and biotic factors such as dispersal limitation on the spatial abundance patterns of *shola* tree and shrub species. This is done by modelling environmental and spatial (dispersal) effects on *shola* species using canonical ordination, Moran's Eigenvector Maps (MEMs) and variation partitioning (Dray et al. 2006). In a novel methodological application, MEMs (or spatial predictors) are built to explicitly test spatial hypotheses based on seed dispersal, including a new approach that models topographic resistance to disperser movement using a Circuit Theory (McRae et al. 2008). Each of the models is tested against observed species abundance data for the selection of the best environmental and spatial model. This analysis improves on previous variation partitioning studies of tropical forests by: a) including both topographic and edaphic predictors b) using MEMs to build and test specific spatial hypotheses representing dispersal processes in novel ways and c) testing the 'pure space' component of variation in the data for any unmeasured environmental drivers (Diniz-Filho et al. 2012), thereby strengthening the ability to attribute this component to dispersal limitation.

Finally, in the fifth chapter, I examine differences in diversity, composition, stand structure and regeneration between *shola* forests located within a landscape of natural grassland and those located in a converted matrix of tea or wattle plantations. I also examine the relationship between distance to tea plantations and the presence of *Cestrum* sp. which appears to have invaded the *shola* understorey in some areas. I model *Cestrum* abundance as a function of various bioclimatic and habitat factors. Possible ecological mechanisms through which the conversion of the matrix could have caused the observed changes in *shola* communities are discussed.

I conclude with a synthesis of the findings and a discussion on management implications from this study.

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Chapter 2

Topographic and bioclimatic determinants of the occurrence of forest and grassland in tropical montane forest-grassland mosaics of the Western Ghats, India

Introduction

Montane forest-grassland mosaics in the tropics form hotspots within hotspots of global biodiversity (Myers 2003; Bond and Parr 2010) supporting several endemic species (Ramesh and Pascal 1997) and are recognised centres of speciation for some taxa (Narayanan et al. 2013). Both forest and grassland communities are characterised by high spatial turnover in species composition (Nair et al. 2001, Sankaran 2009, Bond and Parr 2010). The complex and heterogeneous terrain on which they occur has the potential to provide important climatic microrefugia (Dobrowski 2011) for tropical biodiversity, especially under climate change.

As in other forest-grassland mosaics (Behling and Pillar 2007, Silva and Anand 2011), there is evidence for climatic control on the distribution of forests and grasslands within mosaics in the Western Ghats. During the Pleistocene, forests spread over grasslands in warmer, wetter phases and contracted during cooler, dry periods (Sukumar et al. 1995, Caner et al. 2007). During episodes of past climate change, topography mediated the extent of change between grass and forest, with forest expansion limited to sheltered valleys, possibly due to the effect of strong winds on steeper slopes and more exposed sites (Caner et al. 2007). There appears to be a strong topographic effect on current vegetation pattern, with forest patches occurring in valleys, depressions and sheltered sites and grasslands occupying ridges, hill tops and exposed areas (Ranganathan 1938; Meher-Homji 1967).

Topographic heterogeneity has complex effects on microclimate (Dobrowski 2011), impacting resource gradients for plants, such as sunlight, soil moisture and nutrients. At large spatial scales, elevation influences temperature and precipitation (Lauer 1981), while at finer scales, topographic position, terrain ruggedness and land surface curvature control the direction, rate and degree of convergence of flow of air and water, as well as mixing between the surface air and free-atmosphere layers (Dobrowski 2011). Consequently, valleys are more weakly linked to regional temperature patterns and have greater diurnal temperature ranges than peaks or ridge tops (Dobrowski 2011). Depressions and valley bottoms are also more frost-prone than elevated areas due to the pooling of cold air (Bader and Ruijten 2008; Dobrowski 2011). Aspect and slope influence solar insolation, thereby affecting local air temperature and soil-water balance through evapotranspiration (Lookingbill and Urban 2004, Bennie et al. 2008). Mid-lower slope positions usually have greater surface soil moisture levels than upland plateaus (Daws et al. 2002, Lookingbill and Urban 2004). Topographically controlled hydrologic sorting of soil particles also affects soil texture, depth, pH and nutrient content at sites (Hook and Burke 2000, Cox et al. 2002, Lippok et al. 2013). Cox et al. (Cox et al. 2002) and Lippok et al. (Lippok et al. 2013) found that levels of pH and exchangeable calcium and magnesium increased from ridge to valley.

Elevation and topography affect the incidence, frequency and spread of disturbance processes such as fire (Geldenhuys 1994; Martin et al. 2007; Wood et al. 2011). Topographic orientation affects the flow of fire-bearing winds (Geldenhuys 1994), while topographic heterogeneity increases frictional drag on winds and creates discontinuities in fuel-load and soil moisture (Stambaugh and Guyette 2008). Wood et al. (Wood et al. 2011) found that after accounting for vegetation type, topographic position, elevation and aspect were important predictors of fire occurrence. Forests occurring in mosaics with more flammable vegetation types are often located in topographic positions that inhibit the spread of fire such as near rocky outcrops, in valleys, depressions and on aspects sheltered from fire-bearing winds (Geldenhuys 1994, Martin et al. 2007, Coblentz and Keating 2008, Wood et al. 2011).

Although many studies have examined the effects of climate on forest-grassland mosaics, there is no quantitative study on the effect of topography on vegetation pattern across the full range of bioclimatic conditions in which these mosaics are found. A better understanding of the importance of various topographic features, how they interact with bioclimate and the spatial measurement scale at which they influence vegetation pattern could provide insights into mechanistic processes maintaining grasses and trees in tropical montane forest-grassland mosaics. Such an analysis could also help inform the management and conservation of these biologically important mosaics, especially in the face of climate change and other anthropogenic factors.

The main objectives of this analysis were to answer the following questions: i) to what extent can topography and bioclimate predict the pattern of occurrence of grass and forest patches within forest-grassland mosaics of the Western Ghats? ii) how does the relative importance of topography and bioclimate vary at different elevations? iii) what are the important interactions between topography and bioclimate for vegetation patterns? iv) what are the relevant measurement scales for topographic predictors that affect vegetation pattern within mosaics?

Materials and Methods

Study Site

The study area encompasses montane forest-grassland mosaics of the Western Ghats between 8°22’-13°31’ latitude and 74°50’-77°30’ longitude (Fig. 2.1). These habitats occur at the tops of the range; the largest expanses occur on high plateaus in the Nilgiris and Anamalai hills. Elevation for the study mosaics varies from approximately 500m to 2695m above mean sea level, while mean annual temperatures vary between 13–25°C, maximum warm season temperatures between 19–33°C, and minimum cold season temperatures between 0–20.5°C. Ground frost occurs at elevations above 2000m between November and February. Mean annual precipitation across the study mosaics ranges from approximately 800mm to above 6000mm.While most of the area receives rainfall primarily during the southwest monsoon (May–September), the eastern mosaics receive an increased proportion of rainfall during the northeast monsoon (October–December).Duration of the dry season ranges from one month in the southernmost mosaics to 4 months in the northernmost ones, and amount of rainfall decreases rapidly from west to east, especially at higher latitudes (Ramesh and Pascal 1997).

The mosaics consist of undulating grasslands interspersed with patches of stunted evergreen forests, locally known as *shola*. The boundary between forest and grassland is abrupt. *Sholas* have been classified as wet montane temperate forests (Champion and Seth 1968), and as tropical montane cloud forests (Bunyan et al. 2012). Trees are stunted (rarely above 15m tall), with relatively small, thick leaves, and trunks and branches covered with bryophytes and epiphytes (Meher-Homji 1967). Dominant families include Lauraceae, Rubiaceae, Myrtaceae

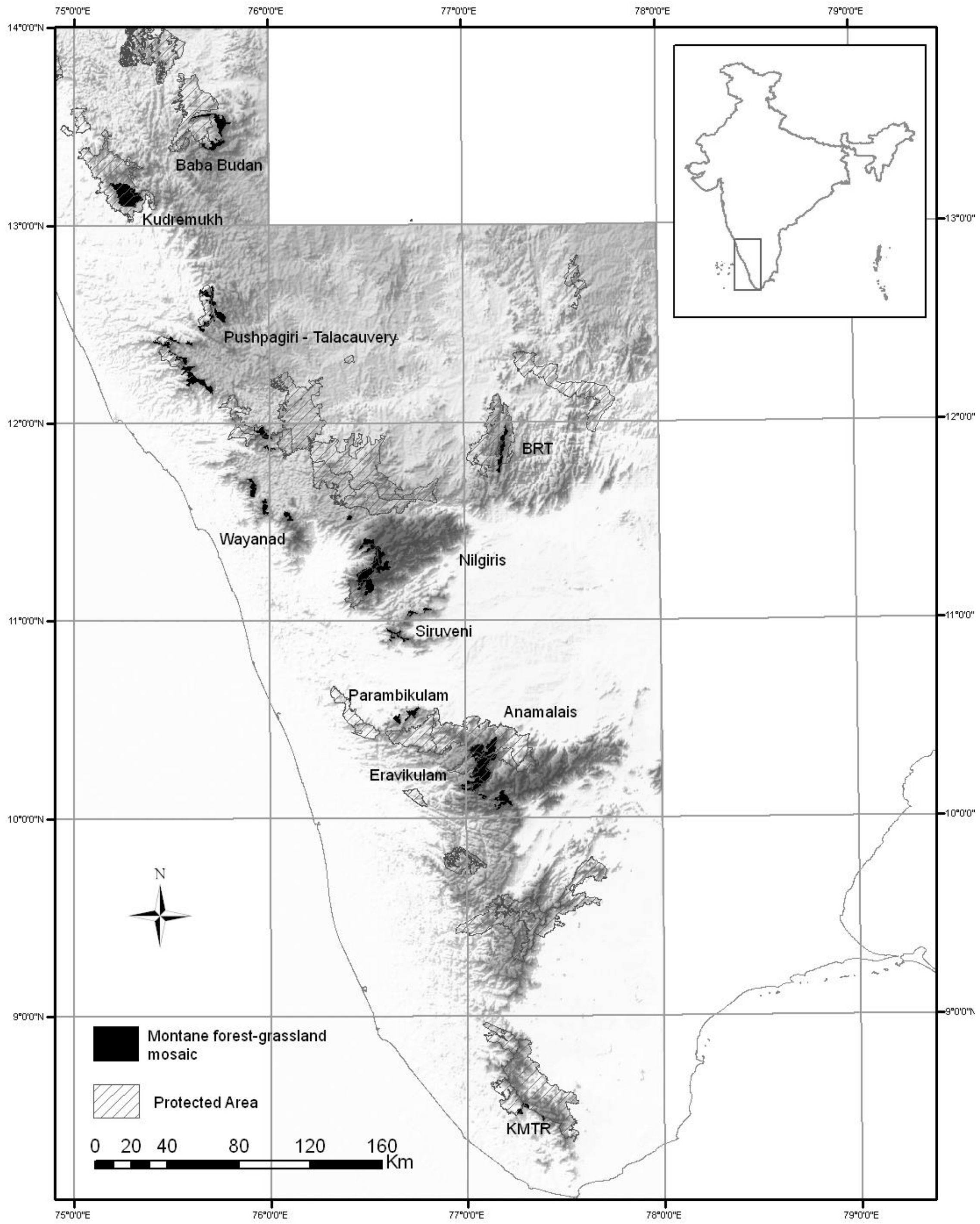

Figure 2.1. Map of the Western Ghats showing locations of montane forest-grassland mosaics and inset showing sampling points spaced 500m apart on one of the study mosaics

and Symplocaceae (Meher-Homji 1967; Nair et al. 2001). The grasslands, which have also been called ‘shrub-savanna’, consist of grass, herb and shrub species (Meher-Homji 1967). These mosaics cover approximately 1% of the Western Ghats but are rich in endemic species, some of which are extremely rare. Cattle grazing and fire are common disturbances across these mosaics and there is very limited understanding of their impact on vegetation dynamics. These mosaics face a number of threats, including large scale land-use conversion, invasion by exotics and climate change (Thomas and Palmer 2007, Bunyan et al. 2012).

Sampling strategy

Delineation of forest-grassland mosaics and extraction of sample points

Mosaics were identified using high-resolution satellite imagery in Google Earth (Google Earth 2013). Polygons were digitised using visual interpretation and their locations and borders refined in consultation with three field biologists who have worked extensively in this habitat across the Western Ghats, in addition to my own experience from previous fieldwork. This analysis represents the current extent of the mosaics and therefore underestimates the full range of topographic and bioclimatic conditions under which these mosaics naturally occur, for which there is insufficient data. In the Nilgiris and Anamalai hills, large areas of grassland, have been converted to exotic tree plantations (Prabhakar 1994). The boundaries of the mosaic on lower slopes where *sholas* merge into continuous forest, were necessarily subjective and were drawn conservatively to restrict the study area primarily to forests that occur within a matrix of grassland. Areas within and around Periyar Tiger Reserve were excluded because some of these grasslands appear qualitatively different from the grasslands in other mosaics (*Personal observation*).

A systematic sample of point locations covering the study area was created in ArcGIS v.10.0 (ESRI 2011), with a random start and spaced 500m apart (deemed adequate for spatial independence since habitat can change from grassland to forest several times over within this distance). The points were overlaid on high-resolution (~2.5m) imagery in Google Earth, and the habitat type of each point was classified as forest (“1”) or grassland (“0”). Points falling within 30m of a forest-grassland edge (since the DEM has an average positional error of about 20m) were eliminated, as were points located in areas concealed by cloud cover. Points falling on rocky outcrops, water bodies and exotic tree plantations were also eliminated.

Extraction and computation of topographic and bioclimatic predictors

A total of 1960 points of the original 2020 points were imported into ArcGIS 10.0 for analysis. A subset of points located in extreme topographic positions was used to confirm that spatial registration of imagery matched that of the DEM. Selection of putative predictors of occurrence of forest and grassland within the mosaic was based on available published literature on the determinants of these patterns in such mosaics globally (Meher-Homji 1967; Geldenhuys 1994; Sukumar et al. 1995; Caner et al. 2007; Martin et al. 2007; Bader and Ruijten 2008; Wood et al. 2011).

The ASTER Global Digital Elevation Model (GDEM) v.2 tiles (30m contour interval) (NASA and METI 2011) for the study area were used to extract the following topographic predictors in ArcGIS using Spatial Analyst and Topography toolbox: elevation, slope, transformed aspect, solar radiation (McCune and Dylan 2002), topographic position index (Jenness 2006), topographic convergence index (Beven and Kirkby 1979), and surface curvature (Table 2.1).

Table 2.1: Topographic and bioclimatic predictors used to predict vegetation pattern in forest-grassland mosaics

Name	Code	Range	Description	Reference
Elevation	elev	455 – 2555m	Elevation of 30m pixel	(NASA and METI 2011)
Slope	slope	0.75 - 62.15 degrees	Local slope at 30m resolution	(METI and NASA 2011)
Ruggedness Index	rugged	4.24 - 157.46m	Terrain heterogeneity over a 3x3 cell neighborhood using a 90m DEM	(Riley et al. 1999)
Sine Aspect/ Cosine Aspect	sin.asp/ cos.asp	-1.00 - 1.00	E-W and N-S transformation of aspect at 30m resolution	(NASA and METI 2011)
Beers Aspect	Beers	0 - 2.00	SW-NE transformation of aspect at 30m resolution	NASA &METI 2011)

Name	**Code**	**Range**	**Description**	**Reference**
Curvature 30m	curve30	-7.9 - 8.45	Combined across and along slope curvature, using a 30m pixel and 3x3 cell window	(NASA and METI 2011)
Curvature 90m	curve90	-3.3 - 4.04	Combined curvature, using a 90m pixel and 3x3 cell window	(NASA and METI 2011)
Local scale topographic position index	tpi3.10	-90.93 - 120.75m	Average difference in elevation between a focal cell and neighborhood defined using an annulus of inner radius 90m and outer radius 300m	(Jenness 2006)
Intermediate scale topographic position index	tpi10.34	-271.77 - 345.8 m	TPI using an annulus of inner radius 300m and outer radius 1020m	(Jenness 2006)
Landscape scale topographic position index	tpi10.67	-384.3 - 508.76 m	TPI using an annulus of inner radius 300m and outer radius 2010m	(Jenness 2006)
TCI 30m	tci30	0 - 366	Topographic convergence index using a 30m pixel	(Beven and Kirkby 1979)
TCI 60m	tci60	-0.03 - 13.21	Topographic convergence index using a 60m pixel	(Beven and Kirkby 1979)
TCI 90m	tci90	-0.56 - 11.02	Topographic convergence index using a 90m pixel	(Beven and Kirkby 1979)
Distance to coast	coast.dist	25.27 - 174.11 km	Euclidean distance to coast line	
Solar radiation	solar	0.15 - 0.44 MJ/cm^2/yr	Potential annual direct solar radiation based on latitude, slope and aspect.	(McCune and Dylan 2002)
Max. temperature warmest month	max.tmp	19 – 33 ^{o}C		(Hijmans et al. 2005)
Min. temperature	min.tmp	4.1 - 20.5 ^{o}C	Min. temperature in coldest month	(Hijmans et al. 2005)

Name	Code	Range	Description	Reference
Annual temperature range	anntmprng	10.5 - 18.2 ^{o}C		(Hijmans et al. 2005)
Temperature seasonality	tmp.seas	891 - 1783	Temperature seasonality (standard deviation of temperature over the year*100)	(Hijmans et al. 2005)
Mean temperature dry quarter	meantmp.dry	11.9 - 25.5 ^{o}C	Mean temp from Jan-Mar	(Hijmans et al. 2005)
Mean temperature warm quarter	meantmp.warm	13.9 - 27.5 ^{o}C	Mean temp from Mar-May	(Hijmans et al. 2005)
Mean temperature cold quarter	meantmp.cold	11.2 - 24.3 ^{o}C	Mean temp from Nov-Jan	(Hijmans et al. 2005)
Annual precipitation	annprec	754 - 6080 mm	Mean annual precipitation	(Hijmans et al. 2005)
Precipitation CV	prec.cv	50 - 140	Precipitation seasonality (coefficient of variation based on monthly precipitation values)	(Hijmans et al. 2005)
Warm quarter precipitation	warm. prec	165 - 893 mm	Avg. precipitation from Mar-May	(Hijmans et al. 2005)
Dry quarter precipitation	dry.prec	7 - 138 mm	Precipitation from Jan-Mar	(Hijmans et al. 2005)

TPI was calculated at local, intermediate and landscape scales (Table 2.1), defined by field-based observations of approximate distances between local hilltops and depressions and also wider valleys and peaks within some of the mosaics. TCI and surface curvature values for each sampling point were also extracted at different scales, by resampling the DEM to 60m and 90m resolutions. TCI was used as a proxy for soil moisture as it incorporates the upslope flow area above a given cell, identifying convergent points in the landscape which water would flow to. It is also a proxy for areas that are prone to cold air pooling and therefore frost (Bader and Ruijten 2008; Dobrowski 2011). Bioclimatic predictors (Table 2.1) were downloaded from the BIOCLIM global dataset, available at 1km resolution (Hijmans et al. 2005).

Statistical Analysis

Classification trees and random forests

As the dataset comprised several highly correlated predictors likely to have complex interactions, a classification tree (CT) approach (Breiman et al. 1984) was used to explore relationships between the response variable (forest or grass) and the predictors. CTs make no assumptions about underlying response functions and use recursive partitioning to split the data into increasingly homogenous subsets based on predictors. They are a powerful and intuitive method for visualising interactions between predictors (De'ath and Fabricius 2000; Cutler et al. 2007).

CTs based on conditional inference (Hothorn et al. 2006) were constructed in R Statistical Software (R-Development-Core-Team 2013) package "party". Conditional inference was chosen over the Gini index as a splitting criterion because the latter is biased towards predictors measured over larger scales or categorical predictors with many categories (Strobl et al. 2009). Conditional inference trees have a statistical stopping criterion, which prevents over fitting and eliminates the need for pruning (De'ath and Fabricius 2000).

A single CT was found to be quite unstable, with small changes in the training data yielding a different tree. Hence random forests (Breiman 2001) was used to assess: a) relative importance of the topographic and bioclimatic predictors and b) their combined ability to predict where forest and grass occur. Random forests compare favourably in terms of prediction accuracy against other approaches such as GLMs, GAMs and neural networks (Prasad et al. 2006; Cutler et al. 2007). The CTs were built using two-thirds of the data and the remaining third "out-of-bag" data was used to assess prediction error for the random forest. Predictor importance was computed by randomly permuting values of each predictor in turn, thereby removing any association with the response, and then classifying "out-of-bag" samples using each CT and measuring the change in prediction accuracy after the permutation of that predictor (Cutler et al. 2007; Strobl et al. 2009). This was then averaged across all CTs in the forest.

A random forest of 1000 conditional inference CTs was grown using sub-samples of the data (Strobl et al. 2007). For any given node within a tree, a subset of 5 randomly selected predictors was selected for splitting that node (Hothorn et al. 2006). Prediction accuracy was assessed using the “out-of-bag” subset of the data. This was repeated ten times using a different random seed each time, with overall prediction accuracy assessed as the average of ten runs. Predictors of very low importance (near 0) were removed from the data. The list of predictors was then refined by beginning with the most important predictor and eliminating highly correlated (Pearson’s *r* >0.7) predictors that were of lower importance. Random forests was then re-run with this smaller set of predictors and the cross-validated “out-of-bag” prediction accuracy reassessed as described above. Finally, to enhance our understanding of the effects and interactions between predictors, a conditional inference CT was built using the full dataset and the selected subset of predictors.

Generalised linear modelling

Generalised linear modelling (McCullagh and Nelder 1989) was used as a different way of assessing predictor importance based on a) summed Akaike weights (Burnham and Anderson 2002) and b) model averaged, standardised beta coefficients (Zar 1999). GLMs were also used to assess importance of interactions between predictors, many of which were identified using the conditional inference CTs.

To avoid the effects of collinearity and limit the number of predictors, and the number of models considered, we further eliminated predictors based on i) collinearity and ii) very low predictor importance (near 0) as demonstrated by the random forest analysis. Thus, the initial random forest analysis did feed into the GLMs, but not to the extent that it would seriously affect our final inference, since only obviously unimportant predictors were eliminated. Model-averaged estimates of each standardized beta coefficient were obtained as a weighted (using Akaike weights) average across all models containing that predictor. We also obtained unconditional standard errors (SE), which includes model selection uncertainty (Burnham and Anderson 2002). The 95% confidence intervals based on these SEs were examined to see if they straddled zero. Finally, Akaike weights were summed over all models containing a predictor as a measure of predictor importance. Because we required a balanced set of models where each predictor appeared in the same number of models (Doherty et al. 2010) we fitted all combinations of the predictors, capped at a maximum of 6 predictors per model, allowing us to assess the importance of each predictor based on the summed Akaike weights (Burnham and Anderson 2002). This analysis was implemented in R using the package “MuMIn”.

We note that neither the CT nor GLM approaches as used by us represent confirmatory analyses (Nichols et al. 2012) to test specific a priori hypotheses based on current understanding. While we did use available information to select putative predictors of the occurrence of forests or grasslands, the balanced set of models we assessed using GLMs is not a ‘candidate set’ (sensu Burnham and Anderson 2002) where each model represents a specific scientific hypothesis, but a way to assess the importance of different predictors while ensuring that our inferences are not influenced by variable representation of different predictors within the set.

As the factors affecting vegetation pattern are likely to differ at low-medium versus high elevations (e.g. frost occurs only above a certain elevation), we assessed the change in the relative importance of topographic and bioclimatic predictors with elevation by repeating the above analyses for a subset of the data representing forest-grassland mosaics in the Nilgiris and Eravikulam plateaus above 1500m elevation (Fig. 2.1). These high-elevation mosaics are also of particular conservation and management interest.

Results

Random Forests: Classification accuracy and predictor importance

The sample points (grass *n* = 1000, forest *n* = 960) cover a wide range of topographic and bioclimatic conditions (Table 2.1). The results of the random forest runs with the full dataset indicated a mean overall prediction accuracy for the “out-of-bag” data of 68.6%, (mean prediction accuracy for grass = 69.7%, forest =67.6%). Random forest runs using only topographic predictors had lower mean prediction accuracy (66.5%; grass = 67.1%, forest = 65.8%).

Permutation variable importance values averaged over 20 random forests runs indicated that elevation was the most important predictor, followed by local-scale TPI (tpi3.10). Predictors with the lowest importance values were TCI (30m pixel), curvature (30m pixel), sine aspect, slope and Beers aspect (Fig. 2.2a).

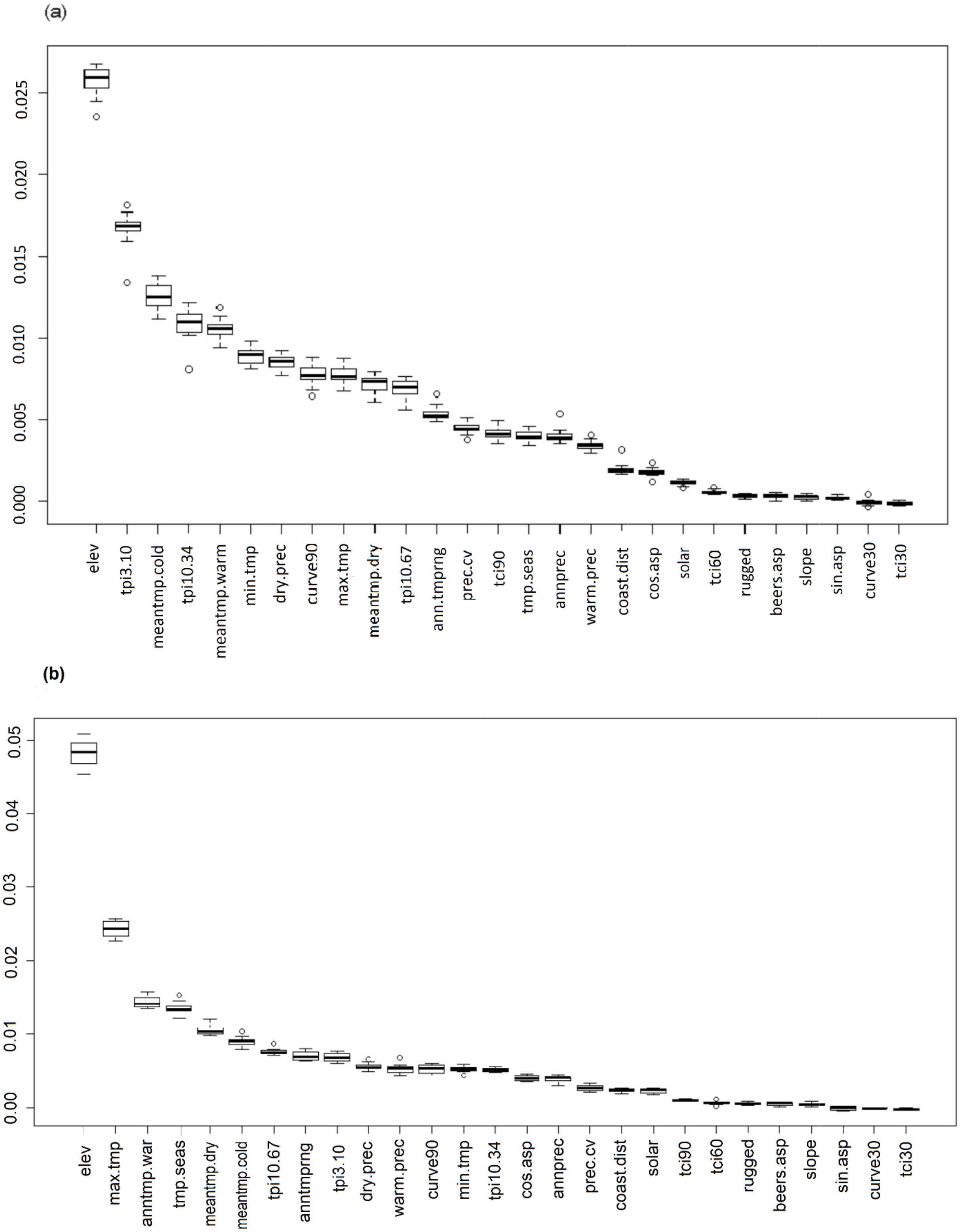

Figure 2.2: Boxplots showing distribution of permutation-based variable importance measures for each predictor derived from multiple random forest runs for a) all mosaics b) Nilgiris and Eravikulam subregions. Please refer to Table 2.1 for explanation of predictor codes.

Based on collinearity and the results of the permutation variable importance, the following subset of 11 predictors was chosen: elevation, local-scale TPI (tpi3.10), dry quarter precipitation, curvature (90m pixel), landscape-scale TPI (tpi10.67), annual temperature range, TCI (90m pixel), annual precipitation, distance to coast, cosine aspect and ruggedness. A marginal improvement in mean prediction accuracy was achieved over ten random forest runs for the "out-of-bag" data with this subset of predictors (69.2%; grass = 70.1%, forest = 68.3%).

For the Nilgiris-Eravikulam subset, (*n* = 783; 43% forest, 57% grass), the full set of predictors had an overall mean prediction accuracy of 72.1% (grass = 80.3%, forest = 63.9%), with many forest points misclassified as grass. Elevation was the most important predictor, followed by maximum temperature of the warmest month (Fig. 1.2b). Predictors related to temperature (most of which were very highly correlated with elevation (Pearson's $r \geq 0.95$)), gained importance over local-scale TPI. Landscape-scale TPI was more important than local-scale TPI at high elevations (Fig. 1.2b). Cosine aspect, gained importance in the higher elevation dataset – and was negatively correlated with solar radiation (Pearson's $r = -0.67$). Annual precipitation and dry quarter precipitation were less important at higher elevations (Fig. 1.2b).

Based on collinearity and the results of the permutation variable importance measure, the following subset of 12 predictors was chosen for Nilgiris-Eravikulam mosaics: elevation, temperature seasonality, landscape-scale TPI (tpi10.67), annual temperature range, local-scale TPI (tpi3.10), dry quarter precipitation, curvature (90m pixel), cosine aspect, annual precipitation, distance to coast, TCI (90m pixel) and ruggedness. A higher overall mean prediction accuracy of 73.1% (grass = 81.4%, forest = 64.8%) was achieved with this subset of predictors and the "out-of-bag" data.

Conditional inference classification trees: interpretation of predictor effects and possible interactions

The conditional inference CT for the full dataset, using the subset of 11 predictors, indicated that local-scale TPI (tpi3.10) and elevation were important splitting variables followed by dry quarter precipitation and cosine aspect (Fig. 1.3). The initial split made on tpi3.10, indicates that relatively small differences in local TPI are important. Another main split was based on elevation of about 2000m. The majority of points with higher tpi3.10 and elevations ≥ 2038m were classified as grass, with high node purity. Above 2000m, only 28% of the sample points were forest compared to about 50-60% in mosaics below 2000m. Slight, local topographic depressions (tpi3.10 ≤ -3.8m) below 2041m elevation were more likely to be identified as 'forest' compared to those above 2041m (Fig. 1.3, Nodes 4-7 vs. Nodes 9-12), indicating an interaction between elevation and tpi3.10.

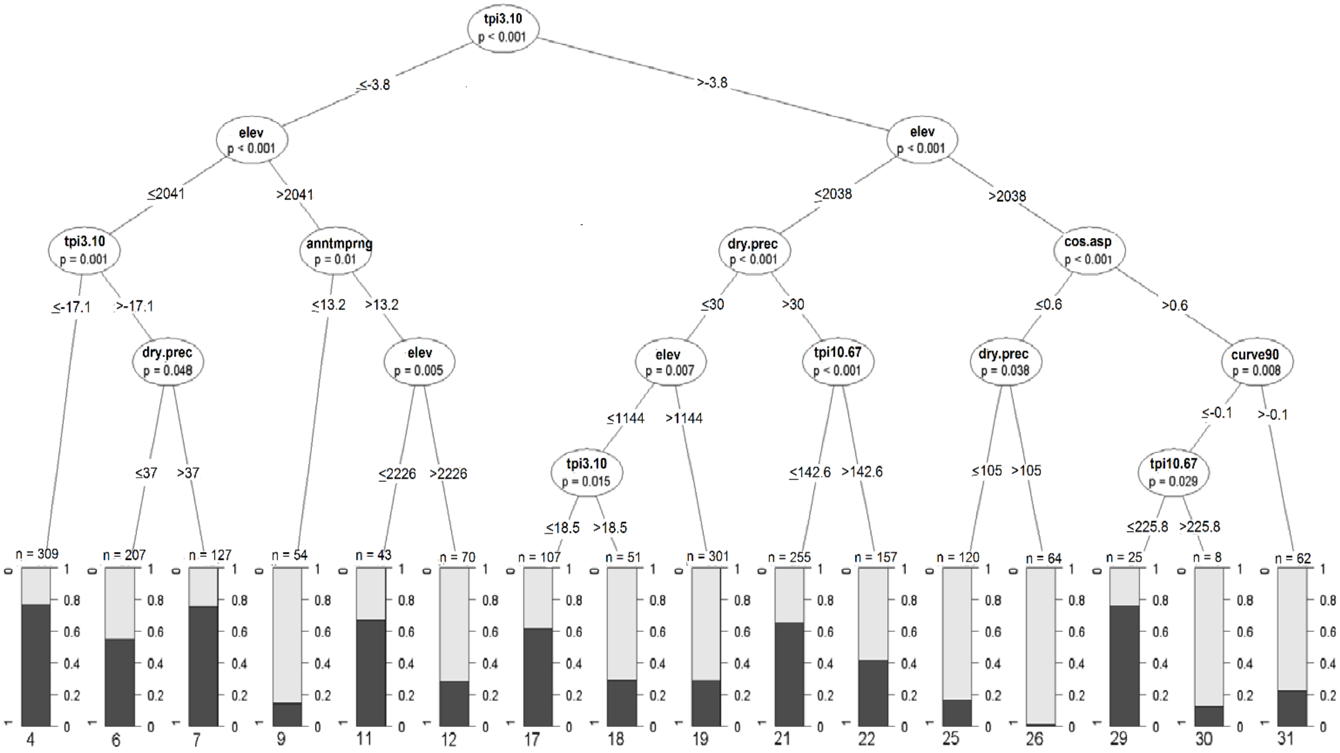

Figure 2.3. Conditional inference classification tree for forest and grassland points in forest-grassland mosaics of the Western Ghats**.** Node purity of terminal nodes depicted in bar charts with dark grey assigned to "forest" and light grey to "grass". Terminal node identity numbers are given below each bar chart. For geographic breakdown of data points in each terminal node see Appendix 1. Please refer to Table 2.1 for explanation of predictor codes.

Sites between 1144–2038m elevation, with flat or elevated topographic positions and dry quarter precipitation ≤ 30mm,were predominantly grassland (Fig. 2.3, node 19), as were most sites with high landscape-scale TPI (e.g. hilltops; tpi10.67 > 142.6m), in areas with dry quarter precipitation >30mm. Below 1144m, points with dry quarter precipitation < 30mm, that had large positive differences in local-scale TPI (tpi3.10 > 18.5m) (e.g. local ridge) were more likely to be grass. Therefore, where dry quarter precipitation was higher, landscape-scale TPI influenced whether a site held grassland or forest, whereas when dry quarter precipitation was low, differences in local-scale TPI had an impact on cover type (Fig. 2.3).

There seemed to be complex interactions among topographic variables as well as between elevation and annual temperature range (Figs. 2.3 and 2.4). For higher elevation points, elevation, annual temperature range, cosine aspect, curvature (90m pixel) and landscape-scale TPI (tpi10.67) were important splitting variables.

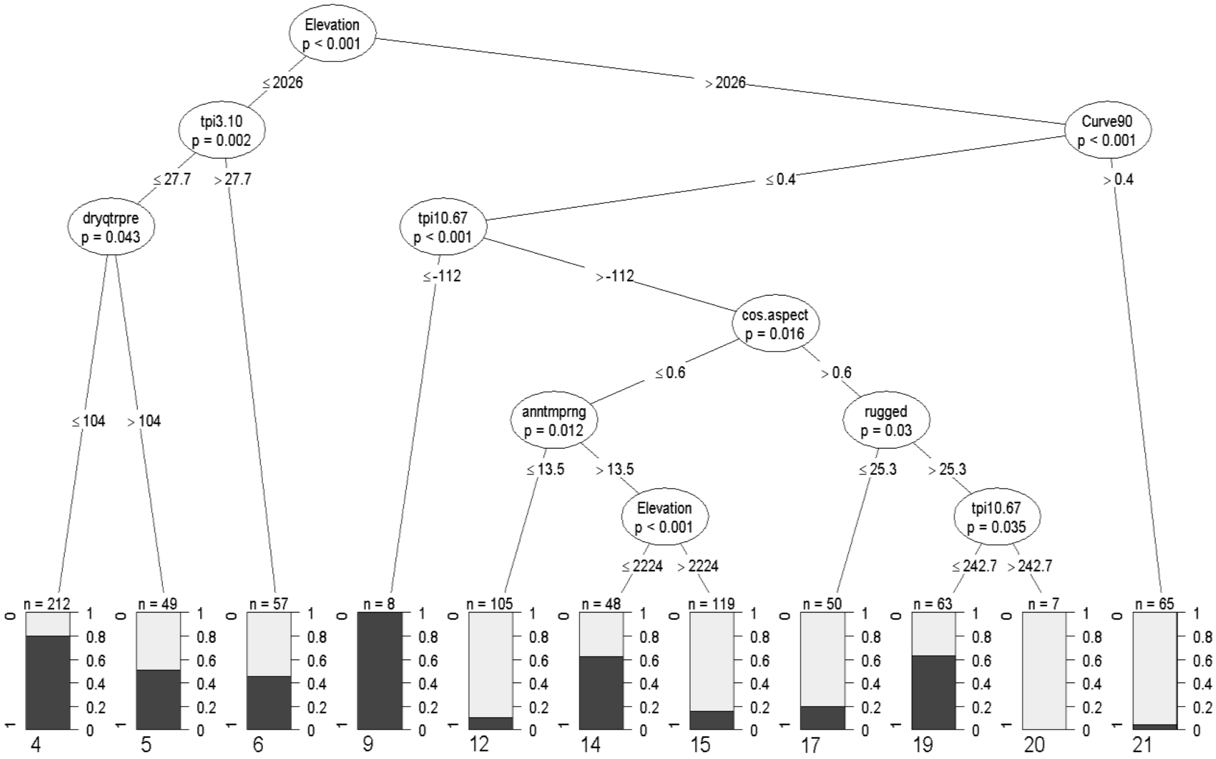

Figure 2.4. Conditional inference classification tree for forest and grass points in forest-grassland mosaics of the Nilgiris and Eravikulam (> 1500m elevation). Purity of terminal nodes depicted as a bar chart with dark grey assigned to “forest” and light grey to “grass”. Terminal node identity numbers are given below each bar chart. Please refer to Table 2.1 for explanation of predictor codes.

The CT built from the subset of 12 predictors for Nilgiris-Eravikulam, showed that between 1500–2555m, elevation was the most important splitting variable, followed by local-scale TPI at lower elevations and local curvature (curve90) at higher elevations (Fig. 2.4). Points between

1500m–2026m were mostly classified as forest, particularly when they had lower tpi3.10 values. Grasslands in this elevation band were not classified well, as shown by the high level of node impurity (Nodes 5 and 6 in Fig. 2.4). Points > 2026m elevation and with convex curvature (i.e. curve90 > 0.4) were classified as grass with high node purity (Node 21 in Fig. 2.4). Points > 2026m elevation were classified as forest with high node purity only when they lay on flat or concave local curvature and at relatively low landscape-scale TPI, i.e. deeper valleys (Node 9 in Fig. 2.4). Above 2026m, forest points fell mostly on NE to NW aspects. More south-facing sites with annual temperature range >13.2^{o}C, above 2224m elevation, were classified as grass with very high node purity (Node 15 in Fig. 2.4).

Generalised linear models: predictor importance

The analysis on the full dataset (*n* = 1960) using 11 predictors and interactions between some of the predictors, indicated that the two best models had the following predictors for occurrence of forest: elevation, dry quarter precipitation, local-scale TPI, annual temperature range, interaction between annual temperature range and dry quarter precipitation, curvature (90m pixel) and cosine aspect. Predictors with highest summed Akaike weights were: elevation, dry quarter precipitation, local-scale TPI, annual temperature range, an interaction between annual temperature range and dry quarter precipitation, curvature (90m pixel) and cosine aspect (Table 2.2). Beta coefficients of the top three predictors supported their importance.

Table 2.2: Importance of topographic and bioclimatic predictors used in GLM analysis of forest-grassland mosaics in the Western Ghats. Columns show summed Akaike weights, standardized beta coefficients averaged across models and unconditional standard errors (SE) in parentheses and 95% confidence intervals (CI) based on the unconditional SEs.

Predictor[a]	**Summed Akaike weight**	**Standardized, model-averaged beta (SE)**	**Model averaged 95% CI**
elevation	~1	-1.014 (0.094)	-1.199 : -0.829
dry.prec	~1	0.92 (0.117)	0.69 : 1.15
tpi3.10	0.999	-0.449 (0.085)	-0.616 : -0.283
anntmprng	0.999	0.36 (0.08)	0.204 : 0.516

Predictor[a]	**Summed Akaike weight**	**Standardized, model-averaged beta (SE)**	**Model averaged 95% CI**
anntmprng:dry.pre	0.999	0.323 (0.056)	0.214 : 0.432
curve90	0.579	-0.259 (0.063)	-0.383 : -0.136
cos.aspect	0.379	0.204 (0.05)	0.107 : 0.301
elevation:tpi3.10	0.029	0.19 (0.055)	0.082 : 0.298
annprec	0.008	-0.304 (0.099)	-0.498 : -0.109
coast.dist	0.002	0.202 (0.087)	0.031 : 0.372
elevation:dry.prec	0.0009	-0.173 (0.077)	-0.323 : -0.022
tci90	0.0003	0.091 (0.056)	-0.018 : 0.2
tpi10.67	0.0002	-0.091 (0.062)	-0.211 : 0.03
dry.prec:tpi3.10	0.0001	0.061 (0.056)	-0.05 : 0.171
rugged	0.0001	0.003 (0.05)	-0.096 : 0.102
dist.coast:elevation	0.0001	-0.571 (0.113)	-0.792 : -0.35
cos.aspect:elevation	~0	0.163 (0.051)	0.063 : 0.263
elevation:tci90	~0	-0.209 (0.055)	-0.318 : -0.1
curve90:elevation	~0	0.051 (0.058)	-0.063 : 0.165
dry.prec:tci90	~0	-0.108 (0.06)	-0.226 : 0.01
cos.aspect:coast.dist	~0	0.062 (0.052)	-0.04 : 0.164

[a] Please refer to Table 2.1 for explanation of predictor codes

Important bioclimatic predictors not highly correlated with elevation were dry quarter precipitation and annual temperature range (Table 2.2). Both show a strong latitudinal gradient, with dry season precipitation decreasing and annual temperature range increasing with latitude (Pearson's r = -0.93 and 0.72, respectively).

The analysis for the Nilgiris-Eravikulam mosaics (n = 783) indicated that the best model based on AIC had the following predictors: elevation, annual temperature range, curvature (90m pixel), cosine aspect, distance to coast, and an interaction between cosine aspect and distance to coast.

These predictors also had the highest summed Akaike weights (Table 2.3). Beta coefficients of the top five predictors supported their importance. Compared to the full data set, the importance of annual temperature range, cosine aspect, curvature (90m pixel) and distance to coast increased, while that of local-scale TPI, dry quarter precipitation and its interaction with annual temperature range decreased.

Table 2.3: Importance of topographic and bioclimatic predictors used in GLM analysis of forest-grassland mosaics above 1500m elevation in the Nilgiris & Eravikulam. Columns show summed Akaike weights, standardized beta coefficients averaged across models (unconditional standard errors SE in parentheses) and 95% confidence intervals (CI) based on the unconditional SEs.

Predictor[a]	**Summed Akaike weight**	**Standardized, model-averaged beta (SE)**	**Model averaged 95% CI**
elevation	1	-1.529 (0.14)	-1.804 : -1.254
anntmprng	0.999	0.819 (0.169)	0.489 : 1.15
cos.aspect	0.999	0.42 (0.088)	0.247 : 0.592
curve90	0.996	-0.489 (0.117)	-0.718 : -0.259
coast.dist	0.537	0.248 (0.112)	0.029 : 0.467
cos.aspect:coast.dist	0.377	0.269 (0.091)	0.09 : 0.447
tci90	0.223	-0.189 (0.106)	-0.397 : 0.019
tpi3.10	0.187	-0.214 (0.111)	-0.433 : 0.004
elevation:curve90	0.172	-0.191 (0.094)	-0.375 : -0.006
elevation:tci90	0.094	-0.319 (0.121)	-0.557 : -0.082
dry.prec	0.058	0.308 (0.233)	-0.149 : 0.765
anntmprng:curve90	0.057	-0.152 (0.111)	-0.37 : 0.066
tpi10.67	0.053	-0.14 (0.106)	-0.349 : 0.068
elevation:tpi3.10	0.039	0.227 (0.102)	0.026 : 0.428
cos.aspect:elevation	0.035	0.098 (0.1)	-0.098 : 0.294
annprec	0.025	-0.043 (0.11)	-0.259 : 0.173

Predictor[a]	**Summed Akaike weight**	**Standardized, model-averaged beta (SE)**	**Model averaged 95% CI**
anntmprng:elevation	0.024	-0.054 (0.136)	-0.321 : 0.213
rugged	0.023	0.029 (0.093)	-0.154 : 0.213
coast.dist:elevation	0.014	0.182 (0.122)	-0.057 : 0.422
cos.aspect:tci90	0.010	-0.167 (0.087)	-0.338 : 0.003
cos.aspect:tpi3.10	0.009	0.13 (0.095)	-0.056 : 0.316
dry.pre:elevation	0.001	0.016 (0.134)	-0.248 : 0.28
anntmprng:dry.pre	0.001	0.025 (0.201)	-0.371 : 0.42

[a] Please refer to Table 2.1 for explanation of predictor codes

Interactions between topographic and bioclimatic predictors

The conditional inference CTs indicated complex interactions between elevation, local-scale TPI, dry quarter precipitation and annual temperature range (Fig. 2.3); however the results of the GLM provided only limited support for this (Table 2.2), possibly due to the limited ability of GLMs to model the complex interactions indicated by the CTs. Other than the interaction between annual temperature range and dry quarter precipitation, none of the interaction terms tested on the full dataset was rated as important predictors by the GLMs. However, the 95% confidence intervals for standardised beta coefficients of the interactions between elevation and local-scale TPI, elevation and dry quarter precipitation and elevation and distance to coast did not straddle zero, indicating some support in the models (Table 2.2).

For Nilgiris-Eravikulam mosaics, the interaction between distance to coast and cosine aspect was the most important of the interactions (Table 2.3), however this was not detected by the CT (Fig. 2.4). There was some support for interactions between elevation and curvature (90m pixel) and elevation and TCI (90m pixel). The interaction between elevation and curvature (90m pixel) had a higher summed Akaike weight but a smaller beta co-efficient than the interaction between elevation and TCI (90m pixel) (Table 2.3).

Scale of topographic control on vegetation pattern

The results indicated that topographic pattern within a 300m neighbourhood, was important for vegetation pattern, as measurement of topographic features at this scale (i.e. tpi3.10, curve90 and tci90) was the most relevant for prediction of forest and grassland patches (Fig. 2.2, Table 2.2). Local hills and depressions (tpi3.10) and surface curvature (curve90) seemed to be more influential than prominent peaks and valleys (tpi10.67), though importance of the latter increased in mosaics above 2000m (Fig. 2.2b, Table 2.3).

Discussion

Topography and bioclimate were able to predict the occurrence of grass and forest within forest-grasslands mosaics of the Western Ghats with approximately 70% accuracy. Prediction accuracies were higher for grass compared to forest and for mosaics at higher elevations (1500–2000m). Topography alone was able to predict forest and grassland pattern well, however inclusion of bioclimatic predictors that captured latitudinal gradients in climate improved predictive accuracy.

The misclassification of high elevation forest points may be due to the fact that the predictors measured at the given scales were unable to correctly classify many of the smaller sized (< 2 ha) forest patches that occur in these mosaics. The inclusion of microclimatic data (Dobrowski 2011) could improve classification accuracy for forest patches at higher elevations. Classification accuracy was lower for the lower elevation mosaics between 12° to 13°12’ latitude that lie closer to the coast (Supporting Information S1), indicating that the predictors chosen for this study were unable to characterize vegetation pattern in these mosaics as well.

Overall, the instability found in the CT analysis indicates regional differences in predictor effects and interactions between topography and bioclimate across the range of these mosaics. Hence the same pattern of grassland and forest seems to be generated by different sets of mechanisms across the Western Ghats.

Elevation and bioclimate

Sankaran et al. (2005) demonstrated that mean annual precipitation is the main driver of tree cover in African savannas with low rainfall. In tropical montane forest-grassland mosaics with high mean annual precipitation, elevation is an important predictor of vegetation pattern. Specifically, in the Western Ghats, there seems to be a shift in pattern at about 2000m elevation, above which there is a much lower occurrence of forest. This indicates a climatic effect on tropical evergreen tree growth and survival (Ohsawa 1991). Since bioclimatic predictors related to temperature showed the strongest correlation with elevation, it seems that temperature, rather than precipitation, is the main proximate climatic driver of pattern in high elevation mosaics. The relative importance of elevation and correlated temperature variables increases with elevation, further supporting the view that temperature has an important influence on vegetation pattern in Nilgiris and Eravikulam (Caner et al. 2007).

Temperature is the major limiting factor for tree growth at treelines (Körner 1998). While the mosaics of the Western Ghats are well below the climatically defined treeline in the tropics (Ohsawa 1991, Körner 1998), lower average air and soil temperatures above 2000m may limit most tropical tree species' establishment and survival (Ohsawa 1991, Körner and Paulsen 2004). This is supported by the observation that tree species composition within *shola* patches in the Western Nilgiris shows high turnover between 1900-2000m (please see Chapter 3), with an increasing component of upper montane taxa and frost-resistant species above 2000m (Mohandass and Davidar 2010). Ohsawa (Ohsawa 1991) posits that the thermal limit for lower montane tropical trees occurs at 2,500m in equatorial mountains, with mean annual temperatures of 12°C and 10°C in the coldest month. Mosaics above 2000m have mean annual temperatures of 14.1°C and an average minimum temperature of 7.1°C in the coldest month. Caner et al. (Caner et al. 2007) report that temperatures during the Last Glacial Maximum were about 5°C lower than present day in the Nilgiris, with grassland probably covering most parts of the plateau above 1800m.

The climate signal implied by this altitudinal shift in the occurrence of forest lends support to the role of frost in restricting forest above 2000m (Ranganathan 1938). It is unlikely that the predominance of grassland, noted in historical accounts and palaeoclimatic reconstructions

(Ranganathan 1938, Sukumar et al. 1995, Caner et al. 2007), can be explained solely by increase in the frequency of disturbance (Bor 1938) in these mosaics, when compared to those at lower elevations. Fire frequency in these mosaics over the last 30-40 years should be lower, as they are sparsely populated and have been managed as protected areas where fire suppression is practiced (Srivastava 2001).

Mohandass and Davidar (2010) found evidence to suggest that *sholas* expand into grassland through succession beginning with establishment of frost-resistant woody species in grasslands, and subsequently creating suitable conditions for establishment of lower montane species. An analogous process of forest expansion occurs in subtropical forest-grassland mosaics of Southeastern Brazil, where fire has a major influence on vegetation pattern (Müller et al. 2012).

In mosaics below 2000m, dry season precipitation is an important predictor of forest occurrence. There is some evidence that its influence is mediated by both topographic position and elevation (Fig. 2.3). This could imply a fire-related mechanism in maintaining grasslands at middle and lower elevations, where lower dry season precipitation allows for greater incidence and spread of fire (Bond and Parr 2010). This could prevent forests from establishing in topographic positions that they might otherwise occupy in mosaics with higher dry season rainfall.

Finally, the importance of the interaction between dry quarter precipitation and annual temperature range on the presence of forest implies that forests at mid-elevation (approx. 1000–2000m) areas of the central Western Ghats such as the Nilgiris plateau and the Siruveni hills could be more strongly influenced by these bioclimatic factors than elsewhere (Fig. 2.1).

Topographic effects

As expected, topographic position is an important predictor of vegetation pattern in these mosaics - certainly as a main effect, possibly also in interaction with elevation. Sites with lower topographic position were associated with forest. This could indicate an effect of soil moisture, especially in mid-lower elevation mosaics. Local depressions and valleys are likely to be wetter and therefore less vulnerable to fire (Wood et al. 2011). However, local topographic depressions above 2000m were more likely to contain grass than forest, possibly due to waterlogging and frost (Bader and Ruijten 2008, Dobrowski 2011, Fletcher et al. 2014). At elevations above 2000m, relative topographic position at the landscape scale (300-2010m neighbourhood) and concave surface curvature are more important predictors of forest than local topographic position, corroborating field observations. Larger patches of forest in these mosaics are often confined to sheltered valleys (*pers. obs*.). The greater importance of local curvature in high elevation mosaics could reflect the influence of concave depressions along hill slopes (Ranganathan 1938) that provide adequate soil moisture while allowing for drainage, thus preventing the negative effects of waterlogging or frost on tree growth (Bader and Ruijten 2008, Fletcher et al. 2014).

It is interesting that local topographic position and surface curvature were more important predictors of vegetation pattern than topographic convergence, as previous studies have found topographic convergence to be an important predictor of forest occurrence (Bunyan et al. 2015, Bader and Ruijten 2008).

Aspect, specifically northness, is an important predictor of forest in high elevation mosaics, which has been attributed to differences in radiation exposure (Bader and Ruijten 2008). The histogram of aspect values (cosine transformed) for the sample points indicates an equal representation of both northern and southern aspects in the dataset. Bunyan et al. (2015) find a similar result for these high elevation mosaics. The greater solar radiation received on south facing slopes could increase water stress or desiccation, thus limiting for tree growth (Dobrowski 2011). Drier southern aspects could also be more prone to fire. Wood et al. (Wood et al. 2011) demonstrated that rainforests occurring in a matrix of moorland in Tasmania were restricted to southern aspects and topographic positions very similar to those found in this study, as these places formed fire refugia. Prevailing wind direction may be important as southern and western slopes are affected by strong monsoon winds, while northern and eastern aspects are more sheltered (Caner et al. 2007). The importance of northness and distance to coast in predicting forest at high elevations provides some support for this (Table 2.3). The role of aspect in these mosaics should be investigated further using field experiments and measurement of microclimatic conditions.

Fletcher et al. (2014) show that a transition from one vegetation state to another can be generated by one set of factors and regulated by another. The initial climatic constraint on forests in high-elevation mosaics could be maintained under present climate by cumulative effects of low temperature, frost, fires and wind. Topographic heterogeneity can modulate the intensity and spread of each, possibly helping to create sharp boundaries (Geldenhuys 1994, Martin et al. 2007, Wood et al. 2011). Vegetation pattern in these mosaics could be maintained by a group of interacting factors acting in a spatially heterogeneous manner- determined by topography- and in feedback with vegetation type (Martin et al. 2007), rather than by a single limiting mechanism - be it frost (Ranganathan 1938), fire, grazing (Bor 1938), wind (Caner et al. 2007) or soil (Jose et al. 1994). This analysis provides strong support for topographic control on processes maintaining vegetation pattern in these systems.

The need for data

A major limitation of this study is that it does not consider resource and disturbance gradients such as soil characteristics, fire and grazing, that have been found to be critical in shaping vegetation pattern in other forest-grassland systems (Behling and Pillar 2007, Wood et al. 2011, Müller et al. 2012). Much of the misclassification of vegetation pattern, particularly at lower elevations, could be due to the effects of these factors. Lower elevation mosaics are more exposed to anthropogenic disturbance. At present the required data are not available at relevant scales across the study area.

There is an urgent need for accurate, high resolution spatio-temporal datasets on disturbance, particularly fire, across the study area. We found that global satellite-derived burned area products largely underestimated fire frequency in several mosaics, precluding their use in this analysis.

Implications for management and conservation

The results indicate that ongoing *shola* restoration efforts by State Forest Departments in mosaics above 2000m, should be focused on north-western to north-eastern aspects. Given past conversion of large areas of grassland into exotic tree plantations, recent global trends of forest expansion into grasslands (Bond and Parr 2010, Silva and Anand 2011) and palaeoclimatic trends of forest expansion during warming climates (Sukumar et al. 1995), it is important that restoration of *shola* does not take place at the expense of existing grasslands.

As mosaics differ widely in the extent and manner in which topography and bioclimate influence vegetation pattern (Supporting Information S1), management plans should be tailored to the elevation and geographic position of individual mosaics, with different management guidelines for the more strongly climatically determined mosaics (above 2000m). A better understanding of the role of fire in the maintenance of grasslands is essential (Behling and Pillar 2007, Bond and Parr 2010).

The importance of local topography indicates that microclimate (Dobrowski 2011) regulates vegetation pattern in these mosaics. Projections of vegetation range shifts for these habitats should therefore account for variation in topography and its interaction with changing regional climate and disturbance regimes (Dobrowski 2011, Lippok et al. 2013). The results support the potential role of topographic heterogeneity in creating climatic microrefugia for vegetation within these mosaics that may allow species and plant community types to persist for longer periods of time. Hence, it is important to continue to protect forest-grassland mosaics in the Western Ghats and to increase coordinated research, monitoring and conservation efforts in these habitats.

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Chapter 3

Tropical Montane Cloud Forest (*Shola*) Tree Species Diversity and Distribution at the Regional and Metacommunity Scales

Introduction

Tropical montane cloud forests (TMCF) are ecologically unique and hydrologically important (Bruijnzeel and Proctor 1995) habitats that are restricted to approximately 0.14% of earth's land surface (Scatena et al. 2010). Found between 30^{o}N and 30^{o}S latitudes in Africa, Asia, Northern Australia, Oceania and the Americas, they mostly occur between 1200-2800m in elevation with some records as low as 400m and others as high as 3500m, (Scatena et al. 2010, Jarvis and Mulligan 2011). Most TMCF are found north of the equator (Jarvis and Mulligan 2011).The largest existing area of TMCF is found in Asia (43.2%), mainly in Indonesia and Papua New Guinea, followed by the Americas (40.8%). In Asia TMCF constitutes only 5.9% of all tropical montane forests (Scatena et al. 2010). They are mostly found at higher altitudes, closer to the coast and in areas with higher rainfall and lower seasonality of precipitation than other tropical montane forest types (Jarvis and Mulligan 2011).

Compared to lowland evergreen forests, TMCF largely lack an emergent tree layer in the canopy. There are also fewer species with buttressed trunks, compound leaves or cauliflory (Scatena et al. 2010). The density of woody climbers is lower, while that of non-vascular epiphytes such as mosses and liverworts is much higher (Ashton 2003, Scatena et al. 2010). The stand characteristics of TMCF vary with temperature and humidity along the elevation gradient, with decreasing canopy height and leaf size, increasing leaf thickness, simpler stand structure and increasing density of non-vascular epiphytes (Frahm and Gradstein 1991, Ashton 2003, Scatena et al. 2010). TMCF is therefore further divided into lower montane, upper montane based on these characteristics (Scatena et al. 2010).

The stunted evergreen forests, also called *sholas* (Schimper and Fisher 1902), found at higher elevations in the Western Ghats (WG) have been classified as TMCF (Bunyan et al. 2012) and alternatively as wet montane temperate forests (Champion and Seth 1968) or southern wet temperate forests (Nair et al. 2001). These forest formations are characterized by stunted trees (rarely above 15m tall), with relatively small (microphyllous), thick leaves, dense crowns and trunks and branches covered with bryophytes and epiphytes (Meher-Homji 1967, Nair and Khanduri 2001). The stand structure of these forests closely fit the characteristics of lower and upper TMCF described above. *Sholas* often occur in a matrix of grassland and occupy valley slopes and concave depressions along hill sides (Ranganathan 1938, Nair and Khanduri 2001). The ecologically apt term *shola,* derived from the Tamil word 'Cholai' or 'Chola' in Malayalam, refers to a shaded, wet grove and directly associates this vegetation type with a water source (Nair and Khanduri 2001).

Vegetation zonation along the elevation gradient and the transition from Lower-Upper tropical montane forests in South and East Asia

The altitudinal boundaries of TMCF are determined by the interaction of landform with climate and are largely found to coincide with the upper and lower boundaries of cloud banks, (Grubb and Whitmore 1966, Bruijnzeel and Proctor 1995, Ashton 2003, Jarvis and Mulligan 2011). Cloud condensation and the temperature lapse rate vary with the size of a mountain range and its distance from the coast (Grubb and Whitmore 1966, Jarvis and Mulligan 2011). More humid air condenses at lower elevations while drier air masses require cooler temperatures and higher elevations to form clouds. Temperature lapse rates on smaller mountains may be steeper owing to the "Massenerhebung" effect (Jarvis and Mulligan 2011) which allows plants to extend their ranges upslope on larger mountains (Scatena et al. 2010, Jarvis and Mulligan 2011). Conversely, this also creates a lower cloud condensation level on smaller mountains than on larger ones, leading to a decrease in the lower elevation boundary for TMCF on smaller, isolated mountains, especially those closer to the coast (Grubb and Whitmore 1966).

The transition from lowland tropical forest to lower montane forest is found to occur consistently between 900-1300m elevation across south and east Asian mountains, while the transition from lower to upper montane occurs between 1400-2300m on equatorial mountains, depending on topography, site conditions and the definition of upper-montane formations adopted (Ohsawa 1991, Ashton 2003). According to Ohsawa (1991) subalpine vegetation occurs above 2800m on equatorial mountains.

In his comparative studies of zonation of south and east Asian mountain flora, Ohsawa (1990, 1991) suggests that such zonation, "*results from replacement of related taxa with altitude. This pattern is in tandem with a tendency of impoverishment of floristic diversity through elimination of accessory taxa in the forests at increasingly higher altitudes*" (Ohsawa 1991, p. 5). This pattern is unlike that found in temperate mountains where each zone is "*composed of different floristic elements having contrasting life-forms*" and results from a series of "impoverishment processes" in both structure and diversity from low altitudes to higher ones. Ashton (2003), in his discussion of the boundary between lower and upper montane forests, further elucidates this observation by stating that upper montane formations are marked by, "*the presence of taxa, generally recognised as species or subspecies, which form sister pairs with lowland taxa, in large genera including Syzygium (Myrtaceae), Memecylon (Melastomaceae), Rhododendron and Vaccinium (Ericaceae), Elaeocarpus (Elaeocarpaceae) and Ilex (Aquifoliaceae). Compared with lowland sister taxa they almost without exception share smaller concave leaves with revolute margins and obtuse or retuse apices, and shorter internodes including greatly shortened rachises*." (Ashton 2003, p. 98).

The characteristics of the transition between lower and upper montane forests on Asian mountains therefore include a reduction in species richness and stand structure (Ohsawa 1991), replacement of species by closely related congeners (Ohsawa 1991) with certain functional traits (Ashton 2003) and a change in the physiognomy of trees (Ohsawa 1991, Ashton 2003), as well as the increased density of epiphytes and bryophytes on trees (Frahm and Gradstein 1991, Ashton 2003). On tropical mountains below 20°N, lower montane forests are dominated by notophyllous, taller trees of Lauro-fagaceous affinity, whereas microphyllous, small trees of the genera *Symplocos, Rapanea, Eurya* and *Ilex* that are common in East Asian subtropical and lowland warm temperate forests, are found at the tree line (3800m) and form an important part of upper montane forests (Ohsawa 1991, 1995).

Tree and Shrub species of tropical montane cloud forests (shola) in Central and Southern Western Ghats: Biogeography and endemism

The floristic composition of *shola* forests in the Central and Southern WG is relatively well studied. A compilation of species lists from 17 sources, including regional floras and field studies, reveals that there are at least 278 species of trees and shrubs that occur in these forests (Appendix 3.1). The biogeographic distributions of these species (Fig. 3.1) ranges from Pantropical (1 species) to those that are very narrowly restricted to only the southern WG (16 species). Eighty species (29%) are endemic to the central and southern WG alone, while approximately 65% of the species have ranges that are limited to peninsular India and Sri Lanka. A total of 48% (134 species) are endemic to the WG – Sri Lanka biodiversity hotspot (Myers et al. 2000). The assessment presented here indicates that an even larger component of the tree and shrub flora of *sholas* in the central and southern WG is endemic to peninsular India and Sri Lanka than previously thought by authors working in parts of the central WG (Suresh and Sukumar 1999). Rates of endemism reported in the literature on *sholas* vary widely according to study site and area sampled (Bunyan et al. 2012). The assessment presented here appears to be the first such regional assessment based on species lists compiled from several studies.

The majority of the tree and shrub genera in *sholas* has an Indo-Malayan affinity (Meher-Homji 1967, Suresh and Sukumar 1999). Lauraceae is the most species rich family (41 species), followed by Rubiaceae (24 species) and Acanthaceae (18 species). Dominant genera include *Litsea*, *Cinnamomum*, *Strobilanthes* and *Symplocos*. There are also distinct Himalayan elements, as represented by the genera *Berberis, Rhododendron, Celtis*, *Lonicera, Mahonia, Hypericum, Sarcococca* and *Viburnum* (Meher-Homji 1967). These species are found mostly along the *shola*-grassland edge or in open areas (Meher-Homji 1967, Suresh and Sukumar 1999). Further, a subtropical-warm temperate evergreen element is represented by genera such as *Eurya, Rapanea, Daphiphyllum*, *Ilex, Symplocos*, *Ternstroemia*, *Vaccinium, Rubus. Ardisia* and *Hedyotis* (Ohsawa 1991, Suresh and Sukumar 1999, Ashton 2003). The highest levels of endemism are in the genera *Strobilanthes*, *Cinnamomum*, *Actinodaphne*, *Litsea*, *Euonymus*, *Lasianthus* and *Hedyotis*.

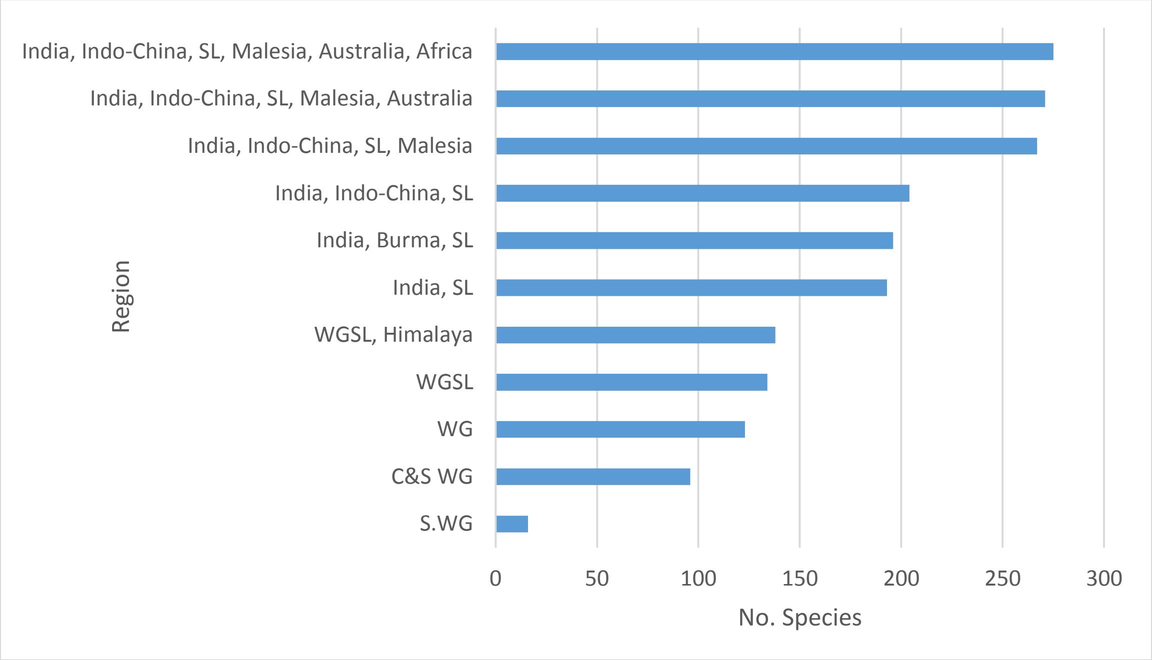

Figure 3.1: Bar chart showing the biogeographic affinities of the tree and shrub species recorded from sholas in the central and southern Western Ghats, from larger to smaller geographic areas. (WG = Western Ghats, SL= Sri Lanka).

The metacommunity framework and its relevance to sholas of Upper Nilgiri Plateau

The recent extension of metapopulation theory to community ecology has provided useful heuristic tools to assess community level patterns at multiple scales (Leibold et al. 2004). Liebold et al. (2004) define a metacommunity as a "*set of local communities that are linked by dispersal of multiple potentially interacting species*". The study of metacommunities attempts to draw inferences about processes structuring communities at different spatial scales by studying variation in the pattern of species distributions from local to regional scales and the feedback between local and regional scale variation (Leibold et al. 2004). Hence two broad frameworks have been adopted for studying metacommunities: a process-based mechanistic framework (Leibold et al. 2004) and a pattern-based one (Leibold and Mikkelson 2002, Presley et al. 2010). Here I apply the pattern-based framework, which compares observed species occurrence patterns to theoretical, idealized distribution patterns, especially in respect to environmental gradients, and tests this against null models (Presley et al. 2010).

Six theoretical patterns of species distributions identified include (Leibold and Mikkelson 2002, Presley et al. 2010):

a) Clementsian (Clements 1916), where communities are well-defined cohesive units in which co-occurring species occupy similar ranges along an environmental gradient and range boundaries coincide.
b) Gleasonian (Gleason 1926), where each species responds to environment differently. Communities lack distinct boundaries as cohesive units of co-occurring species and co-existence is the result of overlapping species ranges along the gradient.
c) Evenly-spaced (Tilman 1982), where strong interspecific competition gives rise to trade-offs that allow species co-existence in evenly-spaced distributions along a gradient.
d) Checkerboard pattern (Diamond 1975), where strong pairwise inter-specific competition results in mutually exclusive species' ranges along a gradient. Such mutually exclusive species pairs occur at random with respect to each other.
e) Nested subsets (Patterson and Atmar 1986), where variation in species traits related to dispersal or competitive ability leads to patterns of species loss along a gradient and species-poor communities are constituted by a subset of species from more species-rich communities.
f) Random patterns, where species co-occurrences are independent of one another and any gradients and cannot be distinguished from random simulations of species presences in the community.

Three characteristics of species distribution patterns assessed are: coherence, turnover or nestedness and range boundary clumping (Leibold and Mikkelson 2002). The concept of coherence arises from the assumption that species are continuously and normally distributed through their range and with respect to an environmental gradient. At the metacommunity level, coherence emerges when most or all of the species in a community respond to the same environmental gradient (Presley et al. 2010). Only metacommunities exhibiting coherence can be meaningfully assessed for turnover and boundary clumping

(Presley et al. 2010). Most metacommunities do exhibit coherence (Leibold and Mikkelson 2002). Turnover is the replacement of species along an environmental gradient. High or positive values of turnover indicate the presence of Clementsian, Gleasonian or evenly-spaced structures. Low or negative turnover may indicate nested patterns where sites with low richness are composed of a subset of species found in richer sites (Presley et al. 2010). Finally, the aggregation of range boundaries is used to distinguish between Clementsian (highly aggregated boundaries), evenly-spaced (hyperdispersed boundaries) or Gleasonian (randomly distributed boundaries) structures (Leibold and Mikkelson 2002, Presley et al. 2010).

The metacommunity framework applies well to the *shola* tree community of the Upper Nilgiris, as multiple tree species co-occur in discrete, stable, island-like patches of varying size and proximity that are set in a distinct habitat matrix of grassland, tea or exotic tree plantations. Most species are bird dispersed (Ganesh and Davidar 2001) and therefore likely to have dispersal distances that encompass one or more *shola* patches. Finally, there are important environmental gradients present in the study area such as elevation and rainfall.

Objectives

The objectives of the analysis in this chapter were to answer the following questions:

i) What is the tree and shrub species diversity, distribution and species composition of the *sholas* in the Upper Nilgiris based on both presence-absence and abundance data?

ii) What is the metacommunity structure of *shola* vegetation and how does it relate to large-scale environmental gradients?

iii) What is the nature of community change with elevation and which are the dominant species associations in the study area?

iv) Can a transitional ecotone between lower and upper montane *shola* forest communities be defined for the the study area based on species turnover and changes in floristic composition?

Methods

Study Area

The study area is located between 11.17°N, 76.77°E and 11.50°N, 76.43°E on the western Upper Nilgiri Plateau (1800-2630m elevation, average elevation 1980m). Most of the survey was conducted on the western and southern parts of the plateau that contain the largest stretches of intact *shola* grassland mosaics (Fig. 3.2). This region is rich in endemic plants. Blasco (1971) has recorded 223 plant species known only from the *sholas* and grasslands of the higher altitude ranges of the Western Ghats. The area is known for its extraordinary vertical and horizontal physiographic differentiation and has three main rainfall regimes (von Lengerke 1977, Caner et al. 2007). The western side of the plateau receives the highest rainfall (5000-2500mm) mainly from the southwest monsoon, the southern and eastern portions of the plateau receive 2000-1500mm annually from both the southwest and northeast monsoon and the central Nilgiris receive 1200-900mm on average (Fig. 3.2). Caner et al. (2007) propose that this spatial variation in rainfall across the plateau has possibly existed since the Last Glacial Maximum (LGM; 20,000 years BP) as it is largely controlled by orography. The dry season lasts for 3-4 months mainly between December and March. Temperature ranges from a mean maximum of 24°C in April to a mean minimum of 5°C in December. Frost occurs between November and March and mainly in the valleys rather than the higher hill slopes (von Lengerke 1977, Caner et al. 2007). Ranganathan (1938) notes that *shola* habitat on the Nilgiri Plateau extends from 1500-2590m. The elevation range covered in this study extends from 1800-2400m.

The major land cover types in this area are: agriculture, tea plantation, forest plantation (eucalyptus and black wattle *Acacia mearnsii*) and *shola* grassland (Prabhakar 1994). The landscape contexts within which natural *shola* forest is located are very varied.

Sampling Protocol

A stratified random sampling design was used to collect *shola* vegetation data from 20x20 m plots, based on slope, aspect, and landscape context. A minimum of four plots were placed within each combination of landscape context and topographic class, with the exact location of plots determined by accessibility and steepness of terrain. In large *shola* patches (> 60 ha), three transects of plots were placed at a minimum of 250 m apart, with a distance of at least 50m between each plot along the transect. All individuals > 0.5m in height were censused within the plots, with species name, diameter at breast height x,y location within the plot and height recorded. For individuals between 0.5-1.3m height, only height was recorded. In addition the distance to the nearest edge of the *shola* fragment was noted as well as the GPS location of the plot corner, elevation, slope and aspect. Two parallel seedling transects of four 1x1m plots were laid, perpendicular to the plot edge, within each plot to census tree seedlings. A total area of 3.48 ha (87 plots) was censused.

Data Analysis

Rarefaction, richness and diversity indices

Species richness was estimated and diversity indices such as Shannon's, Simpson's and Fisher's alpha (Magurran 2004) were calculated. A sample-based rarefaction curve with the x-axis standardized to number of individuals (Gotelli and Colwell 2001) was plotted using the Mao-Tau estimator as implemented in the software EstimateS (Colwell et al. 2012, Colwell 2013). A number of complementary beta diversity indices were calculated to measure variation in community structure across the sample plots based on the species presence-absence matrix (Anderson et al. 2011). These included: Whittaker's beta, Sorenson's Index, Simpson's Index, parameter z in Arrhenius species-area model (Koleff et al. 2003) and Raup-Crick Dissimilarity index. The latter represents the probability that two sampling units have dissimilar species composition. It is computed using a null modelling approach and accounts for differences in alpha diversity between samples (Anderson et al. 2011).

Community compositional analysis: relative abundance, IVI, clustering analysis, spatial distribution of clusters and dominant species' associations

A ranked abundance curve (Whittaker 1965) was plotted to visualize the abundance distribution of species in the study area (Magurran 2004). The observed distribution was tested against various theoretical models of species abundance (i.e. brokenstick or null model, pre-emption, log-normal, Zipf and Zipf-Mandelbrot models of species abundance), using maximum likelihood estimation with a poisson error distribution. The model that best fit the observed rank-abundance distribution was selected using Akaike's Information Criterion (AIC) values (Wilson 1991).

Basal area, Relative density, Relative frequency, Relative Dominance and Importance Value Index (IVI) were calculated for each of the species across all the plots (Ganesh et al. 1996). The following formulae were used:

- Basal area (m^2) = 0.00007854 x dbh^2 (where r is radius of the plant girth at breast height) Basal area represents dominance of a plant species.
- Density = total number of plants of any species/ number of plots
- Frequency = (number of plots with the presence of a species/number of plots) x 100
- Relative dominance = (dominance of a plant species/ total dominance of all plant species) x 100
- Relative frequency = (frequency of a plant species/ total frequency of all plant species) x 100
- Relative density = (density of a plant species/ total density of all plant species) x 100
- Importance Value Index (IVI) = Relative dominance+ Relative frequency+ Relative density

Clustering analysis was conducted to examine groupings of plots based on species composition. Hellinger-transformed (square root of proportional abundance value of each species in a plot) tree species' abundance data (Legendre and Gallagher 2001) was used in an agglomerative clustering framework (Legendre and Legendre 2012). This method hierarchically groups plots based on the similarity between plots in terms of species' abundances. The performance of four clustering algorithms (Legendre and Legendre 2012) was compared using the transformed abundance data: single linkage clustering (based on nearest neighbor distance), complete linkage clustering (maximizes differences among clusters and finds discontinuities in the dataset), Unweighted Pair-Group Method using Arithmetic Averages (UPGMA) and Ward’s Minimum Variance Clustering (based on least squares). The clustering algorithm that performed the best was then chosen to develop a dendrogram of sites. A spatial plot of the final dendrogram was then produced to assess the grouping of sites spatially, based on their species abundances.

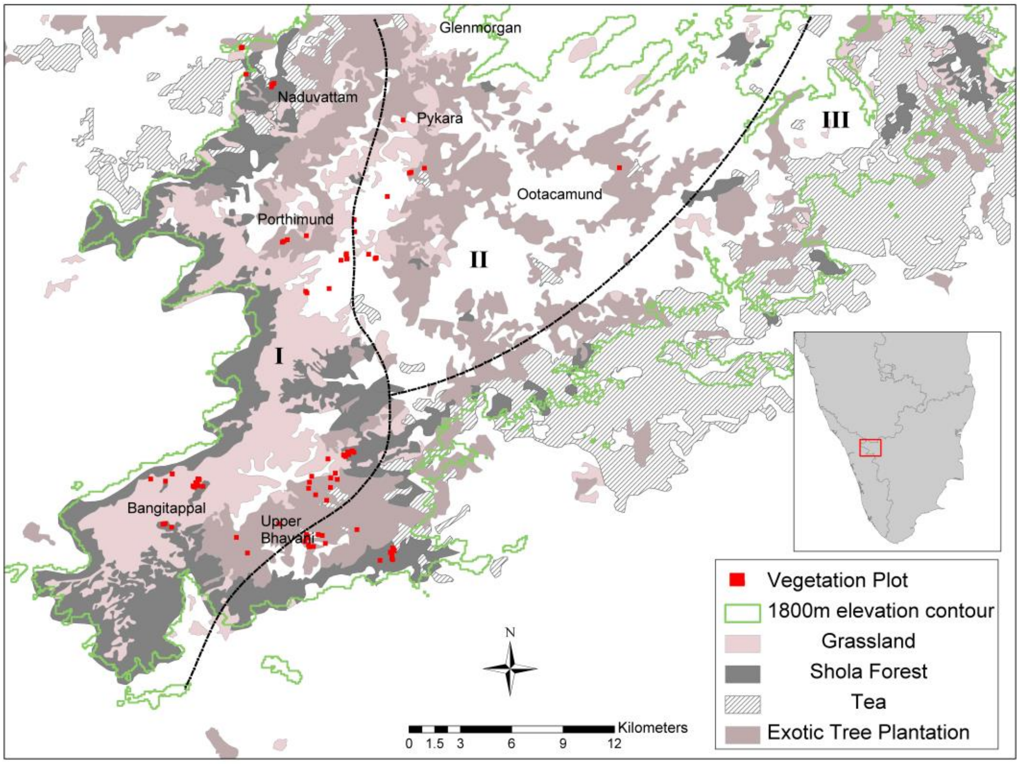

Figure 3.2: Map of the study area in Upper Nilgiris showing locations of surveyed and sampled sholas, major rainfall regimes (Caner et al. 2007) and landcover types (Ramesh et al. 2002)

Kendall’s W coefficient of concordance (Legendre 2005) was used with a parametric *F*-test to identify dominant species’ assemblages using a k-means partitioning (Legendre and Legendre 2012) of the Hellinger-transformed tree abundance data. The number of partitions was determined using the results of the hierarchical clustering and field observations.

The above analysis was conducted in Microsoft Excel and R software (R-Development-Core-Team 2013) using the packages “vegan” (Oksanen 2013) and “cluster”.

Analysis of shola metacommunity patterns: coherence, turnover, boundary clumping

In order to assess properties of the *shola* metacommunity, the “Elements of Metacommunity Structure” (Leibold and Mikkelson 2002, Presley et al. 2010, Dallas 2014) or EMS framework was used. Three metrics (coherence, turnover, and boundary clumping) were calculated from the species presence – absence matrix, with sites as rows and species occurrences as columns (Leibold and Mikkelson 2002, Dallas 2014). The matrix was ordinated (to identify the major axis of variation) using reciprocal averaging (Gauch 1982), so that species with similar ranges and sites with similar species compositions were placed together. The statistical significance of these metrics was tested against randomized null matrices in which row and column totals were held constant (“fixed-fixed null” model of Ulrich and Gotelli 2013) using a z test.

Relating metacommunity turnover to the elevation gradient and assessing species compositional changes with elevation

The ordination scores from the EMS analysis were related to elevation and precipitation variables using a Spearman’s rank correlation test to assess whether these factors form structuring gradients (Presley and Willig 2010, Dallas 2014). In addition, Mantel’s tests (Legendre and Fortin 1989) were performed to assess whether Bray-Curtis distance among plots was correlated to difference in elevation and alternately geographic space. Partial mantel’s tests (Legendre and Legendre 2012) were then used to control for the effect of spatial distance and *shola* fragment area on the relationship between species composition and elevation.

Finally, the nature of floristic compositional change across the elevation gradient was examined at the Family level, using the total basal area divided by the area sampled within 3 elevation zones, and at the species level using the presence-absence matrix with sites (rows) ordered by increasing elevation and species (columns) ordered by range extent at lower elevations. The elevation zone with highest level of turnover was verified by comparing the average values of three pair-wise dissimilarity indices (Bray-Curtis, Jaccard and Raup-Crick) for pairs of plots falling in different elevation zones.

Results

Richness, diversity and endemism in the Tree and Shrub Community of the Western Upper Nilgiris

A total of 95 tree and shrub species are recorded from the *shola* forests in the study area (combined results from this study and those by Suresh and Sukumar 1999 and Mohandass and Davidar 2009). These belong to 34 families and 61 genera (Appendix 3.2). Approximately 53% of the species are endemic to the Western Ghats and Sri Lanka. The dominant families in terms of species number and basal area are: Lauraceae, Rubiaceae, Myrtaceae, followed by Symplocaceae, Acanthaceae, Celastraceae and Sapotaceae (Fig. 3.3). These are also among the families with the highest levels of endemism. Magnoliaceae and Ericaceae are interesting as they are represented by one and two species respectively which are entirely endemic to just the central and southern WG (Fig. 3.3). Elaeocarpaceae is also represented by endemic species. *Cinnamomum* was the most species-rich genus, followed by *Syzygium* then *Litsea* and *Symplocos*. The full list is presented in Appendix 3.2 and has been compiled from the results of the present survey as well as a recent vegetation study conducted by Mohandass & Davidar (2009) in the Upper Bhavani area.

The vegetation plots yielded a count of 25,008 individuals which were identified to yield 81 tree and shrub species (Fig. 3.4). Owing to the difficulties in identification to the species level within certain shrub genera (i.e. *Psychotria, Strobilanthes* and *Lasianthus*), these were clubbed together at the genus level during analysis of the plot data, overall richness is therefore underestimated in this study. However, the rarefaction curve for all samples pooled does reach an asymptote (Fig. 3.4), indicating that the sample size sufficiently captures the tree species' richness of the study area.

Based on the vegetation plots, the species diversity estimate for the study area according to various common diversity indices is: Fisher's Alpha = 10.4, Shannon-Weiner Index (H′) = 3.46, Simpson's (Inverse) Diversity Index = 21.6.

Beta diversity values measured using presence-absence data indicate that there is species turnover in the study area, possibly due to the effect of spatial or environmental gradients (Table 3.1). The high value for parameter *z* in Arrhenius species-area model (represents the steepness of the species area curve), in particular indicates the presence of a structuring gradient as the value for *z* in island systems is approximately 0.3 (Oksanen 2013).

Table 3.1: The value of beta-diversity indices calculated from vegetation plot data

Index	**Estimate**	**Reference**
Whittaker's Beta (β_w)	3.05	(Whittaker 1960)
Pairwise Sørenson's dissimilarity	0.52 (mean)	Sørensen (1948), Koleff et al. (2003)
Pairwise Arrhenius species-area model (parameter *z*)	0.59 (mean)	Koleff et al. (2003)
Pairwise Simpson's Index	0.43 (mean)	Simpson (1943)
Pairwise Raup-Crick dissimilarity	0.39 (mean)	Raup-Crick (1979)

Patterns of tree and shrub dominance and distribution in the shola community

The average number of indviduals ≥ 1cm dbh per plot, was 190.5 ± 95.13_{SD}, (minimum 37, maximum 573). This converts to a mean density of 4762.5 individuals/ha. The average stand basal area was 68.78 m^2/ha ±19.4_{SD}. There is wide variation in the stem density and basal area across plots in the Upper Nilgiris *sholas*. Plots located in larger *shola* fragments were found to have a greater number of species per unit area ($R^2 = 0.26$, $P < 0.001$).

While several species had intermediate abundances in the study area (Figs 3.5 and 3.6), many were locally distributed and rare and some were widespread but not very abundant (Figs 3.5 and 3.6). The rank-abundance curve for the data was best fit by a log-normal distribution (Fig. 3.5). The most abundant tree species were *Symplocos foliosa* Wight and *Litsea wightiana* (Nees) Hook. f., while some of the rarer species in the study plots were: *Syzygium densiflorum* Wall. ex Wight & Arn., *Elaeocarpus recurvatus* Corner, *Isonandra montana* (Thwaites) Gamble, *Schefflera capitata* (Wight & Arn.) Harms, *Olea paniculata* R.Br., *Prunus ceylanica* (Wight) Miq., *Beilschmiedia wightii* Benth. & Hook. and

Actinodaphne sp. Species such as *Syzygium grande* (Wight) Walp., *Syzygium calophyllifolium* (Wight) Walp., *Litsea oleoides* Hook.f., *Cryptocarya lawsonii* Gamble and *Michelia nilagirica* Zenker**,** are relatively widespread and represented by very large mature trees with high basal area and therefore high IVI (Table 3.2, Fig. 3.6). There is wide variation in the relative abundances and IVI of endemic species. The most dominant species are all endemic to the WG and Sri Lanka. While some endemics like *Mahonia leschenaultii* (Wall. ex Wight & Arn.) Takeda, *Elaeocarpus recurvatus* and *Gordonia obtusa* Wall. ex Wight have relatively lower abundances and importance values, there are several endemics that show greater abundances and IVIs compared to more cosmopolitan species such as *Ilex denticulata* Wall. ex Wight, *Eurya nitida* Korth. and *Ternstroemia gymnanthera* (Wight & Arn.) Sprague.

Table 3.2: Species Importance Value, Relative Frequency and Relative Density calculated from vegetation plot data in Upper Nilgiris

Genus	**Species**	**Abundance**	**Prop. plots present**	**Rel. Dens**	**Rel. Freq.**	**Rel. Dom.**	**IVI**
Psychotria	*sp.*	2186	0.79	14.06	3.82	1.84	19.72
Symplocos	*foliosa*	1551	0.90	9.97	4.32	5.39	19.68
Syzygium	*grande*	495	0.66	3.18	3.16	9.47	15.81
Lasianthus	*sp.*	1376	0.86	8.85	4.15	2.71	15.71
Litsea	*wightiana*	1203	0.90	7.74	4.32	2.90	14.95
Syzygium	*calophyllifolium*	237	0.52	1.52	2.49	9.23	13.24
Cinnamomum	*sp.*	610	0.82	3.92	3.93	3.68	11.54
Cryptocarya	*lawsonii*	408	0.44	2.62	2.10	6.74	11.47
Litsea	*oleiodes*	255	0.63	1.64	3.05	5.23	9.92
Meliosma	*simplicifolia*	337	0.85	2.17	4.10	3.61	9.88
Neolitsea	*cassia*	606	0.59	3.90	2.82	2.40	9.12
Michelia	*nilagirica*	64	0.44	0.41	2.10	5.55	8.07
Saprosma	*ceylanicum*	464	0.56	2.98	2.71	1.76	7.45
Cinnamomum	*macrocarpum*	317	0.49	2.04	2.38	2.92	7.34
Rapanea	*wightiana*	273	0.75	1.76	3.60	1.67	7.02
Ilex	*denticulata*	65	0.43	0.42	2.05	4.43	6.90
Daphniphyllum	*neilgherrense*	267	0.68	1.72	3.27	1.32	6.30
Microtropis	*ramiflora*	226	0.66	1.45	3.16	1.62	6.23
Mahonia	*leschenaultii*	373	0.60	2.40	2.88	0.71	5.99
Casearia	*thwaitesii*	180	0.62	1.16	2.99	1.76	5.90
Cinnamomum	*wightii*	203	0.48	1.31	2.33	1.49	5.12
Litsea	*floribunda*	328	0.49	2.11	2.38	0.48	4.97
Nothapodytes	*nimmoniana*	299	0.41	1.92	1.99	0.49	4.41
Syzygium	*densiflorum*	96	0.40	0.62	1.94	1.85	4.40
Turpinia	*cochinchinensis*	179	0.31	1.15	1.50	1.31	3.96

Genus	Species	Abundance	Prop. plots present	Rel. Dens	Rel. Freq.	Rel. Dom.	IVI
Symplocos	*macrophylla*	197	0.47	1.27	2.27	0.30	3.84
Isonandra	*perrottetiana*	118	0.16	0.76	0.78	2.14	3.67
Litsea	*stocksii*	405	0.08	2.60	0.39	0.64	3.63
Symplocos	*obtusa*	275	0.30	1.77	1.44	0.36	3.57
Vaccinium	*leschenaultii*	80	0.34	0.51	1.66	1.13	3.31
Cestrum	*aurantiacum*	271	0.20	1.74	0.94	0.36	3.05
Ilex	*wightiana*	24	0.16	0.15	0.78	1.96	2.89
Eurya	*nitida*	118	0.33	0.76	1.61	0.37	2.73
Elaeocarpus	*recurvatus*	40	0.22	0.26	1.05	1.40	2.71
Microtropis	*microcarpa*	78	0.25	0.50	1.22	0.31	2.02
Ternstroemia	*gymnanthera*	23	0.16	0.15	0.78	1.09	2.01
Tarenna	*asiatica*	109	0.14	0.70	0.66	0.24	1.61
Neolitsea	*scrobiculata*	118	0.13	0.76	0.61	0.18	1.55
Excoecaria	*oppositifolia*	182	0.03	1.17	0.17	0.10	1.43
Glochidion	*neilgherrense*	23	0.17	0.15	0.83	0.44	1.41
Cinnamomum	*sulphuratum*	33	0.11	0.21	0.55	0.61	1.38
Syzygium	*lanceolatum*	52	0.06	0.33	0.28	0.67	1.28
Olea	*paniculata*	32	0.11	0.21	0.55	0.50	1.26
Rhodomyrtus	*tomentosa*	43	0.16	0.28	0.78	0.17	1.23
Photinia	*intergrifolia*	12	0.10	0.08	0.50	0.62	1.19
Actinodaphne	*bourdillonii*	81	0.07	0.52	0.33	0.32	1.17
Schefflera	*sp.*	13	0.09	0.08	0.44	0.64	1.16
Cryptocarya	*neilgherrensis*	108	0.07	0.69	0.33	0.12	1.15
Euonymus	*crenulatus*	20	0.17	0.13	0.83	0.17	1.13
Sarcococca	*saligna*	84	0.09	0.54	0.44	0.09	1.08
Rhododendron	*arboreum*	9	0.05	0.06	0.22	0.77	1.05
Gordonia	*obtusa*	7	0.02	0.05	0.11	0.87	1.03
Prunus	*ceylanica*	23	0.15	0.15	0.72	0.12	0.98
Hedyotis	*articularis*	33	0.15	0.21	0.72	0.03	0.96
Isonandra	*montana*	10	0.07	0.06	0.33	0.51	0.90
Maesa	*Indica*	28	0.08	0.18	0.39	0.33	0.90
Celtis	*tetrandra*	26	0.08	0.17	0.39	0.23	0.79
Memecylon	*randeriana*	33	0.08	0.21	0.39	0.04	0.64
Acronychia	*pedunculata*	57	0.05	0.37	0.22	0.02	0.61
Symplocos	*cochinchinensis*	29	0.05	0.19	0.22	0.13	0.54
Canthium	*dicoccum*	35	0.02	0.23	0.11	0.19	0.53
Isonandra	*lanceolata*	7	0.03	0.05	0.17	0.31	0.52
Phoebe	*paniculata*	10	0.07	0.06	0.33	0.05	0.44
Gomphandra	*coriacea*	7	0.06	0.05	0.28	0.11	0.44
Actinodaphne	*sp.*	9	0.02	0.06	0.11	0.22	0.39
Unknown	*sp6*	9	0.06	0.06	0.28	0.00	0.34
Casearia	*sp.*	24	0.02	0.15	0.11	0.07	0.34
Scolopia	*crenata*	18	0.02	0.12	0.11	0.11	0.33
Microtropis	*sp*	7	0.06	0.05	0.28	0.00	0.32
Unknown	*sp9*	8	0.02	0.05	0.11	0.10	0.26
Sideroxylon	*tomentosa*	4	0.01	0.03	0.06	0.18	0.26
Trichilia	*connaroides*	3	0.03	0.02	0.17	0.05	0.24

Genus	**Species**	**Abundance**	**Prop. plots present**	**Rel. Dens**	**Rel. Freq.**	**Rel. Dom.**	**IVI**
Beilschmeida	*wightii*	2	0.03	0.01	0.17	0.00	0.18
Melicope	*lunu-ankenda*	7	0.02	0.05	0.11	0.00	0.16
Meliosma	*pinnata*	1	0.01	0.01	0.06	0.09	0.15
Unknown	*sp7*	6	0.01	0.04	0.06	0.00	0.10
Syzygium	*cumini*	2	0.01	0.01	0.06	0.01	0.08

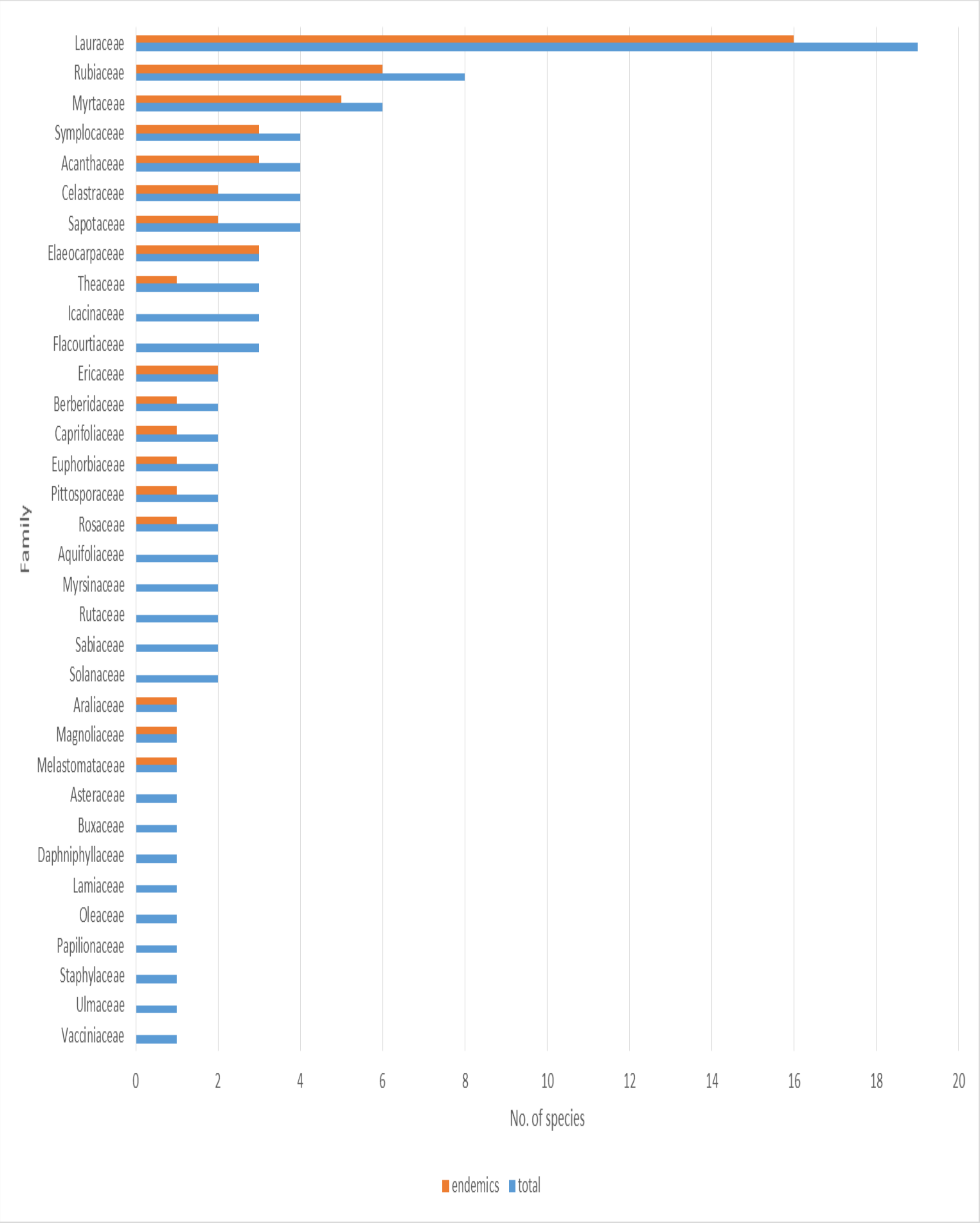

Figure 3.3: Number of tree and shrub species per family and levels of endemism in the tree community of Upper Nilgiri *sholas* (see Appendix 3.1 for details)

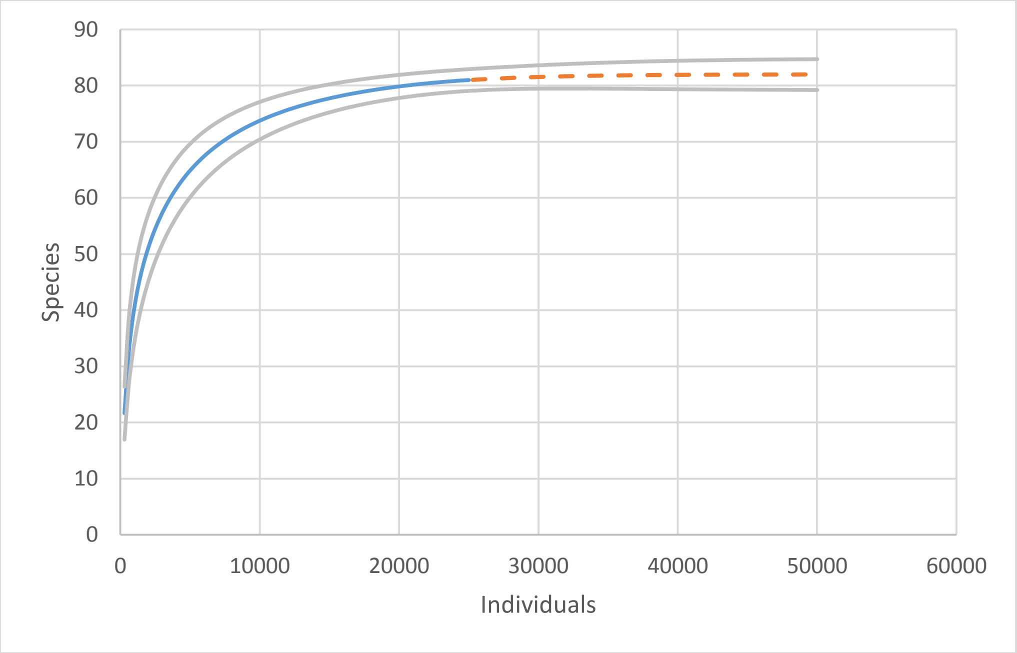

Figure 3.4: Sample-based rarefaction curve for Upper Nilgiri shola tree & shrub species with x-axis rescaled to number of individuals based on the avg. no. ind/sample. Gray lines represent 95% CI, blue solid line represents the sample-based rarefaction, while broken orange line represents extrapolation to double the sample size.

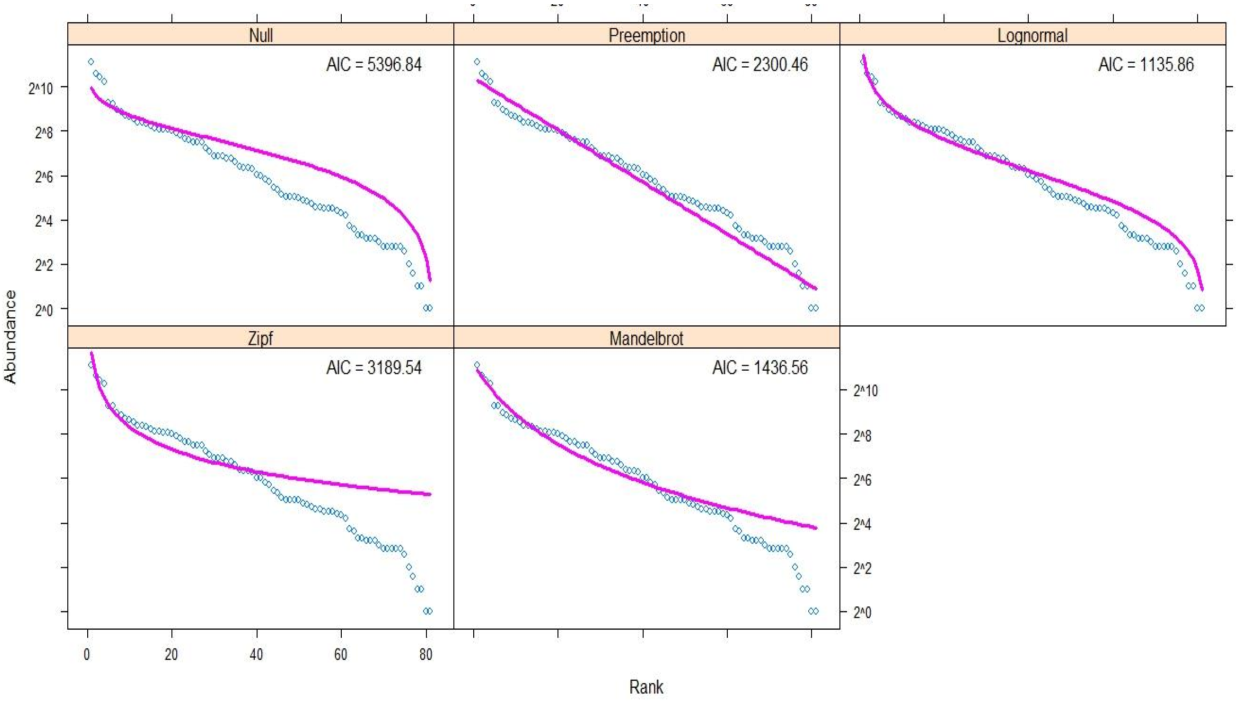

Figure 3.5: Rank-abundance curves (log abundances against species rank order) for tree and shrub species in the Upper Nilgiris, fitted against different theoretical models. Lognormal model shows the best fit with the lowest AIC value.

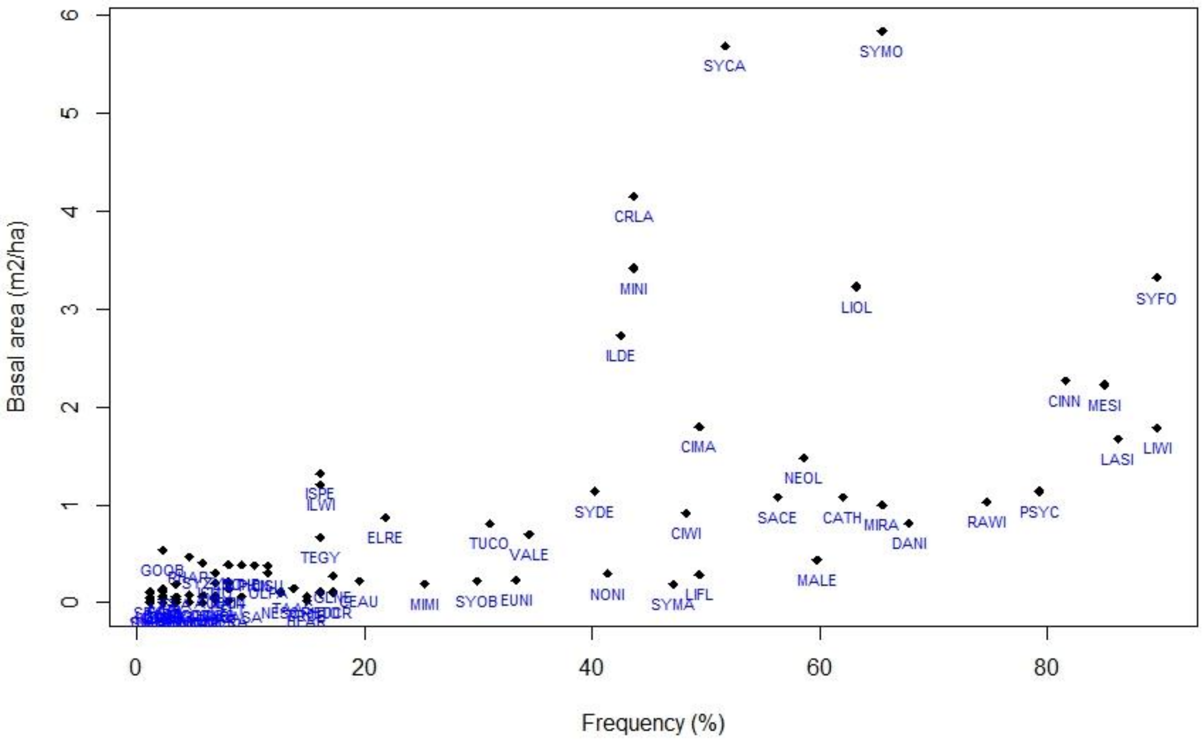

Figure 3.6: Plot of *shola* species basal area by frequency (defined as % of samples in which species occurred)

Clustering analysis of plots based on species abundance data

The most effective clustering method was UPGMA, based on a comparison of Pearson's *r* correlations between the original Hellinger distances and matrices of cophenetic distances (distance at which 2 sites become members of the same group) of the dendrograms produced by each of the four linkage methods (Fig. 3.7). The lower elevation plots (1700-1950m) were clearly separated out from the plots located at and above 2000m by the clustering analysis (Fig. 3.8). Further, plots located between 2000-2150m also seemed to differ in their tree community from the plots at and above 2200m (Fig. 3.8).

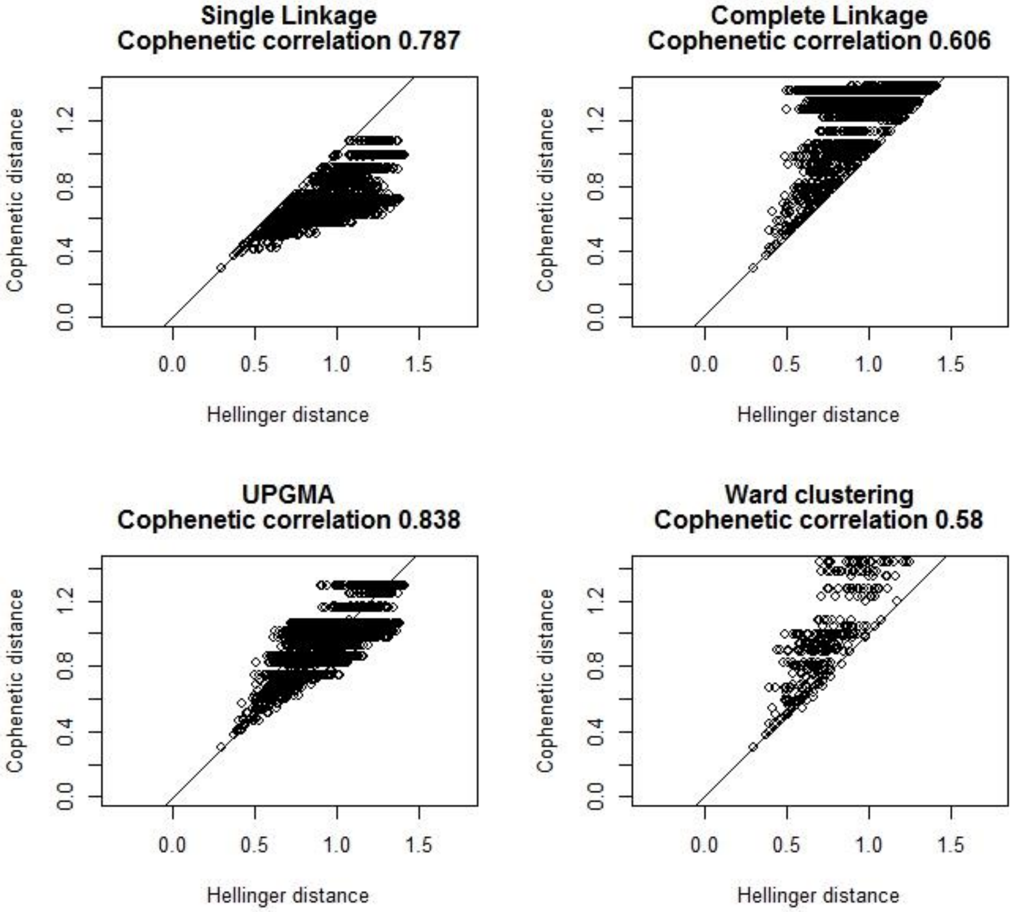

Figure 3.7: Comparison of 4 hierarchical clustering methods using the cophenetic correlation.

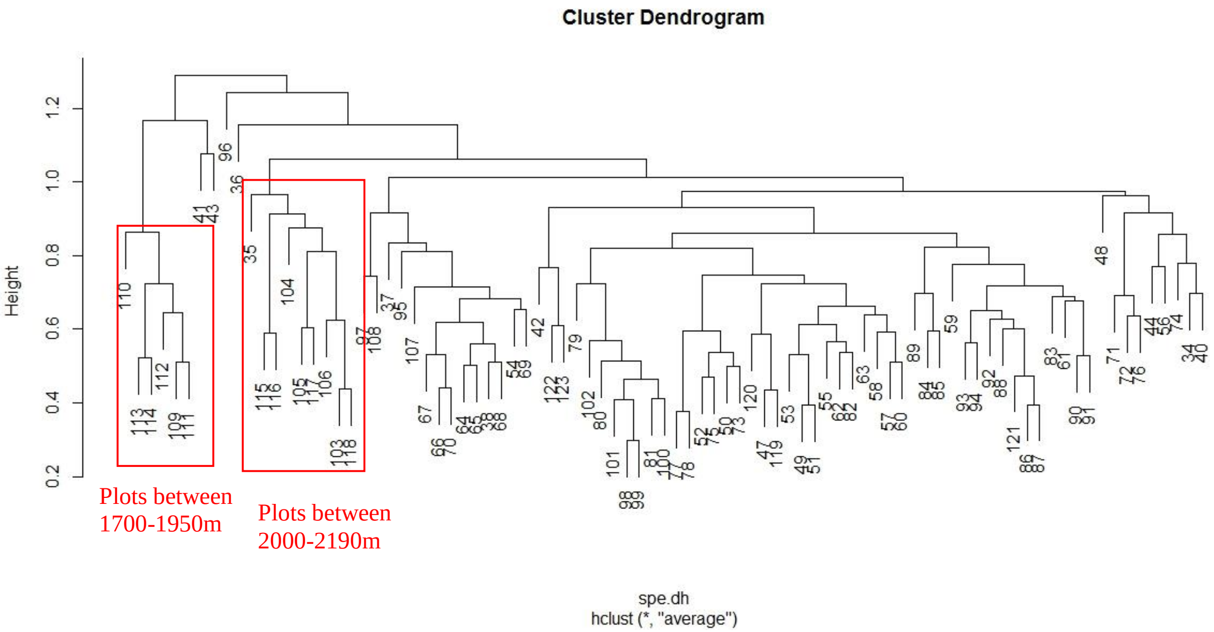

Figure 3.8: Dendrogram showing results of UPGMA clustering of vegetation plots based on Hellinger-transformed species abundance data; showing a clustering out of lower elevation plots and indicating an elevation gradient in community composition

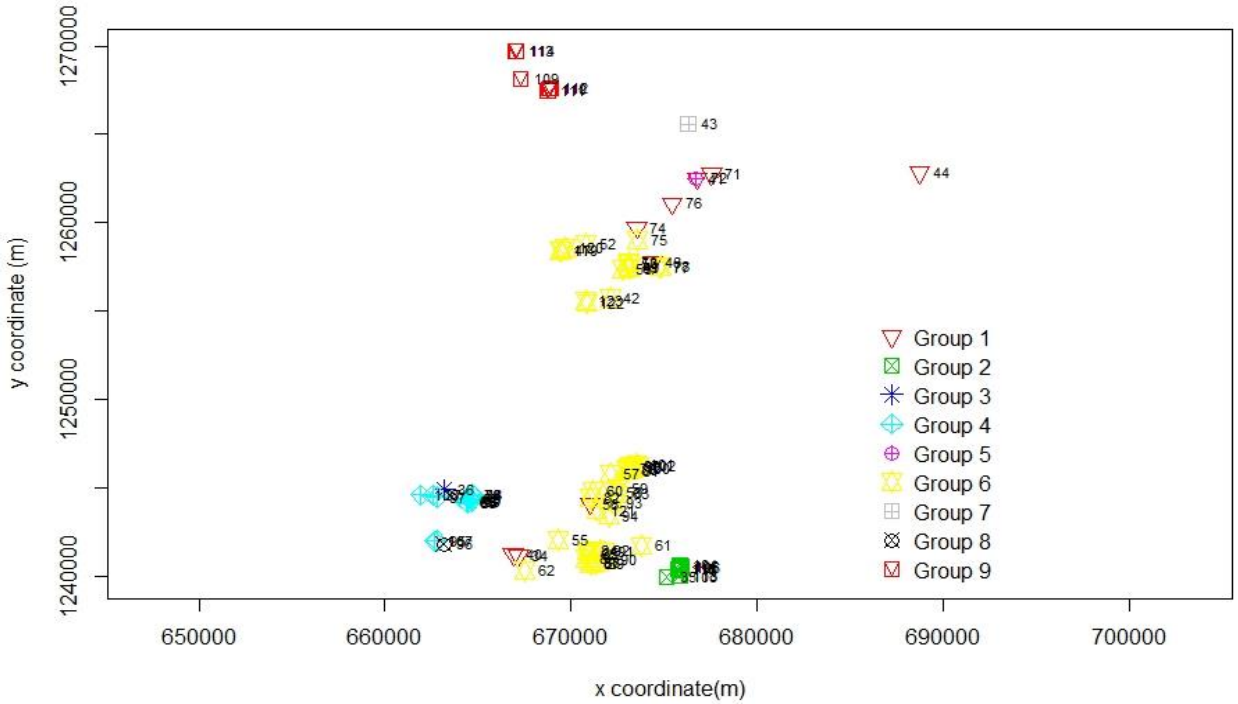

Figure 3.9: Map of the locations of plots in UTM coordinates showing their membership across 9 clusters based on species abundance data using UPGMA clustering

Characterization of metacommunity patterns: coherence, turnover and boundary clumping

The "Elements of Metacomunity Analysis" framework analysis run on the ordinated species presence-absence matrix (Fig. 3.10) indicates that the metacommunity contained fewer embedded absences than expected under null model simulations (z = 2.49, *P* = 0.013). This implies positive coherence. There were also more species' replacements than expected (z = -4.85, *P* < 0.001), implying significantly high turnover among sites. Finally, species range boundaries were highly clumped and significantly different from the null expectation (Morisita's index = 3.52, *P* = 0). These results indicate that at the scale of the study area, the metacommunity exhibits a Clementsian structure possibly in response to one or more structuring environmental gradients.

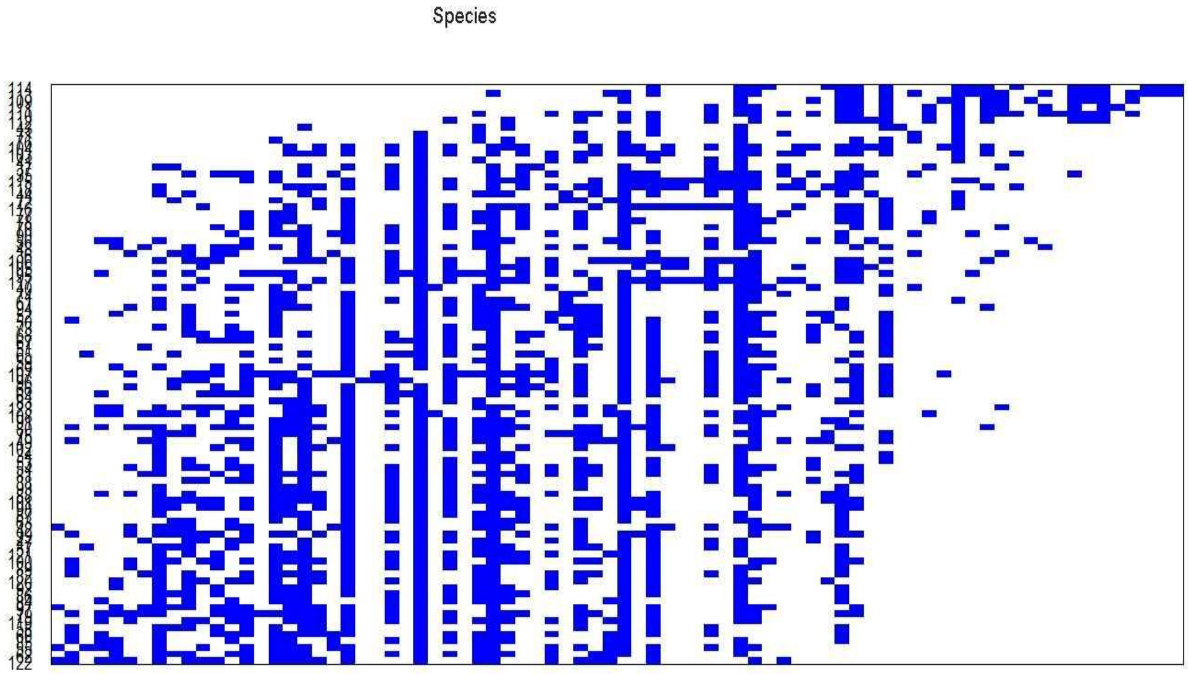

Figure 3.10: Matrix visualization of presence-absence data ordinated by reciprocal averaging, with numbered sites as rows and species as columns. Blue rectangles indicate a species occurrence at a site.

Elevation as a structuring gradient in sholas communities

The site scores obtained from ordination (reciprocal averaging) of the presence-absence matrix (Fig. 3.10) were found to be significantly correlated with elevation values (R_S = -

0.496, $P < 0.001$) and to a lesser degree with mean annual precipitation ($R_s = -0.268$, $P = 0.012$).

The presence of an elevation gradient was also supported by analysis of plot abundance data as indicated by the results of the clustering analysis (Fig. 3.8). Both field observations and plot data indicate a large and rather abrupt change in the *shola* tree community composition between 1900-2100m in the study area.

Finally, the Bray-Curtis distance between pairs of plots was plotted against difference in elevation (Fig. 3.11a). The plot shows an increase in BC dissimilarity with increasing difference in elevation between plot pairs (Mantel's $R_M = 0.5$, $P < 0.0001$). Partial Mantel's tests controlling for the effect of geographic distance (Fig. 3.11b) and *shola* fragment size also verified that greater differences in elevation were correlated with greater differences in species composition (Partial Mantel's $R_M = 0.38$, $P < 0.001$ for elevation and geographic distance, Partial Mantel's $R_M = 0.5$, $P < 0.001$ for elevation and patch area).

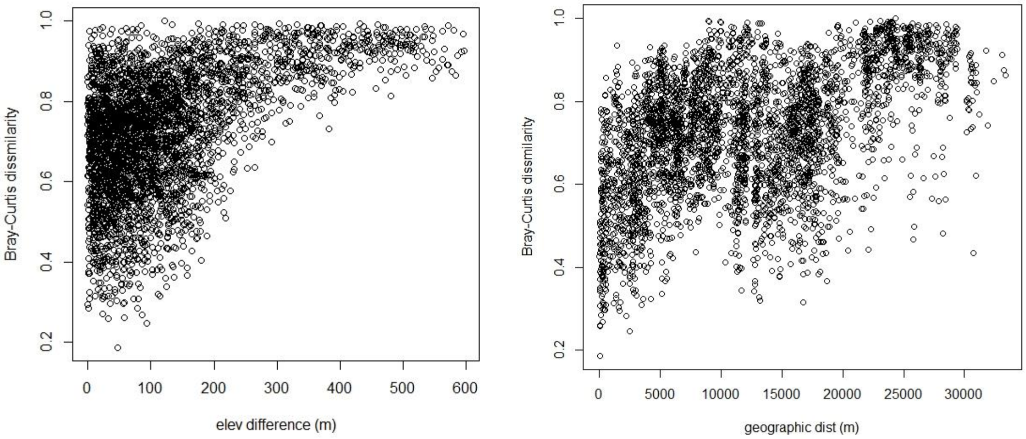

Figure 3.11: Scatter-plot of pairwise site values for Bray-Curtis dissimilarity plotted against pair-wise difference in elevation (left) and geographic space (right)

Floristic change in shola communities along the elevation gradient

The family-wise distribution of total basal area of tree and shrub species in the Upper Nilgiris indicates that dominant families such as Lauraceae, Myrtaceae and Symplocaceae, show changes with elevation. Lauraceae basal area increases between 2000-2200m and then decreases above 2200m. Basal area of Myrtaceae however shows an increase with elevation as does that of Symplocaceae, Magnoliaceae and Celastraceae. Ericaceae and Berberidaceae have low basal area in the study plots but do show an increase with elevation. Theaceae, Araliaceae, Oleaceae, Sapotaceae and Rutaceae show the largest declines in basal area with elevation (Fig. 3.12).

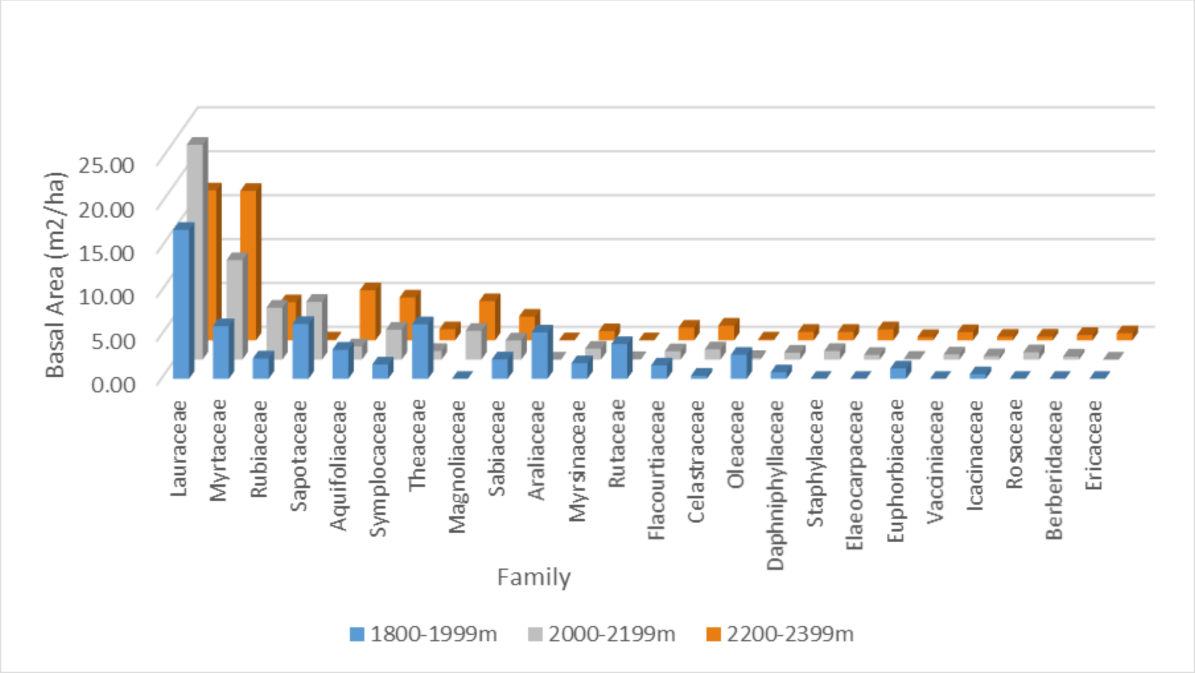

Figure 3.12: Bar chart showing tree and shrub basal area by Family across plots in each of three elevation zones in the Upper Nilgiris *sholas*.

Re-configuration of the presence-absence matrix with rows (sites) ordered by elevation and species (columns) ordered by lower elevation range extent, indicates that at least 12 species are not detected in any of the plots above 2100m. These include: *Litsea stocksii* Hook.f., *Canthium dicoccum* (Gaertn.) Merr., *Scolopia crenata* Clos, *Syzygium lanceolatum* (Lam.) Wight & Arn., *Isonandra lanceolata* Wight, *Syzygium* cumini (L.) Skeels, *Actinodaphne sp.*, *Meliosma pinnata* (Roxb.) Maxim**.** The first four species are both common and abundant in the plots between 1700-1800m and then completely absent above this elevation – indicating an altitudinal range boundary for these species (Fig. 3.13). There are also several species that appear frequently in plots above 1900m that were not encountered below this elevation. These include: *Litsea wightiana*, *Cryptocarya* *lawsonii*, *Mahonia leschenaultii*, *Saprosma ceylanicum* (Gardner) Bedd., *Michelia nilagirica*, *Ilex wightiana* Wall. ex Wight, *Syzygium grande*, *S. calophyllifolium*, *Symplocos macrophylla* Wall. and *S. obtusa* Wall. However it should be noted that far fewer plots fell below 2000m than above (Fig. 3.13). Seven species were only detected above 2100m elevation, constituting the highest elevation group: *Microtropis ramiflora* Wight, *Vaccinium leschenaultii* Wight, *Elaeocarpus recurvatus, Sarcococca saligna* Müll. Arg., *Ternstroemia gymanthera, Hedyotis articularis* R.Br. ex G.Don and *Rhodomyrtus tomentosa* (Aiton) Hask. Finally *Rhododendron arboreum* ssp. *nilagiricum* (Zenk.) was only detected above 2200m (Fig. 3.13). Some species such as *Isonandra perrottetiana* A.DC., *I. montana* (Thwaites) Gamble, *Memecylon randerianum* S.M.Almeida & M.R.Almeida and *Neolitsea scrobiculata* Gamble appear to have narrower elevation ranges between 1900 and 2200m in the study area.

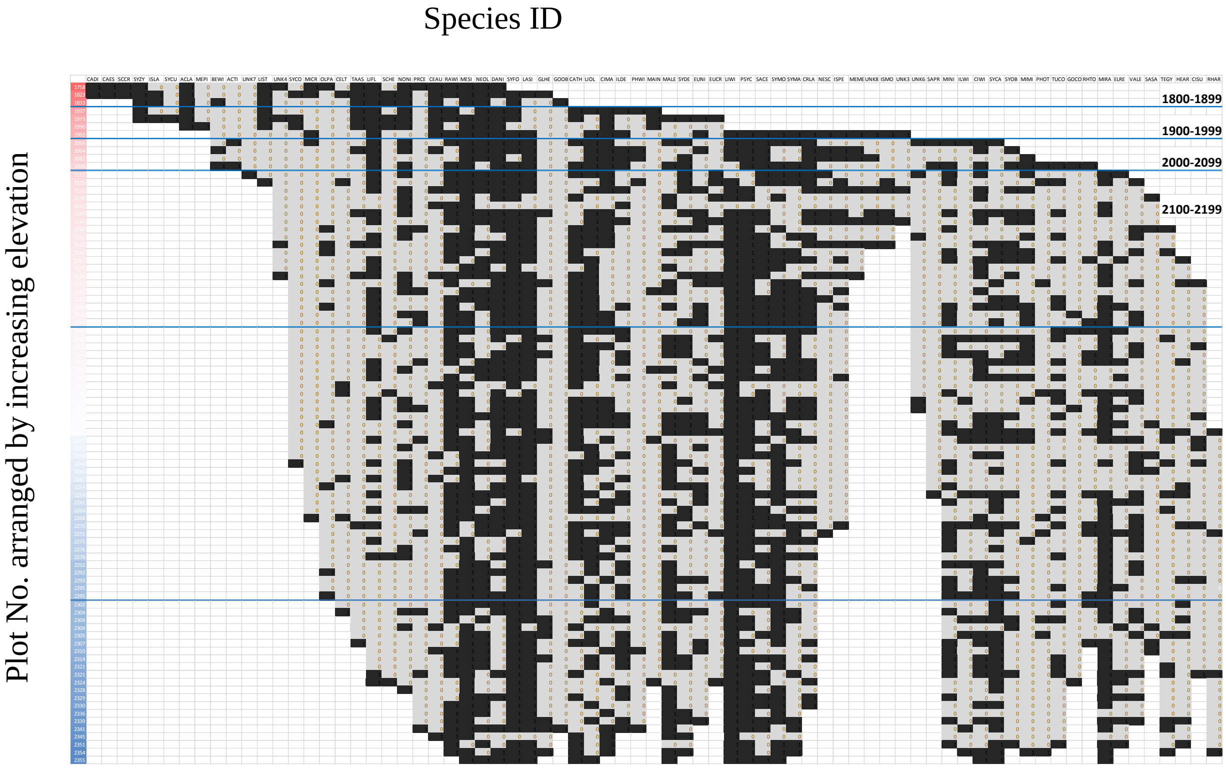

Figure 3.13: Species presence absence matrix with species in columns, arranged by range extent, and plots in rows, arranged in ascending order of elevation value (red-blue). Black squares indicate presence and light grey squares indicate an embedded absence in the species range as indicated by the plot data. Blue horizontal lines indicate 100m elevation intervals, starting at 1800m.

The highest turnover in species composition occurs in the 1900-2100m elevation zone (Fig. 3.13) especially in the genera *Syzygium* (Myrtaceae), *Litsea* (Lauraceae) and *Symplocos* (Symplocaceae). This is supported by a comparison of average values for three pairwise dissimilarity indices across groups of plots in each of three elevation zones. On average, there is greater dissimilarity in species composition between plots at 1800-1999m and those at 2000-2199m than there is between plots at 2000-2199m and those between 2200-2400m, across all three dissimilarity indices (Fig. 3.14). The difference is particularly obvious in the case of the Raup-Crick dissimilarity index which accounts for differences in alpha diversity between plots.

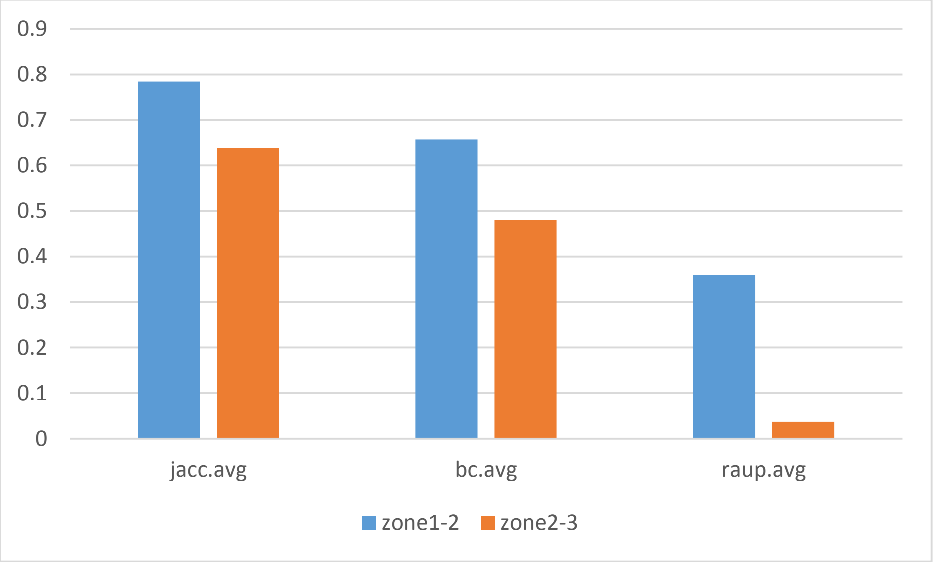

Figure 3.14: Bar chart showing average pair-wise dissimilarities between plots in elevation zones 1 (1800-1999m) and 2 (2000-2199m) and zones 2 and 3 (2200-2400m) according to the Jaccard, Bray-Curtis and Raup-Crick dissimilarity measures.

The number of species encountered is highest between 2100-2200m (62 species). Beyond this elevation zone the number of species recorded in the plots declines with elevation with the plots in the highest elevation zone (>2300 m) having a subset of the species present in the 2200-2300m elevation zone (Fig. 3.13).

Dominant community associations

Four major species' associations were identified based on the abundances of the 50 most abundant species, and the clustering analysis presented above. The assemblages for these associations were tested using Kendall's W coefficient of concordance (Assemblage 1: $F= 3.98$, $P < 0.001$, Assemblage 2: $F= 4.19$, $P < 0.001$, Assemblage 3: $F= 4.48$, $P < 0.001$, Assemblage 4: $F= 3.16$, $P < 0.001$).

Assemblage 1 consisted of: *Litsea floribunda* Gamble, *Cryptocarya lawsonii*, *Neolitsea scrobiculata*, *Isonandra perrottetiana*, *Memecylon randerianum.* This association characterizes plots at about 2000m elevation in the Thia *shola* forest (Group 2 in Fig. 3.9).

Assemblage 2 consisted of: *Psychotria sp.*, *Lasianthus sp.*, *Cinnamomum sp.*, *Symplocos macrophylla*, *Symplocos obtusa*, *Turpinia cochinchinensis* (Lour.) Merr., *Syzygium calophyllifolium*, *Michelia nilagirica*, *Microtropis microcarpa* Wight, *Rhodomyrtus tomentosa*. This association was primarily found at and above 2200m (Group 4 and Group 6 in Fig. 3.9).

Assemblage 3 association consisted of: *Litsea stocksii*, *Nothapodytes nimmoniana* (J.Graham) Mabb., *Actinodaphne sp.*, *Canthium dicoccum*, *Scolopia crenata*, *Symplocos cochinchinensis* and *Syzygium lanceolatum.* This species' association was found in plots between 1700-1900m elevation in the Naduvattam area (Group 9 in Fig. 3.9).

Assemblage 4 consisted of: *Litsea wightiana*, *Symplocos foliosa*, *Syzygium grande*, *Meliosma simplicifolia* (Roxb.) Walp., *Mahonia leschenaultia*, *Sarcococca saligna*. This association was relatively widespread in the study area above 2100m (Group 6 in Fig. 3.9).

Discussion

Comparison of Nilgiris shola diversity and composition with sholas in the Central and Southern WG

The results fall within the range of values for alpha diversity, floristics and stand structure obtained by other researchers working on high elevation *sholas* in the central and southern WG (Table 3.3). The species richness and β diversity reported here are higher than estimates of Jayakumar & Nair (2012) for *sholas* in the Nilgiris, possibly owing to the fact that their sampled area (3 ha) was concentrated in a much smaller geographic extent. Like this study, Mohandass & Davidar (2009) find a log-normal abundance distribution for the Upper Bhavani *sholas*, indicating that the abundance distribution pattern is constant across the larger geographic extent sampled here. Stem density and basal area reported from this study are on the higher side compared to other surveys, including that of Mohandass & Davidar (2009) (Table 3.3). Blasco (1971) reported a stem density of 2000 individuals per ha (>3.8 cm dbh) from the Nilgiris. A great deal of variation was observed across the study area in terms of stand structure, particularly so for the understorey. *Sholas* surrounded by a human-dominated landscape tended to have a dense shrub understorey compared to *sholas* set in grassland or plantation mosaics. Also the presence and abundance of *Cestrum aurantiacum* Lindl., an invasive exotic, was higher in these *sholas* (please see Chapter 5).

At the family level, Lauraceae is consistently found to be dominant (Nair and Menon 2001, Sudhakara 2001, Swarupanandan et al. 2001, Davidar et al. 2007a, Mohandass and Davidar 2009) except in the case of Menon's (2001) study of Eravikulam *sholas*, where he found Myrtaceae to be dominant. Rubiaceae is consistently dominant in the understory (Ashton 1988, Nair et al. 2001). The genus *Cinnamomum* seems to be among the dominants in *sholas* throughout the region (Table 3.3).

Myrtaceae however, seems to be patchier in its dominance, being displaced in some regions by Rubiaceae, Euphorbiaceae or Flacourtiaceae (e.g. Pambadam *shola*) (Nair and Menon 2001, Sudhakara 2001, Swarupanandan et al. 2001, Davidar et al. 2007a).

Symplocaceae appears to be more consistently dominant in the Upper Nilgiris and the Wayanad region than it is further south (Nair and Menon 2001, Swarupanandan et al. 2001, Vidyasagaran and Gopikumar 2001, Mohandass and Davidar 2009). Euphorbiaceae is the second-most dominant family in some *sholas* of the Anamalais but poorly represented in the Upper Nilgiris (Sudhakara 2001, Swarupanandan et al. 2001). Representation of Oleaceae is reported to be higher by at least one study in the southern WG (Swarupanandan et al. 2001) than it is in the central WG (Mohandass and Davidar 2009, this study).

Many of the same tree species are found in *sholas* in the Nilgiris and Eravikulam regions (Nair et al. 2001, Mohandass and Davidar 2009, and this study). Twenty-seven of the 29 species reported from Eravikulam by Nair & Menon (2001) are also found in the Upper Nilgiris. Mohandass & Davidar (2009) report a 47% overlap in species between *sholas* in the Nilgiris and in the Palni hills.

However, several authors have noted the remarkable turnover of dominant species in evergreen forests across different regions (Pascal 1988, Nair and Baburaj 2001, Nair and Menon 2001, Sudhakara 2001, Pascal et al. 2004, Jayakumar and Nair 2012). This is also true of *shola* forests (Table 3.3). At the regional scale in the WG, studies have shown that rates of species turnover and endemism in evergreen forests are largely determined by climatic factors such as variation in total annual rainfall, length of the dry season, and adiabatic lapse rate in temperature with increase in altitude (Ramesh and Pascal 1997, Gimaret-Carpentier et al. 2003, Davidar et al. 2007b). However, this and other such studies conducted over smaller geographic areas (Nair and Menon 2001, Swarupanandan et al. 2001, Vidyasagaran and Gopikumar 2001, Bunyan 2009) point to high turnover in dominance patterns even over short distances (5-10 km). In the Nilgiris, *Beilschmeida wightii* goes from being very rare in Upper Bhavani (Mohandass and Davidar 2009 and this study) and Bangitappal (this study) to being a frequent and even dominant species in Sispara (Nair and Menon 2001). *Syzygium calophyllifolium* is a dominant species in Bangitappal, with a stem density of 75 per ha, however Mohandass et al. (2009) list it as being less common than *S. grande* in Upper Bhavani and having a stem density of 46.7 per ha. Another dominant from the Sispara area, *Ardisia rhomboidea* Wight, was not reported from Upper Bhavani (Mohandass and Davidar 2009) and neither was it detected in any of the plots from this study. *Ilex wightiana* is reported to have much higher frequency in Sispara compared to Upper Bhavani (Nair and Menon 2001, Mohandass and Davidar 2009). While it was observed at the edges of several *sholas* and as solitary trees in the grasslands of Bangitappal, it was not recorded from most plots in this study.

Nair and Menon (2001) report neither *Syzygium calophyllifolium* nor *S. grande* from any of their Sispara or Eravikulam plots. Instead, they report *S. densifolium* as one of the dominant species in Sispara. This species also appears to be dominant in the Eravikulam *sholas* (Menon 2001), which is not the case in the Upper Nilgiris. Conversely, *Symplocos foliosa*, dominant in the Upper Nilgiris, is reported as being rare in Eravikulam (Nair and Menon 2001). Ranganthan (1938) notes variation in species distributions across both the altitudinal and longitudinal gradient in the Upper Nilgiris, with *Mahonia leschenaultii* confined to the western plateau and *Hydnocarpus alpina* Wight restricted to the eastern plateau.

The results also indicate strong spatial autocorrelation in species' distributions across the study area. This could be due to topographically induced variation in meso-climate or edaphic conditions at a landscape scale or even dispersal limitation. Further, landscape context (as a proxy for disturbance) could potentially mediate processes such as dispersal (Kupfer et al. 2006), which in turn affect the degree of spatial autocorrelation in species' distributions. The following chapters examine the influence of various environmental factors and those possibly related to dispersal in greater detail and in a spatially explicit manner.

Metacommunity patterns in the Nilgiris: elevation as a structuring gradient

Several authors have noted the existence of an altitudinal gradient in *shola* vegetation (Ranganathan 1938, Sudhakara 2001, Swarupanandan et al. 2001). However, the nature of the metacommunity response to this gradient has not been examined till now. At the scale of the study area, the *shola* tree metacommunity in the Upper Nilgiris appears to exhibit positive coherence, significant positive turnover along a gradient and highly significant clumping of species' range boundaries. This coincides more with a

Table 3.3: Results from previous plot-based inventories of *shola* forests in high elevation S. Western Ghats

Site	Area Sampled (ha)	Elevation (m)	No. sp‡	α diversity	Stem Dens (ind/ha)	Basal Area (m^2/ha)	Dominant sp.	Author(s)
Brahmagiri	0.1	approx., 1600	56	5.45 (H′)	2533 (>3cm dbh)	73.55	*Cinnamom perrotettii, Actinodahne salicina, Microtropis stocksii, Ligustrum perrottetti*	Vidyasagaran & Gopikumar 2001
Eravikulam	0.7	NR	49	NR	1268**	25 (avg) range: 14.17-32.75	*Syzygium densiflorum, Ixora nottoniana, Mahonia leschenaultii, Maesa indica Cinnamomum wightii, Microtropis ramiflora*	Menon 2001
Eravikulam & Mannavan	1.25	1750-2100	112	2.5-3.38 (H′)***	18,100* (avg)	74 (avg): range 17-89.2	*Mastixia arborea, Syzygium densiflorum, Hydnocarpus alpina, Isonandra candolleana, Turpinia cochinchinensis*	Swarupanandan et al. 2001
Eravikulam	0.49	1900-2400	36	3.24 (H′)**	NR	NR	*Cinnamomum perrotettii, C. sulphuratum, Microtropis ramiflora, Ilex wightiana, I.denticulata, Elaeocarpus recurvatus*	Nair & Menon 2001
Pambadam	0.23	1750-1950	45	4.53 (H′)	21,894*	114.94 (total)	*Scolopia crenata, Actinodaphne bourdilloni, Psychotria nilgiriensis, Neolitsea fischeri*	Sudhakara 2001
Sispara	0.49	2000-2400	37	3.03 (H′)**	NR	NR	*Ilex wightiana, C. perrotetti, S. densiflorum, Beilschmeida wightii, Michelia nilagirica,, Litsea floribunda,*	Nair & Menon 2001
Upper Bhavani	11.5	>2000	69	9.03 (Fisher's α)	2540*	58.97	*Psychotria nilgirensis, Lasianthus venulosus, Litsea wightiana, Symplocos foliosa, Mahonia leschenaultii, Neolitsea cassia, Syzygium grande*	Mohandass & Davidar 2009
BRT, Pambadam Eravikulam	0.3	<1500 to 2200m	77	3.96 (H′)	1711**	15.5 - 78.5 (avg)	NR	Bunyan 2009
Kukkal (Palnis)	1.08		67	12.1 (Fisher's α)	1972*	62	*Psychotria nilgirensis, Maesa indica, Xantolis tometosa*	Davidar et al. 2007

* >1cm dbh, ** >5 cm dbh, ***>10cm dbh
‡ trees and shrubs, NR- not reported

Clemenstian distribution, with several non-overlapping range boundaries, than a Gleasonian one (Leibold and Mikkelson 2002). There appear to be distinct assemblages of species in the *sholas* of the western Upper Nilgiris which are distributed according to both altitudinal and rainfall gradients. The environmental gradient most strongly correlated with the main axis of variation is elevation. This is further supported by the conclusion that sites that differ more in terms of elevation tend to differ more in their species composition.

Metacommunities can exhibit different structures at different spatial scales and in response to different gradients (Presley and Willig 2010, Presley et al. 2010). Indeed, Mohandass & Davidar (2010) find evidence that the *shola* community between 2200-2400m in the Upper Bhavani landscape (a subset of the current study area) exhibits a pattern of nestedness along a patch-size gradient, where the species composition of smaller *shola* patches represent nested subsets of the larger patches. In this study, the plots above 2200m show a reduction in species richness and could be considered a nested subset of the elevation zone below (with the exception of *Rhododendron*). However, it is not possible to separate the effects of the elevation gradient from those of the patch-size gradient above 2200m as *shola* fragments show a decrease in size in the highest elevation zone (2300-2400m). It is possible to say that the clearest pattern emerging for the metacommunity at the scale of the study area, is a Clementsian structure along the elevation gradient (between 1800-2200m), with possible nestedness (Patterson and Atmar 1986) at a smaller scale (especially above >2200m).

Such a pattern points to niche-based processes driving turnover along the gradient. Gimaret-Carpentier et al. (2003) demonstrate that endemic species of the genus *Syzygium*, which are among the dominants in the study area, show much higher levels of niche separation along an elevation gradient in the WG compared to *Litsea* and *Diospyros*. This is supported by the present study, where *S. cumini* and *S. lanceolatum* are completely replaced above 2000m by *S. calophyllifolium*, *S. densiflorum* and *S. grande*. The increasing dominance of *Syzygium sp*. with elevation is also observed in the Anamalai hills (Swarupanandan et al. 2001), as is the peak in abundance and basal area for *Isonandra sp*. (Sapotaceae) that occurs between 1950 and 2100m (Sudhakara 2001, Swarupanandan et al. 2001), similar to the Upper Nilgiris. Endemic species of the genus *Litsea* show some niche separation along both altitudinal and rainfall seasonality gradients in the WG, though to a much lesser extent than those of *Syzygium* (Gimaret-Carpentier et al. 2003). In the study area, *L. stocksii* does not occur above 2100m and appears to be replaced by *L. wightiana* and *L. oleiodes* above 2000m. However *L. floribunda* is found throughout, even above 2300m. Similarly, *Symplocos cochinchinensis* appears to be replaced by *S. obtusa* and *S. foliosa* above 2000m.

This broadly matches the pattern of zonation described for south and east Asian tropical mountains (Ohsawa 1991, Ashton 2003), where pairs of closely related congeneric taxa replace each other with increase in elevation. The species which replace their sister taxa tend to have smaller or thicker leaves with revolute margins (Ashton 2003).

Finally, there are several narrowly endemic species that appear to be restricted to above 2000m in the Upper Nilgiris. These include: *Michelia nilagirica, Mahonia leschenaultii, Hedyotis sp., Cryptocarya lawsonii, Elaeocarpus recurvatus*, *Saprosma ceylanicum* and *Rhododendron arboreum spp. nilagiricum*.

Jayakumar and Nair (2012) recorded a decline in species richness in evergreen forests along the elevational gradient (400-2600m) in the Western Nilgiris. Swarupanandan et al. (2001) and Sudhakara (2001) observed a similar decline in tree species richness and increasing dominance above 1850m in the Anamalai hills. They also report a decline in plot basal area at higher elevations, which was not observed in this study. There is no significant decrease in tree height along the range of elevation gradient (1800-2400m) in this study. However Sudhakara (2001) and Swarupanandan et al. (2001) do report decreasing tree height and simplifying stand structure between 1500-2100m in the Anamalai hills. Their results are consistent with the structural transitions observed in other montane forests of tropical Asia (Ohsawa 1991, Ashton 2003).

Ecotonal boundary between shola communities in the Upper Nilgiris

While many authors have used various altitudinal thresholds to define the lower boundary of *sholas* in the WG (1500m in Ranganathan 1938 and Meher-Homji 1967, 1700m in Bunyan et al. 2012, 1800m in Nair & Khanduri 2001), vegetation zonation *within shola* habitats and specifically distribution of ecotonal boundaries between lower and upper montane *shola* formations are not well known.

The transition observed in the *shola* tree and shrub community of the Upper Nilgiri plateau has the floristic characteristics of an ecotonal transition between lower and upper montane *shola* communities as described by other authors (Ohsawa 1991, 1995, Werner 1995, Ashton 2003). Ohsawa (1991) associates the increased dominance of Symplocaceae and Ericaceae with upper montane formations. In this study, basal area of Symplocaceae and Ericaceae increases with elevation. Basal area of Aquifoliaceae (*Ilex*) is also higher at higher elevations (Ohsawa 1995). Finally, incidence and increased abundance of frost-tolerant genera with Himalayan affinities (Meher-Homji 1967) such as *Mahonia*, *Berberis* (Berberidaceae), *Rhododendron* (Ericaceae) and *Rubus* (Rosaceae) is observed above 2100m in the study area, but not below this elevation. Field observations indicate that structural characters such as tree height, size and thickness of leaves and density of non-vascular epiphytes also match those of upper montane cloud forests as described by Scatena et al. (2010).

The elevation zone at which an ecotonal transition occurs in the Nilgiris is between 1900 and 2100m. Therefore formations above 2100m could be considered to be upper montane *shola* communities that are structurally and floristically distinct from those below 1900m. Werner (1995) notes a similar ecotonal transition within the upper montane formations of Sri Lanka above 2,000-2,100m. However he locates the actual boundary between lower and upper montane forest at 1,500m, based on the lower limit of cloud cover. Interestingly, Jarvis and Mulligan (2011) in their global study of the climatic conditions under which TMCF occur, find that high cloud cover (> 60%) is frequent at more than 80% of the sites (*n* = 526) in their study that lay above 2000m and within 100km from the coast. These conditions match those of the observed transition zone in the Upper Nilgiris. However, further ecophysiological and mechanistic studies are needed determine whether this transition is being driven by mist immersion or change in temperature, or both. In general, the mechanisms behind the transition from lower to upper montane forest types remain unresolved and poorly understood (Foster 2001, Ashton 2003). Another interesting observation is that the forest-grassland mosaic in which these *sholas* occur also shows a greater predominance of grassland to forest above the same altitudinal threshold of 2000m (please see results from Chapter 2).

The *shola* communities above 2000m are of particular interest from a conservation and management perspective owing to the restricted area that they occupy in the WG, the high levels of endemism (particularly narrowly distributed endemics) and their critical hydrologic functions (Nair and Khanduri 2001). While species richness in these forests is lower than other tropical montane forests (Sudhakara 2001, Swarupanandan et al. 2001, Jayakumar and Nair 2012), rates of endemism are higher (Jayakumar and Nair 2012). This analysis provides insights into the spatial turnover in *shola* tree and shrub species along the elevation gradient that should be of use to forest managers and conservation planners.

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Chapter 4

Relative Influence of Environment and Dispersal on Plant Community Composition in Shola Forests

Introduction

The relative roles of niche and neutral processes in the assembly of tropical plant communities has received much attention in the ecological literature over the last two decades. Classical models have invoked deterministic processes in explaining community structure, such as resource competition (Tilman 1982) and abiotic physiological tolerance to the environment (Keddy 1992), which imply that differences in species' niches influence distribution and abundance (Schwilk and Ackerly 2005). Neutral models on the other hand argue that species compositional differences among sites are unrelated to differences in the environment or to species interactions and that ecological drift coupled with speciation and dispersal limitation can alone explain patterns of species composition and turnover (Hubbell 2001). The theory has drawn considerable attention (Condit et al. 2002, Dexter et al. 2012) and led to a proliferation of empirical studies aimed at testing hypotheses in different ecosystems (Rosindell et al. 2011). The debate over whether neutral or niche processes predominate has subsequently shifted towards a consensus that most communities are structured by both (Condit et al. 2002, Gravel et al. 2006, De Cáceres et al. 2012, Brown et al. 2013). Thus recent studies have focused on the relative roles of niche and neutral factors in community assembly.

Environmental determinism has been the most widely investigated process structuring species composition and turnover in tropical forests. Several studies have demonstrated that topographical heterogeneity, soil properties, and successional history can explain differences in species composition and abundance in tropical forests to varying extents (Clark et al. 1998, Harms et al. 2001, Potts et al. 2002, Phillips et al. 2003, Paoli et al. 2006, Dexter et al. 2012, Baldeck et al. 2013). While a few environmental variables such as soil exchangeable phosphorus and moisture availability can play a dominant role in influencing species distributions (Engelbrecht et al. 2007), several environmental variables may have smaller but significant effects at a wide range of spatial scales (Phillips et al. 2003, Tuomisto and Ruokolainen 2006, John et al. 2007, Jones et al. 2008, Baldeck et al. 2013). However, observed spatial patterns in community composition are also influenced by dispersal limitation (Condit et al. 2002, Tuomisto et al. 2003) and biotic interactions (Pitman et al. 1999, 2001), and the relative importance of these processes in driving species turnover is not well understood.

The hypotheses and mechanisms of niche and neutral models predict distinct spatial patterns of species composition. For instance, in communities that are strongly influenced by biotic interactions, a few competitively superior species could dominate landscapes leading to more uniform species composition over large areas. Alternately, if dispersal limitation is strong in communities where species are competitively equivalent, species composition should vary random but in a spatially autocorrelated fashion that shows no trend. Finally, if environmental control is a dominant factor, species distributions in space should be strongly correlated to environmental conditions.

Quantifying the importance of each process requires the use of methods which disentangle their contributions to spatial variance in community composition. The most widely used method is variation partitioning (Legendre et al. 2005, Peres-Neto et al. 2006), which is an extension of partial canonical ordination techniques (Rao 1964, Ter Braak 1986). The power of variation partitioning methods to distinguish between environmental control of community composition and spatial autocorrelation arising from dispersal limitation has been widely discussed in the literature (Tuomisto and Ruokolainen 2006, Smith and Lundholm 2010, Gilbert and Bennett 2010). There are two broad approaches that have been used: (i) canonical analyses (e.g., RDA) using raw-data on species occurrence/abundance (Borcard et al. 1992) and (ii) univariate or multivariate regression analyses with distance data on species, environmental variables, and pure space (e.g., Mantel tests) (Duivenvoorden et al. 2002, Tuomisto and Ruokolainen 2006). These approaches test fundamentally different predictions of the ecological hypotheses on variation in species composition and abundance among sites (Tuomisto and Ruokolainen 2006). The former tests the variation in community composition among sites as a function of variation in environmental conditions or neutral community dynamics, while the latter examines variation in the *differences* in community composition between two sites as a function of variation in the *differences* in environmental conditions or geographical distance. Empirical evidence from studies that use these approaches have shown a wide range of patterns, from strong environmental control on variance in community composition among sites (Phillips et al. 2003, Svenning et al. 2004, Paoli et al. 2006, Jones et al. 2008, Baldeck et al. 2013) to a greater role for dispersal in determining variation in the differences in composition between sites at given distances (Condit et al. 2002, Vormisto et al. 2004, Chust et al. 2006).

Despite the increase in studies using variation partitioning to test the relative importance of neutral and niche processes on the spatial variance in species composition, some important concerns regarding this approach remain. Firstly, the manner in which environment and space are modelled has a strong influence on the outcome of the analyses (Jones et al. 2008, Chang et al. 2013), where the effect of unmeasured environmental factors can manifest as the influence of pure space. For example, (Baldeck et al. 2013) show that the contribution of environmental factors almost doubled on including soil variables along with topographical variables, resulting in comparable decreases in the contribution of pure space. Most studies do not account for effects of soil characteristics and are therefore likely to underestimate the importance of environmental factors at fine and intermediate scales (Chang et al. 2013). The confounding effect of unmeasured environmental factors on assessments of pure spatial effects, which are typically interpreted as dispersal related, poses a challenge for evaluating the roles of environment and dispersal on species turnover.

Secondly, the spatial scale of analysis also influences these assessments (Legendre et al. 2009, De Cáceres et al. 2012, Garzon-Lopez et al. 2014). DeCaceres et al. (2012) analysed beta diversity across a global network of forest plots and found that spatial factors, independent of spatially induced environmental effects, increase in importance at finer sampling scales (10 x 10m), while environmental factors (i.e. topographic heterogeneity) were more influential at larger observation scales (plot sizes ≥ 50 x 50m). Further, soil resource availability tends to increase in importance at fine spatial scales (~10m) while topographic heterogeneity usually matters at larger scales (>50m). On both counts, spatial scale appears to be critical in distinguishing the effects of niche and neutral processes (Garzon-Lopez et al. 2014). It is important that the approach used to model the influence of space allows for a multi-scale description of spatial pattern.

Finally, the interpretation of any identified pure space component may be problematic unless the spatial weighting matrix is designed to test specific hypotheses. Even if the importance of unknown environmental effects is evaluated (Diniz-Filho et al. 2012), the specific environmental factors will still need to be identified. Thus, variation partitioning studies would at least need to build and test multi-scale spatial models based on specific hypotheses (e.g., dispersal limitation), while also explicitly estimating the effect of unmeasured environmental variation on the component of variation attributed to spatial predictors.

In order to address these shortcomings, variation partitioning studies should:

a) include soil data to more comprehensively model the role of environmental factors at intermediate and fine scales (Chang et al. 2013).
b) build and test multi-scale spatial models based on specific hypotheses so that these models constitute a direct test of specific spatial processes, such as dispersal, and;
c) attempt to disentangle the effect of unmeasured environmental variation from the component of variation attributed to spatial predictors.

The general framework of Moran's Eigenvector Maps (MEMs) (Dray et al. 2006) provides complex, multi-scale spatial predictors, with the necessary flexibility to model specific spatial hypotheses (e.g. different dispersal scenarios). On the other hand, independent tests of the influence of any effects of unmeasured environmental variables can now also be carried out (Diniz-Filho et al. 2012). MEM consists in the diagonalization of a spatial weighting matrix and has the advantage of allowing for the spatial connectivity among sites to be defined in a variety of ways that would allow tests of competing hypotheses (Dray et al. 2006). For example, in topographically complex landscapes, Euclidean spatial distance may not accurately depict dispersal connectivity, or where sampling has to be perforce irregularly distributed, MEMs may provide the needed flexibility for proper spatial analyses. Further, they have been shown to outperform other approaches in modelling spatial relationships between sites (Jones et al. 2008, Gilbert and Bennett 2010). Surprisingly, despite the strength and flexibility of spatial connectivity matrices in testing specific dispersal processes, they have not been adequately used to study the role of dispersal in variation partitioning studies on plant communities

The following study uses high elevation tropical montane cloud forests of the Western Ghats, India to address existing gaps in variation partitioning studies as stated above. These forests, also known as *sholas*, occur above 1500m elevation in island-like patches, within a mosaic of natural grassland (Meher-Homji 1967, Bunyan et al. 2012). The topographically complex terrain in which they occur creates greater environmental heterogeneity over shorter distances, which has been found to increase the influence of niche-based processes on community assembly at intermediate and large spatial scales (Brown et al. 2013). Species composition and distributions have been described in earlier studies (Meher-Homji 1967, Jose et al. 1994, Suresh and Sukumar 1999, Mohandass and Davidar 2009) and by the same author in earlier chapters, but the relative role of environmental factors, such as climate, topography and soils, and of dispersal in structuring tree communities has not been investigated. *Shola* tree species appear to be strongly influenced by the elevation gradient (please see Chapter 3). Some species found in these forests are frost-adapted, while others show differences in distribution along edge-interior gradients (Meher-Homji 1967, Jose et al. 1994). Related to this, forest fragment size also influences the composition of communities, with larger patches having greater representation of late-successional species (Mohandass and Davidar 2010). Together, these observations and the fact that tropical montane forest soils are known to be nutrient limited (Tanner et al. 1998, Fisher et al. 2013), indicate that environmental filtering should play a strong role in structuring *shola* plant communities. However, the role of dispersal limitation at the landscape scale in this naturally fragmented, patch-island habitat versus the effects of environmental filtering remains unresolved.

In this study I carry out an extensive set of quadrat sampling of species composition, and environmental measurements, to evaluate the contribution of historical and environmental factors, and dispersal to the variation of tree and shrub species composition in this landscape. I evaluate the role of dispersal processes using different spatial connectivity models and employ a framework to simultaneously test dispersal and environment effects on plant community structure. Finally, I estimate what fractions of the variation in composition of *shola* tree and shrub communities can be accounted for by variation in environmental and historical factors relative to dispersal limitation.

Methods

Study area

The study area of approximately 600km^2, is located between latitudes 11.17^{o}N and 11.50^{o}N, and longitudes 76.43^{o}E and 76.77^{o}E on the Upper Nilgiri Plateau at elevations 1800-2630m above mean sea level (m.s.l.). *Shola* forests extend from 1500-2590m (Ranganathan 1938) and most of the survey was conducted on the western and south-western parts of the plateau that contain the largest stretches of intact *shola*-grassland mosaics (Fig. 4.1). Plant endemism is high and Blasco (1971) recorded 223 plant species known only from this region. About 53% of the tree and shrub species in the study area appear to be endemic to the Western Ghats and Sri Lanka (see Chapter 3).

The plateau shows extraordinary vertical and horizontal physiographic differentiation and has three main rainfall regimes (von Lengerke 1977, Caner et al. 2007) - the highest level in the west (5000-2500 mm/yr), decreasing towards the south the east (2000-1500 mm/yr), and lowest in the central part (1200-900 mm/yr) (Fig. 4.1). The dry season lasts 3-4 months (December through March), and temperature ranges from a mean maximum of 24°C in April to a mean minimum of 5°C in December. Frost occurs between November and March and mainly in the valleys rather than the higher hill slopes (von Lengerke 1977, Caner et al. 2007). Geologically, the plateau is made up of deeply weathered, ancient metamorphic rocks called charnockites and the soils are acidic (pH range 4.09-5.56) rich in organic matter. They were most recently classified as non-allophanic andisols (Caner et al. 2000) and earlier as Ultisols (Typic Haplohumults) and Inceptisols (Oxic Humitropepts) (Sehgal et al. 1996). Peat soils occur in swampy areas along valley bottoms.

The area is sparsely populated, and falls under Reserved Forest and also a National Park. Major land cover types are shola-grassland mosaics, forestry plantations (*Eucalyptus* sp. and *Acacia mearnsii*), agriculture, and tea plantations. The grasslands pre-date human settlement and are not considered to be of anthropogenic origin (Sukumar et al. 1995, Caner et al. 2007). However, during the last 150 years, particularly the last 70 years, large stretches of grassland were planted with exotic tree species or converted to tea plantations (Prabhakar 1994).

Vegetation sampling

A stratified random sampling design was used to collect vegetation data from 20 x20 m plots, based on slope, aspect, and landscape context. A minimum of four plots were placed within each combination of landscape context and topographic class, with the exact location of plots determined by accessibility and steepness of terrain. In large *shola* patches (> 60 ha), three transects of plots were placed at a minimum of 250m apart, with a distance of at least 50m between each plot along the transect. Within each plot all individuals > 0.5m in height were identified to species, mapped and diameter at breast height measured for all individuals $\geq$1.3m in height. Species identities were confirmed using field guides, flora (Gamble 1923, Ramesh et al. 2008) and the help of an experienced taxonomist. Distance to the nearest edge of the *shola* fragment was noted as well as the GPS location of the plot corner, elevation, slope and aspect. A total area of 3.48 ha (87 plots) was measured. The minimum distance between plots was 24.4m and the maximum distance was 31km; 16 plots were separated by 100m or less. Most plot pairs were at a distance of 5km apart, followed by 17km apart (Fig. 4.2).

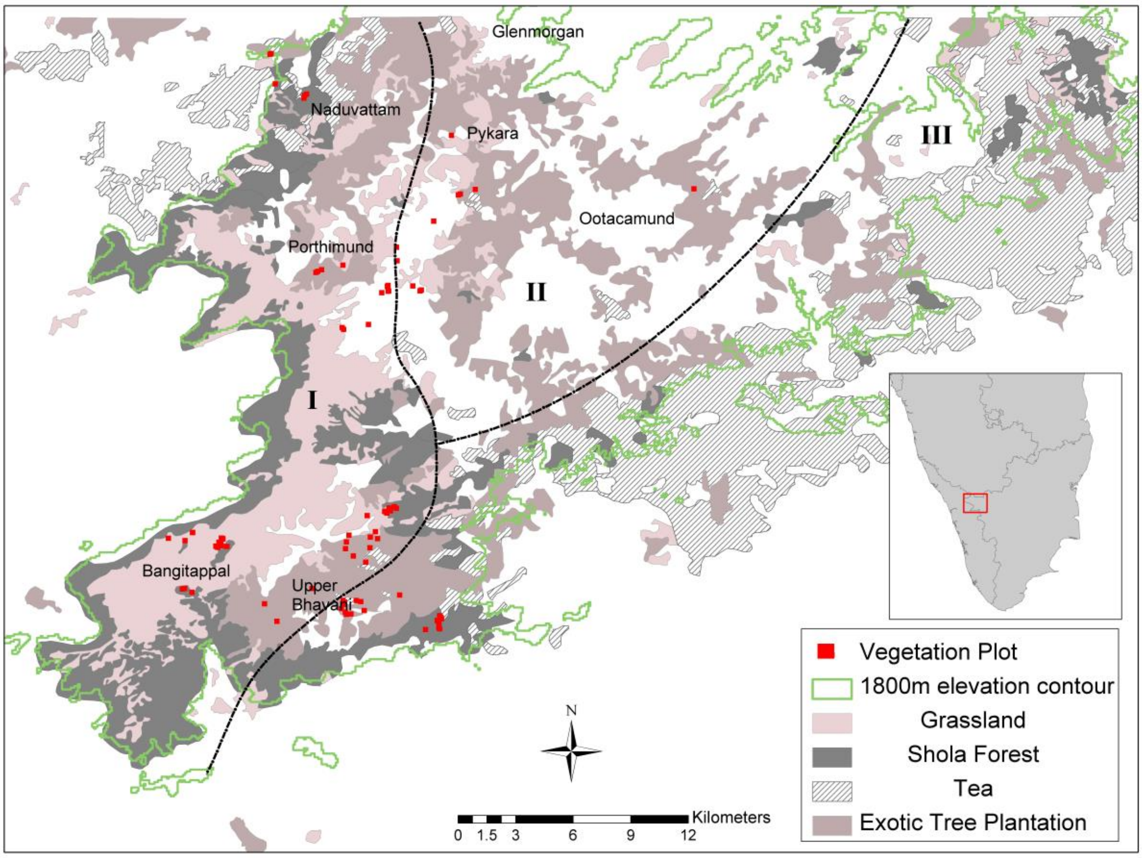

Figure 4.1: Map showing locations of sampled *sholas*, major rainfall regimes (from Caner et al. 2007) and landcover types (Ramesh et al. 2002). Region I rainfall 5000-2500mm, mainly from the southwest monsoon, Region II rainfall 1200-900mm, Region III rainfall 2000-1500mm from both the southwest and northeast monsoon.

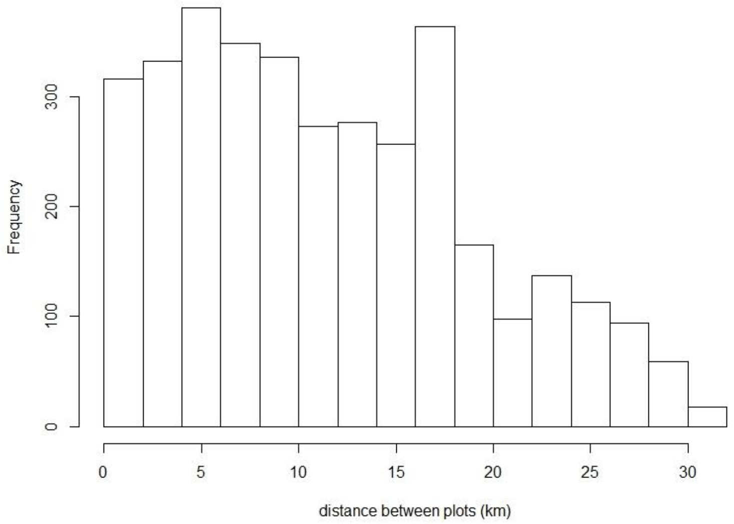

Figure 4.2: Histogram showing distribution of pairwise plot distances

Soil sampling and analysis

Three surface soil samples were collected at regular intervals along the diagonal of each vegetation plot, using a 30cm long iron pipe. The litter layer was cleared and the top 20cm layer of soil was sampled at each point. After collection the samples were stored in airtight plastic containers for analyses in the lab.

In the lab soil samples were processed and texture was measured using the hydrometer method (Sheldrick & Wang 1993; see Appendix 1 for protocol). Most of the plots had soil texture that varied from loamy sand to sandy loam. The mean sand content was 75.13% ± 5.67, mean silt content was 16.75% ± 4.34 and mean clay content was 8.11% ± 2.95. The colour of the samples varied greatly from light brown to very dark brown (almost black). There was also high organic matter content consisting of fine roots or leaf and bark fragments in the samples.

Total soil carbon and nitrogen was measured using a C/H/N analyzer (LECO). Approximately 10g of soil from each plot was first ground to pass through a fine mesh sieve (0.25mm). Approximately 0.15g of this was used for the LECO analysis. Each batch of samples was processed along with a blank as well as a set of known soil standards to calibrate the readings. The results show that the average percent carbon in the samples was 11.27% ± 3.68 and the average percent nitrogen was 0.86 ± 0.22.

The Mehlich III extraction protocol (Trans and Simard 1993) was followed to measure exchangeable soil cation concentrations. The Mehlich extracts were analysed using ICP-Optical Emission Spectrometry (Thermo Fischer ICAP 6000 series). Mehlich extraction was conducted on the dried archived soil samples rather than fresh soil as I did not have access to lab facilities during field sampling. However, after drying and preparation the soil samples set aside for nutrient analysis were kept refrigerated. The readings for potassium were unusually high for several plots and further investigation indicated an error in the ICP readings for potassium in two batches of sample runs. Therefore potassium data was not used in further analysis.

A summary and results of the exploratory analysis with soil predictors are presented in Appendix 2. Except for Cu, which was significantly negatively correlated with elevation (Pearson's r = -0.32), none of the other soil nutrient concentrations showed a significant correlation with elevation. This could be because all of the sites are above 1500m elevation (Tanner et al. 1998, Fisher et al. 2013).

Environmental Data collection

Environmental variables describing plot characteristics (habitat, topography, climate) were extracted using ArcGIS v.10.0 (ESRI 2011) and Google Earth (Google Earth 2013). Variables were plotted to check their distribution and transformed as necessary. Pearson's r was also calculated to assess which of the variables were highly correlated.

The ASTER Global Digital Elevation Model (GDEM) v.2 tiles (30m contour interval) (METI and NASA 2011) for the study area were used to extract the following topographic predictors in ArcGIS using Spatial Analyst and Topography toolbox: elevation, slope, cosine aspect and solar radiation (McCune and Dylan 2002), topographic position index (TPI), (Jenness 2006), topographic convergence index (TCI), (Beven and Kirkby 1979), and surface curvature (Table 4.1). TPI was calculated at the local scale (Table 4.1). TCI and surface curvature values for each sampling point were also extracted at the local scale, by resampling the DEM to 60m resolution. TCI was used as a proxy for soil moisture as it incorporates the upslope flow area above a given cell, identifying convergent points in the landscape which water would flow to. It is also a proxy for areas that are prone to cold air pooling and therefore frost

(Dobrowski 2011). Bioclimatic predictors (Table 4.1) were downloaded from the BIOCLIM global dataset, available at 1km resolution (Hijmans et al. 2005).

Soil data was not collected in 9 of the vegetation plots. For 7 of these plots, inverse-distance interpolation was used to estimate soil texture values and kriging was used to estimate soil cation concentrations. As the remaining 2 sites were located far apart from the rest of the sites, it was not possible to get good estimates for soil predictors for these sites. They were therefore dropped from the dataset and not used in further analysis. This analysis was done in R statistical software v.3.0.2 (R-Development-Core-Team 2013) using the 'GeoR' package.

Table 4.1: Environmental variables used in canonical ordination analysis of shola tree and shrub species abundance data

Variable Code	**Description**	**Units**	**Source/Reference**
Local Habitat			
Ln.area	Shola fragment area calculated from polygons digitized in Google Earth – log transformed	m^2	Google Earth imagery
LS.context	Landscape context, categorical variable: 1-grass, 2-tea, 3-wattle		Field data
Plot.BA	Basal area per unit area of plot	m^2ha	Field data
Dist.edge	Distance from nearest edge of shola	m	Field data
Dist.stream	Measured using Google Earth imagery with a DEM-derived stream layer overlaid and using along ground distance.	m	Google Earth imagery, ASTER DEM
Climate			
coldest.min	Minimum temp of coldest month 1km grid	°C	BIOCLIM, Hijmans et al. 2005
temp.seas	Temperature Seasonality (standard deviation *100) 1km grid		BIOCLIM, Hijmans et al. 2005
ann.prec	Annual precipitation 1km grid	mm	BIOCLIM, Hijmans et al. 2005
prec.cv	Precipitation Seasonality (Coefficient of Variation) 1km grid		BIOCLIM, Hijmans et al. 2005
prec.warmqtr	Warm quarter precipitation 1km grid	mm	BIOCLIM, Hijmans et al. 2005
prec.dryqtr	Dry quarter precipitation 1km grid	mm	BIOCLIM, Hijmans et al. 2005
prec.coldqtr	Cold quarter precipitation 1km grid	mm	BIOCLIM, Hijmans et al. 2005

Soil			
Perc.sand	Percent sand in soil	%	Field data & lab analysis
Perc.silt	Percent silt in soil	%	Field data & lab analysis
Perc.clay	Percent clay in soil	%	Field data & lab analysis
Perc.C	Percent carbon in soil	%	Field data & lab analysis
Perc.N	Percent nitrogen in soil	%	Field data & lab analysis
Ca	Calcium concentration	ppm	Field data & lab analysis
Al	Aluminium concentration	ppm	Field data & lab analysis
Mg	Magnesium concentration	ppm	Field data & lab analysis
Fe	Iron concentration	ppm	Field data & lab analysis
Mn	Manganese concentration	ppm	Field data & lab analysis
B	Boron concentration	ppm	Field data & lab analysis
Zn	Zinc concentration	ppm	Field data & lab analysis
P	Phosphorous concentration	ppm	Field data & lab analysis
Cu	Copper concentration	ppm	Field data & lab analysis
Topography			
Elevation	Measured in field using Garmin GPS eTrex vista H	m	GPS data from field
Slope	Measured in field using a compass	degrees	Field data
Cos.asp	cosine transformation of aspect in radians, 30m DEM resampled to 60m resolution		ASTER GDEM, METI & NASA 2011
TCI	Topographic convergence index using 60m DEM resolution		ASTER GDEM
TPI1.3	Average difference in elevation between a focal cell and neighborhood defined using an annulus of inner radius 60m and outer radius 180m	m	ASTER GDEM, METI & NASA 2011
Curve30	Calculated from ASTER DEM 30m pixel		ASTER GDEM, METI & NASA 2011
Solar60	Potential annual direct solar radiation based on latitude, slope and aspect. Calculated using 60m DEM pixel	MJ/cm^2 /yr	McCune and Dylan 2002

Data Analysis

Assessing relative influence of climate, topography, habitat and soil

Abundance data for 79 tree and shrub species with stems ≥ 1cm dbh, across a total of 85 plots, were used in statistical analysis as recent studies show that environmental filtering affects trees even at early life stages (Baldeck et al. 2013, Brown et al. 2013).

The environmental predictors were grouped into four matrices: “climate”, “soil”, “topography” and “habitat”. Redundancy analysis (RDA) (Rao 1964) was conducted on Hellinger transformed species abundance data (Griffith and Peres-Neto 2006) using the four matrices as predictors. Canonical variation partitioning (Borcard et al. 1992) was used to determine the amount of variation that could be accounted for by each of the predictor matrices. This method runs RDAs based on the full model and then subtracts the components of variation accounted for by each individual matrix, while controlling for the effects of the other matrices through partial RDAs. The analysis was conducted in R statistical software using the package ‘vegan’. The adjusted R^2 (R^2_a) for each component was then calculated (Peres-Neto et al. 2006) and compared.

Selection of best environmental model

To obtain the most parsimonious set of environmental predictors for RDA, we used model selection based on Akaike’s Information Criteria (AIC) (Burnham and Anderson 2002). A set of 102 competing models was formulated using insights from the results of RDAs described above and by building increasing levels of complexity, starting with the broader scale predictors for climate and successively adding different combinations of finer scale predictors based on topography, soil and habitat (see Appendix 4.1 for full model set). Interaction terms between climate predictors were also included.

Selection of best spatial model

Alternative spatial models representing different types and levels of connectivity were formulated based on Dray et al. (2006). Three different model sets (see Appendix 4.2 for illustration) designed to represent different dispersal scenarios were tested. The first defined links between sampling sites based on a Delauney triangulation. Inverse-distance weights were assigned to links using the formula: $1- (d/dmax)^y$. This approach maximizes linkages and therefore connectivity and dispersal across all sites.

The second set of spatial connectivity matrices was defined using a series of 50 threshold Euclidean distances to define connectivity. These distances ranged (in intervals of about 330m) from 3.5km (minimum distance required to ensure that all plots had at least one neighbour) to 20km. The range of distances was decided based on a multivariate variogram of species abundances (Dray et al. 2006). The links were weighted as indicated above. Weights formulated with values for y between 2 and 10 were tested. These models represent dispersal limitation at different distance ranges, with the likelihood of dispersal decreasing non-linearly with distance.

The third spatial connectivity matrix was designed specifically to test topographical effects on dispersal. In topographically complex terrain Euclidean distance between plots may not accurately capture connectivity if significant barriers exist. Hence we defined a connectivity matrix using binary links weighted by slope resistance (Appendix 4.2), instead of Euclidean distance. Resistance values for links between plots were derived using a Circuit Theory approach (McRae et al. 2008). A raster of slope values for the study area, derived from the DEM (resampled to 60m resolution) was used as a resistance surface. This part of the analysis was conducted using Circuitscape software v. 4.0 (McRae et al. 2009). A binary matrix with a threshold distance of 4.8km was created for all the plots. Plots ≤ 4.8 km apart received a value of '1' and those > 4.8km apart received a value of '0'. The threshold distance of 4.8 km was derived by plotting a multivariate variogram of detrended species abundances (Borcard et al. 2011). This matrix was then multiplied (using Hadamard product) by the inverse slope-derived resistance value between each pair of plots, using the same formula as above, to yield the final spatial connectivity matrix. This was done in R using the 'spdep' package.

Spatial predictors in the form of Moran's Eigenvector Maps (MEMs) were derived from each of the above spatial connectivity matrices. Only positive MEMs were selected as the intent was to model positive spatial autocorrelation between plots, driven by dispersal processes. To test competing spatial models, Hellinger-transformed species abundance data was first detrended using plot x and y coordinates, as there was a significant spatial trend present in the data (Borcard et al. 2011). RDAs were run with the detrended data as the response variable and positive MEMs derived from each of the spatial connectivity matrix models as predictors. The model with the lowest AICc values was picked as the best spatial model (Dray et al. 2006). This analysis was conducted in R using packages 'vegan', 'spdep', 'spacemakeR'.

Assessing the relative influence of environment and space

Canonical variation partitioning based on RDAs was used to assess how much of the species abundance data was explained by environment and space. The environmental and spatial models with the lowest AIC values were selected as described above. A third explanatory matrix was also added consisting of the plot x and y locations as a significant spatial trend was present in the data and had to be modelled separately (Borcard et al. 2011). The pure space and pure environment components were determined, and the significance of each of the partitions was assessed by permutation (Borcard et al. 2011).

Finally, we used the method suggested by Diniz-Filho et al. (2012) to test for the presence of unmeasured environmental variation represented in the pure space component. This was done by obtaining species abundances predicted by the pure space component (Diniz-Filho et al. 2012) and then conducting a Mantel's test between a matrix (R) representing the Pearson's correlations between these species' abundances, and a matrix (M) representing the Manhattan distances between species Moran's I correlograms. This analysis was conducted in R using the libraries 'vegan' and 'ncf'.

Results

Data for a total of 15,854 individuals belonging to 79 species, across 85 vegetation plots was used in the analysis. The number of individuals (≥ 1cm dbh) in a 0.04ha plot varied from 37 to 573, with a mean of 182 and median of 165. Species richness in the plots varied from 8 to 33 (mean = 22, median = 21). The most abundant species was a shrub represented by 2186 individuals. There were two species each represented by one and two individuals respectively. The most abundant tree species were: *Symplocos foliosa*, *Litsea wightiana* and *Neolitsea cassia*, while the most abundant shrub species were: *Psychotria nilgiriensis* and *Lasianthus venulosus*.

Relative influence of climate, topography, habitat and soil on species abundances

The results of the RDAs with each set of environmental predictors run separately indicated that all four canonical models were significant ($P < 0.05$). Hence climate, topography, habitat and soil were all important in explaining variation in species abundance. Among the climate predictors the following were significant ($P < 0.05$): an interaction between temperature seasonality and dry quarter precipitation, and annual precipitation. All of the 5 habitat terms used were highly significant ($P < 0.01$). The RDA with soil predictors indicated that simple percentage values for sand clay and soil C, and concentrations of N, Ca, Cu Al, P and Zn were also significant ($P < 0.05$). Finally, of the topographic predictors, elevation was highly significant ($P < 0.01$) with cosine aspect, TCI and slope also showing significant effects ($P < 0.05$).

Variation partitioning indicated that the 31 environmental predictors explained a significant amount of the variation in the tree and shrub abundances ($R^2_a = 42\%$, $P = 0.005$). Among these 6 climate predictors, plus an interaction term between temperature seasonality and dry quarter precipitation, were able to explain the maximum amount ($R^2_a = 26.9\%$, $P = 0.005$), followed by 5 local habitat predictors ($R^2_a = 19.5\%$, $P = 0.005$), 7 topographic predictors ($R^2_a = 14\%$, $P = 0.005$) and 12 soil predictors ($R^2_a = 11.5\%$, $P = 0.005$). Some combinations of environmental factors showed significant effects while others did not. Thus, climate and topography ($R^2_a = 6.3\%$, $P = 0.005$), and climate and habitat were important ($R^2_a = 5.4\%$, $P = 0.005$), while topography and soil was not (Fig. 4.2). Furthermore, significant ($P < 0.01$) proportions of variation were attributable purely to climate ($R^2_a = 8\%$), habitat ($R^2_a = 6\%$), soil properties ($R^2_a = 4\%$), and topography ($R^2_a = 2.8\%$). Climatic and habitat predictors were better able to explain variation in species abundance distributions compared to soil and topographic predictors.

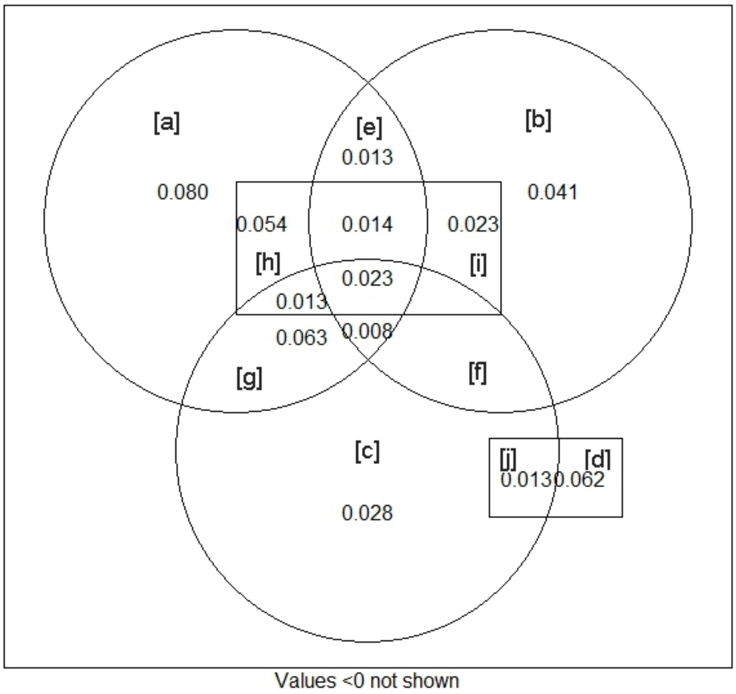

Figure 4.3: Variation partitioning results for Hellinger transformed tree and shrub abundance data with 4 explanatory environmental matrices. The enclosing box represents total variation in composition, of which 42.75% was explained by the environmental datasets The labels for the adjusted R^2 values for each of the partitions are as follows: [a] pure climate fraction, [b] pure soil fraction, [c] pure topography fraction, [d] pure habitat fraction, [e] climate + soil, [f] soil + topography, [g] climate + topography, [h] habitat + climate, [i] habitat + soil, [j] topography + habitat.

Selection of the best environmental model

The full list of 102 models that we built using various combinations of significant predictors is presented in Table S1 with AIC, ΔAIC values, model likelihood, adjusted R^2 and significance level. There were 10 models with ΔAIC < 2, indicating that they were equally good (Table 4.2). The set of predictors that performed best were: an interaction between temperature seasonality and dry quarter precipitation, slope, TCI, percent clay, N, P, Ca, Zn, log of fragment area and landscape context. Elevation, though a strong predictor on its own did not add additional explanatory power when combined with temperature and precipitation variables (Table1). The model with the lowest AIC value has an R^2_a = 40.3% (P = 0.005). Eight of the 14 RDA axes from this model are significant ($P < 0.05$) and the first 4 axes account for 30.5% of the variation.

Table 4.2: Top ten environmental models based on Δ AIC< 2, along with model likelihood, adjusted R^2 values and significance. Please refer to Table 4.1 for variable codes.

Model	**AIC**	**Δ AIC**	**Model lik**	**AIC wt**	***R^2***	***R^2adj***	***P***	**DF**
tmp.seas*prec.dryqt + ann.prec + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont	-85.65	0.00	1.00000	0.109	0.50	0.40	0.005	15
tmp.seas*prec.dryqt + ann.prec + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont + plotBA	-85.43	0.22	0.89474	0.098	0.51	0.40	0.005	16
tmp.seas*prec.cv + ann.prec + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont	-85.21	0.44	0.80148	0.087	0.50	0.40	0.005	15
tmp.seas*prec.dryqt + ann.prec + coldest.min + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont	-85.20	0.46	0.79632	0.087	0.51	0.41	0.005	16
tmp.seas*prec.dryqt + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont	-85.02	0.63	0.72879	0.079	0.49	0.39	0.005	14
tmp.seas*prec.dryqt + coldest.min + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont	-84.86	0.79	0.67326	0.073	0.50	0.40	0.005	15
tmp.seas*prec.dryqt + Slope + TCI60 + elev + Nperc + perc.clay + P + Ca + Zn + ln.area + LS.cont	-84.59	1.07	0.58697	0.064	0.50	0.40	0.005	15
tmp.seas*prec.dryqt + Slope+ TCI60 + elev + Nperc + perc.clay + P + Ca + Zn + Cu + ln.area + LS.cont	-84.18	1.47	0.47837	0.052	0.51	0.40	0.005	16
tmp.seas*prec.dryqt + Slope+ TCI60 + elev + Nperc + perc.clay + P + Ca + Zn + Cu + ln.area + plotBA + LS.cont	-83.93	1.72	0.42293	0.046	0.52	0.40	0.005	17
tmp.seas*prec.dryqt + coldest.min + Slope + TCI60 + Nperc + perc.clay + P + Ca + Zn + ln.area + plotBA + LS.cont	-83.84	1.82	0.40346	0.044	0.49	0.39	0.005	16

Temperature seasonality, fragment area, dry quarter precipitation, Ca and N influence the distribution of sites along the first RDA axis (Fig. 4.4), indicating an association with small forest patches at high elevation. This axis is positively correlated with *Litsea wightiana*, *Psychotria nilgiriensis* and *Symplocos foliosa* abundance (Table 4.3). The second axis is positively correlated with P, Ca, and temperature seasonality, while negatively correlated with dry quarter precipitation and log fragment area (Fig. 4.4). Species strongly negatively correlated with this axis are *Saprosma ceylanicum*, *Cryptocarya lawsonii* and *Psychotria nilgiriensis* (Table 4.3). Indicating that these species have higher abundances in lower dry season rainfall areas, within large fragments with relatively nutrient poor soil. RDA 3 is positively correlated with annual precipitation and TCI and negatively correlated with a landscape context of tea and the interaction between temperature seasonality and dry quarter precipitation. This axis is correlated with *Neolitsea* sp. and *Nothapodytes nimmoniana* (Table 4.3). RDA 4 is influenced by landscape context, mainly separating sites surrounded by *Acacia mearnsii* plantation from those surrounded by tea. It is also positively correlated with N levels and negatively correlated with Zn. This axis is positively associated with shrub species *Psychotria nilgiriensis* and *Lasianthus venulosus*, which have higher abundances in wattle sholas.

Table 4.3: Species with the ten highest scores on first four RDA axes of the best environmental model. Names listed in decreasing order based on the absolute value of the score. Negative scores are indicated in brackets.

RDA1	**RDA2**	**RDA3**	**RDA4**
Litsea wightiana	*Saprosma ceylanicum* (-)	*Neolitsea cassia* (-)	*Psychotria nilgiriensis*
L. stocksii (-)	*Cryptocarya lawsonii* (-)	*Nothopodytes nimmoniana*	*Saprosma ceylanicum* (-)
Psychotria nilgiriensis	*Psychotria nilgiriensis* (-)	*Neolitsea scrobiculata* (-)	*Lasianthus venulosus*
Symplocos foliosa	*Litsea wightiana*	*Isonandra perottetiana* (-)	*Meliosma simplicifolia* (-)
Cestrum aurantiacum (-)	*L. stocksii*	*Symplocos macrocarpum*	*Litsea wightiana* (-)
Mahonia leschenaultii	*Lasianthus venulosus* (-)	*Saprosma ceylanicum*	*Cinnamomum wightiana* (-)
Litsea floribunda (-)	*Mahonia leschenaultii*	*Casearia thwaitesii*	*Casearia thwaitesii*
Lasianthus venulosus	*Cinnamomum macrocarpum* (-v)	*Cryptocarya neilgherrensis* (-)	*Cryptocarya lawsonii* (-)
Syzygium montanum	*Nothopodytes nimmoniana*	*Excoecaria oppositifolia* (-)	*Neolitsea cassia* (-)
Actinodaphne bourdillonii (-)	*Litsea floribunda* (-)	*Litsea floribunda*	*Cinnamomum* sp.

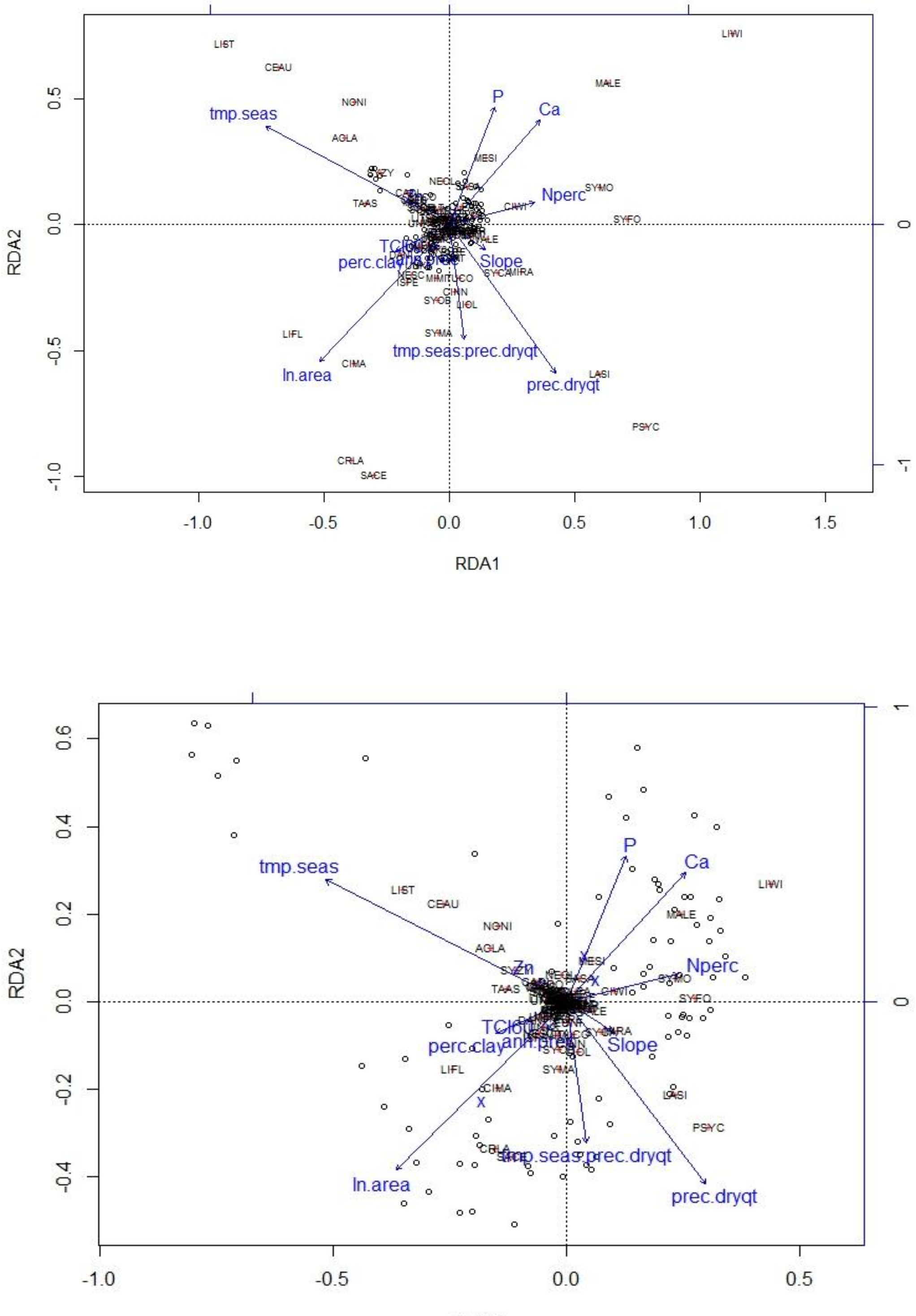

Figure 4.4: Triplots of RDA axes 1 & 2 of Hellinger transformed tree and shrub data constrained by predictors from the best environmental model. Top panel represents the distance biplot (scaling 1) using weighted average scores. Bottom panel represents the correlation biplot (scaling 2) with site scores as open circles.

Selection of best spatial model

The best spatial model in the RDAs between the detrended Hellinger-transformed species data and the respective MEMs, was a model that linked sites at a distance threshold of 4.8 km (Appendix 4.2) and had an inverse distance weighting on the links using the formula 1-(d/dmax)^2. This model yielded the lowest AICc values (Table 4.4) and had 10 positive MEMs (Fig 4.5). The Delauney triangulation models performed the worst, indicating that spatial predictors based on maximum spatial connectivity across all sites and therefore unlimited dispersal, did not model variation in the detrended species abundances as well as the other models. The models derived from slope resistances did not perform as well as the ones based on simple Euclidean distance weights using a threshold for connectivity.

Table 4.4: Competing spatial models with AICc values and number of spatial predictors derived (in the form of positive MEMs). Only variants of the best distance threshold model are shown (i.e. models with threshold = 4.8km)

S.no	Spatial Model	AICc	weight type	No. MEM pred
1	Links thresholded at 4.8 km with inverse Euclidean distance weights	-89.870	1- $(d/d_{max})^2$	10
2	Links with 4.8 km threshold	-88.193	None	8
3	Links thresholded at 4.8 km with inverse slope resistance weights	-87.927	1- $(slope.res/slope.res_{max})$	11
4	Links thresholded at 4.8 km with inverse slope resistance weights	-87.031	1- $(slope.res/slope.res_{max})^2$	8
5	Links thresholded at 4.8 km with slope resistance weights	-83.752	slope resistance	6
6	Inverse Euclidean distance weighted links based on Delauney triangulation	-82.105	1- $(d/d_{max})^2$	6
7	Links based on Delauney triangulation	-81.821	None	8

Relative influence of environment and space on species abundances:

Variation partitioning conducted with 3 predictor matrices: best environmental model, best spatial model, and the spatial coordinates (x, y) of plots, indicated that environmental and spatial predictors together explained 50.8% of the variation in the undetrended tree and shrub data (Fig. 4.6). The environmental variables explained 40.3% of the variation, of which only 5.5% is not spatially structured (pure environment). This fraction likely represents the effects of local environmental conditions. The remaining fractions (Fig. 4.6) represent spatially structured environmental variation (total 27.4%) and are indicative of induced spatial

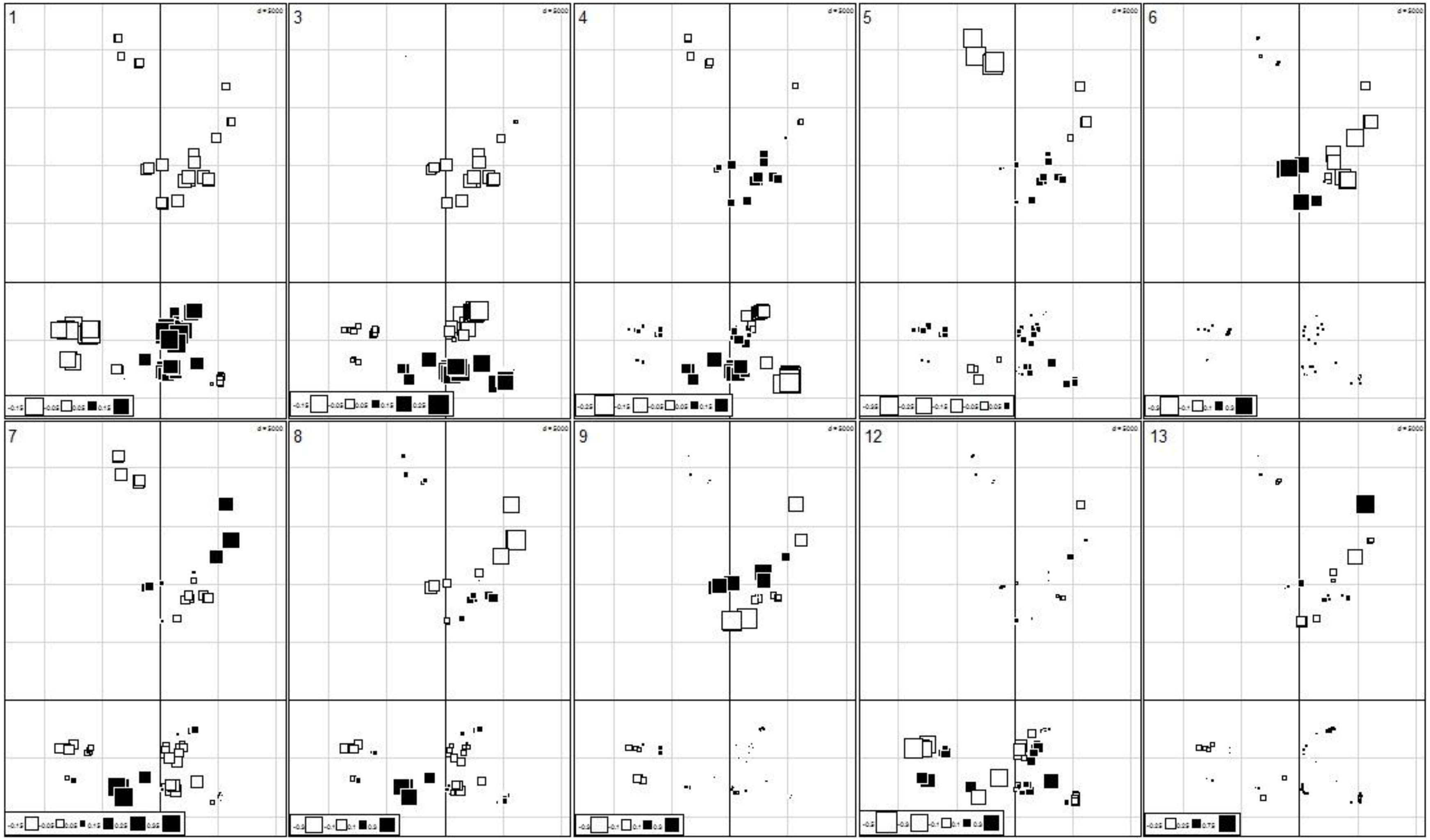

Figure 4.5: Maps of 10 positive Moran's Eigenvectors (MEMs) from the best spatial model (i.e. Euclidean distance threshold of 4.8 km with inverse distance weighted links). Black squares represent positive spatial autocorrelation while white squared represent negative spatial autocorrelation. The size of the squares correspond to the magnitude of the correlation

variation. The pure environment fraction ($R_a^2 = 5.5\%$) and pure spatial ($R_a^2 = 9.4\%$) fraction are both significant ($p < 0.01$), while the pure spatial trend is very small and non-significant, and shows overlap with environmental predictors (Fig. 4.6). The spatial predictors alone account for less than 10% of the variation.

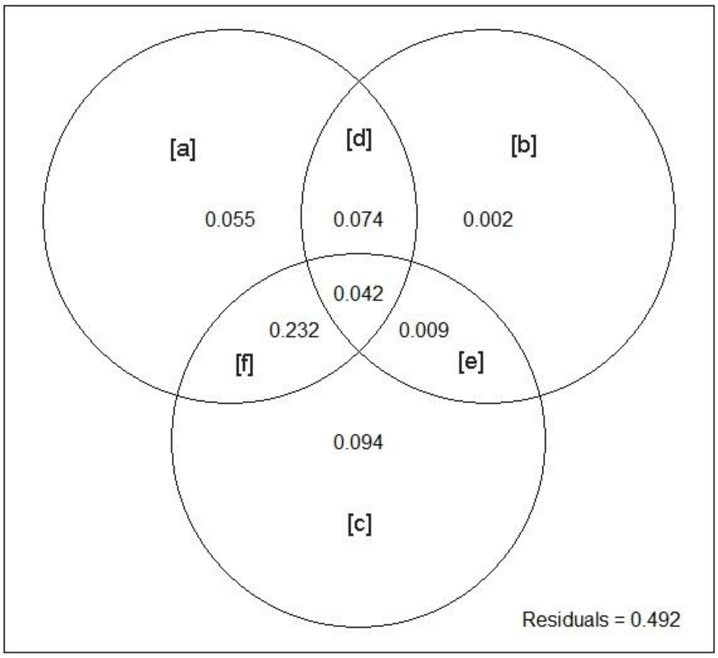

Figure 4.6: Variation partitioning results for Hellinger transformed tree and shrub abundance data with space, environment and plot (x,y) locations. The enclosing box represents total variation in composition, of which 50.8% was explained by the environmental, plot x.y locations and spatial (MEM) data. The labels for the adjusted R^2 values for each of the partitions as follows: [a] pure environmental fraction, [b] pure spatial trend fraction, [c] pure MEM fraction, [d] joint environment and spatial trend fraction, [e] MEM + spatial trend, [f] environment + MEM.

The Mantel's test between the matrix containing the correlations between predicted species abundances (using the pure space component) and another matrix containing the Manhattan distances between Moran's I correlograms for each of the species was non-significant ($r_M = - 0.048$, $p = 0.99$). This indicates that the variation attributed to the pure space component is unlikely to be confounded by unmeasured environmental variables (Fig.4.7).

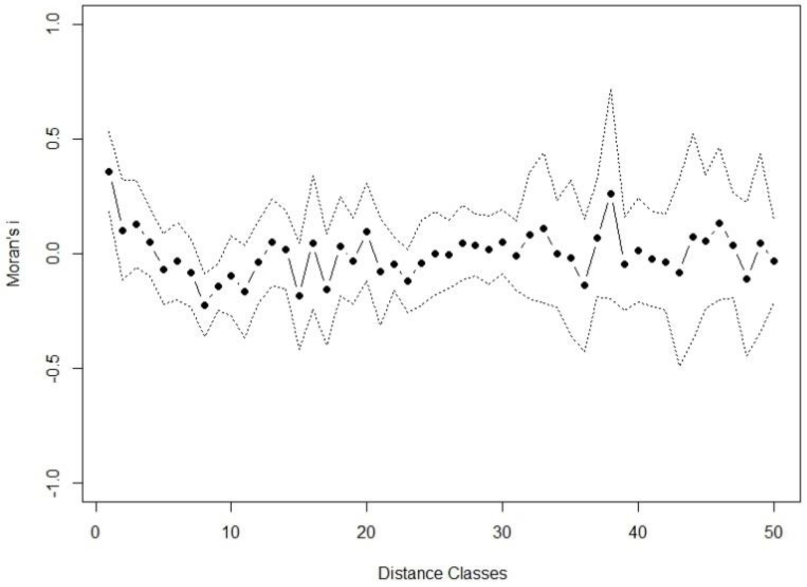

Figure 4.7: Correlogram showing the average Moran's I value for a given distance class. Moran's I calculated based on predicted abundances of 79 tree and shrub species using the pure spatial component from variation partitioning. Increment between distance classes is approximately 620m. Dashed lines represent 1 standard deviation from the mean.

Discussion

This study investigates the importance of environment, space, history, and biotic factors in the organization of plant communities in a unique landscape of montane tropical forest in the Western Ghats of India. The results clearly show that environment, historical factors and space accounted for about half the total variation in shola tree and shrub abundances among sample plots distributed over a 600 km^2 area. The total variation explained in this study is high compared to some studies where both edaphic and topographic predictors were used (Svenning et al. 2004, Jones et al. 2008), and within the range of results found for smaller intensely mapped study areas (24-50 ha) across lowland tropical forests (Baldeck et al. 2012). Although direct comparison of variation partitioning results across studies that differ in scale, spatial structuring of environment and species life-history is not recommended (Smith and Lundholm 2010), the high explanatory power of this analysis may reflect the attempt to include all the important factors that potentially influence plant distributions and abundance.

Importantly, the results demonstrate strong evidence of spatially induced variation in plant community structure. The major influence must therefore arise from spatially structured environmental variation and its interaction with limited dispersal (Smith & Lundholm 2010, Garzon-Lopez et al. 2014). However, at least 9% of the variation in species abundances can be attributed to spatial processes alone (i.e., not due to unmeasured environmental factors) and this is most likely due to dispersal limitation. Thus it could be concluded that dispersal limitation has a relatively small role in determining the extant plant community structure in this landscape, a finding that is consistent with observations that these forest mosaics are tens of thousands of years old (Caner et al. 2007).

Environmental and historical factors that influence shola species abundance

Climate was the most influential environmental factor followed by habitat and then soil. Previous studies had found a strong relationship between variation in climate and tree species distributions at large spatial scales in the Western Ghats (Davidar et al. 2007, Ramesh et al. 2010). The results show that in topographically complex terrain, at high elevations, climate influences species distributions even at scales on the order of tens of kilometres. The elevation-temperature gradient in the study area drives much of the variation in species composition from north to south. Its interaction with the west-east precipitation gradient can explain why the northwestern plots show the greatest difference in species composition with the southeastern ones. Therefore gradients and interactions of temperature and precipitation that shape tree species distributions at regional scales across the entire Western Ghats (Davidar et al. 2007) also affect plant community structure within a single habitat type at much smaller scales, albeit in topographically complex terrain. It should also be noted that the study area covers the high elevation end of the elevation-temperature gradient in the Western Ghats, where many tropical evergreen tree species are at their range boundaries (Ohsawa 1991). Therefore species abundances may respond relatively strongly to changes in precipitation and seasonality in this landscape.

Moisture availability for vegetation may further act through the frequency and duration of mist immersion, a factor that is not fully captured in precipitation data. Such non-precipitating moisture inputs is known to play a critical role in determining dry-season moisture availability in tropical mountains (Goldsmith et al. 2013, Oliveira et al. 2014). Although dry-quarter precipitation does vary between sites in the study area - with lower values for the western edge of the plateau and higher in the southeastern parts - the specific importance of mist immersion needs further investigation.

Apart from the major influence of climate, historical factors appear to have a substantial influence of plant distributions (Svenning et al. 2004, Ramesh et al. 2010, Garzon-Lopez et al. 2014), and this is reflected in the importance of patch area and landscape context. It has been shown that patch size affects both the structure and composition of *sholas* (Mohandass and Davidar 2010). The results are consistent with this observation, and while species such as *Litsea wightiana*, *Symplocos foliosa*, *Mahonia leschenaultii* and *Syzygium grande* are most abundant in the smaller patches, *Cryptocarya lawsonii*, *Cinnamomum macrocarpum*, *Saprosma ceylanicum* and *Litsea floribunda* achieve highest abundance in the largest patches. Life histories of tree species in this region have not been studied in detail, but shade tolerance could be one possible mechanism causing the patch size effect on species composition. Seedling and sapling survivorship in shade is an important influence on species distributions in tropical forests (Svenning et al. 2004, Comita and Hubbell 2009). Smaller patches experience higher influence of edge habitat (Bunyan 2009), which explains the dominance of at least *Litsea wightiana* in these patches (Mohandass and Davidar 2010). *Mahonia leschenaultii*, a species with temperate affinity, is frost-resistant (Meher-Homji 1967) - possibly enabling it to compete better in smaller, ‘edgier’ *sholas*.

Landscape context is confounded with climate, and decisions on the establishment of monoculture exotic tree and tea plantations are influenced by local climate. In addition, plots in sholas surrounded by the nitrogen fixing *Acacia mearnsii* plantations (Forrester et al. 2007) showed higher average values for total soil N, while plots located in a matrix of tea plantations showed higher average P concentrations. Plots in grassland *sholas* had higher concentrations of Al, indicating lower pH levels. Although these differences in soil properties are correlated with differences in abundance of some species, other factors may be also involved in driving broader community-level differences. Thus while *Symplocos foliosa* and *Syzygium grande* were dominant in higher N sites, *Meliosma simplicifolia* and *Neolitsea cassia* were common in higher P sites. An invasive shrub *Cestrum aurantiacum* was most abundant in *sholas* surrounded by tea, followed by wattle plantation sholas and was absent in grassland sholas, but the exact reason for these differences are unknown. The canonical model results show that the effects of landscape context persisted even after accounting for the effects of all environmental predictors. Changes in other factors associated with landscape context, such as disturbance frequency or movement behaviour of seed dispersers (Morales et al. 2013) could also influence species abundances through their effects on regeneration and recruitment.

The importance of total soil N in explaining variation in abundances is supported by findings that high-elevation tropical montane cloud forest soils are N limited (Fisher et al. 2013). *Litsea wightiana* appears to be more dominant in sites with lower total soil N, while *Symplocos foliosa* and *Neolitsea cassia* are more dominant in sites with higher total soil N. Phosphorous limitation is reported to be greater in low-elevation tropical forests, with P availability increasing with elevation in some places (Tanner et al. 1998, Fisher et al. 2013). However, overall P concentrations for the study area seem very low, probably in part due the region's non-allophanic Andisols that are known to have high P retention (Caner et al. 2000), reducing P availability to plants. Species correlated with low P concentrations are *Turpinia cochinchinensis, Symplocos obtusa* and *Syzygium calophyllifolium*, while species correlated with higher P concentrations include *Litsea wightiana*, *Mahonia leschenaultii* and *Casearia thwaitesii.* High Ca concentrations were positively correlated with *Meliosma simplicifolia*, *Saracocca saligna*, *Nothopodytes nimmoniana* and *Isonandra perotettiana* abundances and low Ca concentrations with the abundance of *Microtropis ramiflora, Symplocos macrophylla* and *Vaccinium leschenaultii*. Studies in lowland tropical forests have also found P and Ca to be important in explaining species distribution patterns (Paoli et al. 2006, John et al. 2007, Guèze et al. 2013). Apart from soil nutrients, soil texture (percent clay content), a factor that affects water retention, was important for some species (e.g., *Cinnamomum macrocarpum* and *Litsea stocksii*).

Surprisingly, other than elevation, topographic variables were the least important environmental predictors. Although many studies have found topography to have a strong influence on species abundance patterns, they typically used only topographical predictors within a 25-50 ha scale that were derived using 20m resolution data (Legendre et al. 2009, De Cáceres et al. 2012, Brown et al. 2013). It is possible that the topographical analysis presented here (180 m – 90 m; using a 30m DEM) was too coarse to capture its effects on vegetation measured at the 20m scale. Variation in relative topographic position (within a 180 m neighbourhood), aspect, and surface curvature (over a 90 x 90m neighbourhood) do not seem to influence the distribution of shola species. However, abundances of *Nothapodytes nimmoniana, Symplocos macrocarpum, Saprosma ceylanicum, Casearia thwaitesii* and *Litsea floribunda* are positively correlated with topographic wetness (TCI) at intermediate spatial scales, while slope measured at the plot scale is correlated with *Meliosma simplicifolia* and *Vaccinium leschenaultii* abundance.

RDA-based variation partitioning

Recent simulation studies have questioned the ability of variation partitioning approaches to reliably assess the relative importance of niche and neutral processes (Smith and Lundholm 2010, Gilbert and Bennett 2010). Gilbert & Bennett (2010) found that the RDA-based method tends to underestimate the environmental signal in the data, while over-fitting and inflating the importance of space. The former is due mainly to the limitations of RDA in modelling non-linear species-response curves (Austin 2002, Gilbert and Bennett 2010). I plotted species abundances against important environmental predictors such as elevation and precipitation for the common species and found that in many cases, the response could be approximated by a linear relationship. While this might simply indicate that the environmental gradient sampled here was not large enough to encompass the ranges of most of the study species, the observed linear responses does minimise potential problems with RDA-based analyses. Furthermore, using polynomial transformations of precipitation and log transformations of soil predictors as suggested by (Jones et al. 2008) did not improve the explanatory power of the models (analysis not shown). Therefore the nature of species response curves in this study is unlikely to cause inefficiency or bias in RDA analyses. Since I did not use forward selection analyses, the tendency of MEMs to inflate the proportion of variation accounted for by space is not important (Mundry and Nunn 2009, Gilbert and Bennett 2010).

Interpretation of the pure space component

In variation partitioning studies, the component of variation explained by pure space is most often interpreted as driven by dispersal limitation. In this study I found that a threshold-based and inverse-distance weighted spatial connectivity model performed best in terms of predicting patterns of positive spatial autocorrelation in species abundances. Furthermore, Mantel analyses showed no significant effects of unmeasured spatially structured environmental variables. Therefore I interpret the Euclidean distance-weighted connectivity as a direct measure of the effect of pure space, while the threshold value (here ~4.8 km) appears to indicate an important breakpoint in connectivity between sites in this landscape. Such thresholds could be determined by specific aspects of the topography or the landscape influencing movement of dispersers.

The irregular sampling scheme necessitated in this study prevents the direct interpretation of scale for the spatial predictors used (Borcard et al. 2011), which is indeed a disadvantage. A regular sampling scheme was not feasible in this habitat, given the patchy nature of the forests and the fact that most patches are relatively small and are very irregularly distributed in space. An increase in the proportion of closely spaced plot pairs (≤ 100m apart) may however improve the ability to model dispersal-based processes at this spatial scale.

Possible factors contributing to unexplained variation

Given the large spatial extent of this study, low gamma diversity and high environmental variability, we would have expected the amount of unexplained variation to be lower (De Cáceres et al. 2012, Brown et al. 2013). However substantial variation in species abundances remains unexplained, and some unaccounted factors such as disturbance and historical events may in part be responsible. At broader spatial scales, environmental factors such as wind speed and mist immersion that are important in for montane cloud forests (Goldsmith et al. 2013), were not considered due to lack of data. At intermediate and fine spatial scales, effects of temporal variation in environmental factors such as soil nutrients and moisture (Jones et al. 2008) and the stochastic effects of colonization and gap dynamics could also contribute to unexplained variation (Condit et al. 2002).

Despite these limitations, this study compares well in terms of the comprehensive environmental dataset that could be directly measured and also extracted from secondary sources, when most other studies have relied mainly on topographical predictors (Chang et al. 2013). It is also one of the few studies that has used spatial eigenvectors in a hypothesis testing framework and introduces a novel approach combining Circuit Theory and MEMs to model dispersal in topographically complex terrain.

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Chapter 5

Effects of Conversion of Landscape Matrix from Grassland to Tea and Exotic Tree Plantation on the Shola Tree and Shrub Community in the Upper Nilgiris

Introduction

Fragmentation studies have only recently begun to move away from the patch-island paradigm to investigate the role of the landscape matrix in influencing ecological processes (Driscoll et al. 2013). Rather than viewing the landscape matrix as an inhospitable ‘ocean’ surrounding ‘islands’ of natural habitat, ecologists are now examining the effects of the matrix on processes such as dispersal, pollination and disturbance (Kupfer et al. 2006, Debinski 2006, Bennett et al. 2006, Gardner et al. 2009). Anthropogenic conversion from one matrix land cover type to another does not always result in loss of habitat, or even in the breaking apart of existing habitat (i.e. fragmentation (*sensu* Fahrig 2003), but it may still affect ecological processes at the landscape level, thereby altering resource availability, functional connectivity (Ricketts 2001) and abiotic environments in and around habitat patches (Driscoll et al. 2013).

Studies have found evidence that processes which drive patterns of species abundance and distribution within natural communities are strongly affected by the surrounding landscape matrix (Prugh et al. 2008, Prevedello and Vieira 2010, Watling et al. 2011, Magrach et al. 2012). Watling et. al.’s (2011) meta-analysis found that for 63 studies on terrestrial vertebrate abundance and occupancy, the effect of predictors based on matrix composition was greater than that of binary (habitat-non habitat) predictors. Significant differences in effect sizes across levels of matrix heterogeneity were also found for both abundance and occupancy measures. Their results supported the findings of Prugh et al. (2008), which indicate patch area and isolation alone are poor predictors of occupancy among animal populations; and that landscape context has “*a strong effect on occupancy patterns across many taxonomic groups and ecosystems worldwide*” (Prugh et al. p.20773). Simulation studies indicate that even a small difference in the matrix interaction can significantly affect the chances of survival and persistence for plant metapopulations in a landscape (Loehle 2007).

In the case of plants, the processes that cause these changes include: alteration of edge habitats (Laurance et al. 2011, González-Moreno et al. 2013), increased frequency of disturbances such as fire, grazing and trampling within habitat patches (Laurance et al. 2011), disruption or alteration of plant-animal interactions - through change in herbivore, disperser and pollinator communities and behaviour (Bender and Fahrig 2005, Aguilar et al. 2006, Prugh et al. 2008, McConkey et al. 2012) - and finally, increased competition with invasive exotics (Murphy and Lovett-Doust 2004, González-Moreno et al. 2013). Apart from the effect of each of these processes in isolation, complex and synergistic interactions between them can cumulatively cause major shifts in natural plant communities (Ries et al. 2004, Laurance et al. 2011, Driscoll et al. 2013). For instance, anthropogenic change in landscape context surrounding a forest patch could simultaneously increase its susceptibility to invasion, as well as increase invasive propagule pressure (Didham et al. 2007, González-Moreno et al. 2013).

Importance of naturally fragmented systems for studying impacts of matrix conversion: the shola-grasslands of the Upper Nilgiris

Naturally fragmented forest systems such as the *sholas* of the Western Ghats offer a unique opportunity to study the effects of anthropogenic matrix conversion in a context in which it is far less confounded by other aspects of anthropogenic fragmentation such as habitat loss or partitioning (Ewers and Didham 2006). The *shola*-grassland system is comprised of discrete patches of forest habitat surrounded by a relatively homogenous and structurally distinct matrix of grasslands. Species distributions, interactions and ecological processes are likely to have equilibrated across fragments in these systems over many hundreds of generations (for trees). Subsequent conversion of the natural grassland matrix to exotic tree plantations and tea estates, particularly over the last 100 years (Prabhakar 1994), is very likely to have disrupted this equilibrium in complex and unpredictable ways (Driscoll et al. 2013). For instance, such conversion could have a ‘reverse fragmentation effect’ on processes such as seed dispersal by increasing frugivore density through the introduction of generalist frugivores that are commensal with humans. Conversely, it could also decrease functional connectivity by diverting frugivore movement into matrix habitats, thereby increasing seed rain in these areas, as opposed to within forest patches. Edge effects would certainly be altered, especially in those areas where grassland was converted to wattle (*Acacia mearnsii*) plantations, leading to reduced light, lower wind stress and increased moisture at the forest edge (Bunyan 2009). As this is a naturally fragmented system, several endemic tree and shrub species are adapted to the *shola*-grassland edge (Meher-Homji 1967) and alteration of edge conditions through matrix conversion could impact their distributions.

One obvious and widely acknowledged effect of matrix conversion has been the increase in invasive alien species in the remnant grasslands (Thomas and Palmer 2007, *Personal observation*). In fact, one of the main species of plantation exotics, *Acacia mearnsii,* has been recognized as an aggressive invader of montane grasslands (Thomas and Palmer 2007). However, far less conservation and research attention has been paid to the invasion of *shola* forest patches.

Cestrum: a montane forest invasive in the Upper Nilgiris

The genus *Cestrum* in the Family Solanaceae has 175 known species of shrubs, vines and small trees (de Rojas and D’Arcy 1998, Cuevas-Arias et al. 2008, Monro 2012). The native range for this genus is Central and South America (Monro 2012). Here most *Cestrum* species occur in montane areas, above 800m elevation, in cloud forests and conifer and oak forests (de Rojas and D’Arcy 1998, Cuevas-Arias et al. 2008, Monro 2012). The abundant, attractive and often fragrant flowers of this genus are the reason it has been introduced as an ornamental plant in many regions, where it has subsequently become naturalized, and in several cases, turned invasive in parts of Australia, South and east Africa, Reunion Islands, South Asia, the Pacific islands, Galapagos and Hawaii (PIER 2005, Henderson 2007, Harvey et al. 2012, Gardener et al. 2013, USDA 2013). These species include: *Cestrum laevigatum* Schltdl., *C. parqui* (Lam.) L'Hér., C. *auriculatum* L'Hér., *C. diurnum* L., *C. nocturnum* L., *C. elegans* (Brongn. ex Neumann) Schltdl.**,** and *C. aurantiacum*.

Most of these species bear berries with small seeds that remain viable in the seed bank and are bird dispersed (Marambe et al. 2001, Geldenhuys 2004, Gardener et al. 2013). They are fast-growing, capable of vegetative reproduction (Symon 1981) and tend to form dense mats which can suppress the regeneration of other plant species (USDA 2013). They are also known to be shade-tolerant (Geldenhuys 2004), drought-tolerant, capable of growing on poor soils and have invaded a range of habitats from coastal dunes to savannahs, grasslands, plantations and closed forest (Henderson 2007). Most are quite toxic to livestock and native mammals (de Rojas and D'Arcy 1998, Juyal and Ghildiyal 2013, USDA 2013). For these reasons, they are labelled as noxious weeds with moderate to high invasive potential (Nel et al. 2004, PIER 2005, Henderson 2007, USDA 2013). In South Africa and Australia extensive programs have been undertaken to clear areas of *Cestrum* species (MacDonald and Jarman 1985, Stockard and Shepherd 1996, Marais and Wannenburgh 2008).

Cestrum diurnum, *C. nocturnum*, *C. elegans* and *C. aurantiacum* are reported from many parts of the Indian subcontinent and Sri Lanka, including the Kashmir (Bano et al. 2013) and Nepal Himalayas (Kunwar 2003), Darjeeling (Moktan and Das 2012) and the Western Ghats (Saravanan et al. 2014). In the Western Ghats, Sri Lanka and Darjeeling Himalayas, *Cestrum aurantiacum* and *C. elegans* are reported as invasive weeds (Marambe et al. 2001, Moktan and Das 2012, Sajeev et al. 2012, Saravanan et al. 2014). However no comprehensive effort to study their distribution and impact on native vegetation has been undertaken.

These species seem to occur at higher elevations, between 1500 to above 2000m (Marambe et al. 2001, Moktan and Das 2012, Sajeev et al. 2012, *Personal observation*), and in the Nilgiris have successfully invaded native forest fragments and the understorey of tree plantations (Saravanan et al. 2014, *Personal observation*). They appear to have spread from settled areas and tea plantations, where their abundance is highest (*Personal observation* for Nilgiris) and were likely imported as ornamental plants for the managers' bungalows. *Cestrum aurantiacum* is the more abundant species and where it occurs in large numbers under native forest canopies, seems to dominate the understorey with little native regeneration apparent below it. It appears to be well adapted to the cloud forest environment in its native range in Guatemala and Nicaragua (de Rojas and D'Arcy 1998, Monro 2012), which would allow it to spread from open environments and thrive in the dense shade of *shola* fragments.

Objectives

In this chapter I investigate whether matrix conversion from natural grassland to tea and wattle plantations has had an impact on *shola* plant communities by assessing whether *shola* patches embedded within different landscape matrix types differ in community composition, population structure of tree and shrub species and soil characteristics. I also assess factors related to *Cestrum* invasion and its effects on regeneration of *shola* trees. I discuss possible ecological pathways through which the altered matrix has affected *shola* vegetation in the context of the conceptual framework proposed by Driscoll et al. (2013). My specific objectives can be listed as follows:

i) Assess differences in patterns of species richness and dominance, stand structure and tree size class distribution across *sholas* in the different landscape contexts.
ii) Assess whether *sholas* in different landscape contexts also differ in terms of soil characteristics.
iii) Examine causes of *Cestrum* invasion in *sholas* surrounded by tea plantations and consequences for regeneration of native species.

Methods

Study area

The study area of approximately 600km^2, is located between 11.17^{o}N, 76.77^{o}E and 11.50^{o}N, 76.43^{o}E on the Upper Nilgiri Plateau (1800-2630m elevation). Most of the survey was conducted on the western and south western parts of the plateau that contain the largest stretches of intact *shola*-grassland mosaics (please see Figure 4.1 in Chapter 4 for a map of the study area). *Shola* forests extend from 1500-2590m (Ranganathan 1938). This region is rich in endemic plants. Blasco (1971) has recorded 223 plant species known only from the *sholas* and grasslands of the higher altitude ranges of the Western Ghats. Fifty-three percent of the tree and shrub species in the study area are endemic to the Western Ghats. Most tree and shrub species have zoochorous dispersal with birds and mammals being the main dispersal vectors (Ganesh and Davidar 2001). There are a few wind dispersed species such as *Rhododendron* and *Gordonia obtusa*, however their abundances inside *shola* patches is relatively low. Patch size in the study area varies widely with few very large patches (>100 ha) and several smaller patches (< 10 ha). A detailed description of the climate, geology and soils of the study area can be found in the preceding chapters.

The area is very sparsely populated, and falls under Reserved Forests and also a National Park. Major land cover types are: exotic tree plantations (*Eucalyptus* sp. and *Acacia mearnsii*), agriculture, tea plantation, and *shola*-grassland (Prabhakar 1994). There is evidence that the grasslands have a climatic origin that pre-dates human settlement (Sukumar et al. 1995, Caner et al. 2007). Over the last 150 years, vast stretches of grassland were converted to monoculture exotic tree and tea plantations. One of the plantation species, *Acacia mearnsii* (black wattle), has subsequently invaded large areas of grassland. Most of the conversion to wattle has occurred over the last 70 years (Prabhakar 1994).

Vegetation sampling

A detailed description of the sampling design and data collected from vegetation plots can be found in Chapter 4. In large *shola* fragments (≥ 60 ha), three transects of plots were placed at a minimum of 250m apart, with a distance of at least 50m between each plot along the transect, where possible. One large fragment in each landscape context was sampled. Two transects of four 1x1m seedling plots each were laid across each vegetation plot. All seedlings within these plots were censused. Sampling effort was not equal across all three landscape contexts, owing to their unequal distribution across the region. While there are many *sholas* located within wattle plantations, there are far fewer within grasslands and tea plantations (please see Figure 4.1).

Soil sampling and analysis

Please see Chapter 4 for description of soil data collection in the field. In the lab, soil samples were processed and texture was measured using the hydrometer method (Sheldrick & Wang 1993; see Chapter 4 and Appendix 4.1 for protocol). Most of the plots had soil texture that varied from loamy sand to sandy loam. The mean sand content was 75.13% ± 5.67, mean silt content was 16.75% ± 4.34 and mean clay content was 8.11% ± 2.95. The colour of the samples varied greatly from light brown to very dark brown (almost black). There was also high organic matter content consisting of fine roots or leaf and bark fragments in the samples. Total soil carbon and nitrogen was measured using a C/H/N analyzer (LECO). Approximately 10g of soil from each plot was first ground to pass through a fine mesh sieve (0.25mm). Approximately 0.15g of this was used for the LECO analysis. Each batch of samples was processed along with a blank as well as a set of known soil standards to calibrate the readings. The results show that the average percent carbon in the samples was 11.27% ± 3.68 and the average percent nitrogen was 0.86 ± 0.22.

The Mehlich III extraction protocol (Trans and Simard 1993) was followed to measure exchangeable soil cation concentrations. The Mehlich extracts were analysed using ICP-

Optical Emission Spectrometry (Thermo Fischer ICAP 6000 series). Mehlich extraction was conducted on the dried archived soil samples rather than fresh soil as I did not have access to lab facilities during field sampling. However, after drying and preparation the soil samples set aside for nutrient analysis were kept refrigerated. The readings for potassium were unusually high for several plots and further investigation indicated an error in the ICP readings for potassium in two batches of sample runs. Therefore potassium data was not used in further analysis.

Soil data was not collected in 9 of the vegetation plots. For 7 of these plots, inverse-distance interpolation was used to estimate soil texture values and kriging was used to estimate soil cation concentrations. As one of the sites was located far apart from the others, it was not possible to get good estimates for soil predictors for this sites. It was therefore dropped from the dataset and not used in further analysis. This analysis was done in R statistical software v.3.0.2 (R-Development-Core-Team 2013) using the ‘GeoR’ package.

Environmental Data Collection

Habitat variables describing plot characteristics (*shola* fragment area, topography, climate) were extracted using ArcGIS v.10.0 (ESRI 2011) and Google Earth (Google Earth 2013).Variables were plotted to check their distribution and transformed as necessary. Pearson’s *r* was also calculated to assess which of the variables were highly correlated. The ASTER Global Digital Elevation Model (GDEM) v.2 tiles (30m contour interval) (METI and NASA 2011) for the study area were used to extract the following topographic predictors in ArcGIS using Spatial Analyst and Topography toolbox: elevation, slope and distance to stream, which was used as a proxy for soil moisture (Lookingbill and Urban 2004). Bioclimatic predictors were downloaded from the BIOCLIM global dataset, available at 1km resolution (Hijmans et al. 2005).

Data analysis

Species richness was estimated and diversity indices such as Shannon’s, Simpson’s and Fisher’s alpha (Magurran 2004) were calculated for each landscape context. Plots below 2000m elevation were removed from this analysis. Sample-based rarefaction curves with the x-axis standardized to number of individuals (Gotelli and Colwell 2001) was plotted using the Mao-Tau estimator as implemented in the software EstimateS (Colwell 2013). As the number of grassland *shola* plots was the lowest (*n* = 18), data from the wattle (*n* = 41) and tea *sholas* (*n* = 22) were rarefied to the level of individuals sampled in grassland *sholas* in order to make comparisons of species diversity. Morisita-Horn Index was used to assess the degree of species overlap among the grassland *sholas* and among *sholas* in wattle that occurred above 2000m elevation and in the same rainfall zone (please see Figure 4.1 in Chapter 4). This index of beta diversity was chosen as it is not affected by unequal sample sizes (grass *n* =18 and wattle *n* = 35) (Wolda 1981). The tea estate *sholas* were excluded from this analysis as they occurred in a different rainfall zone (Figure 4.1). Finally, to assess differences in species composition the Importance Value Index (IVI) of each species was calculated for the set of *sholas* (above 2000m) in each landscape context (Ganesh et al. 1996), to compare which species were dominant in each of the landscape contexts.

Stand structure within plots was characterized by number of stems per plot, basal area of the plot, mean dbh of plot, number of large trees (> 40cm dbh), number of seedlings, number of saplings, number of shrubs (belonging to *Psychotria* or *Lasianthus*) and finally number of dioecious individuals present. GLMs with a Poisson error term were used to test whether each of these structural characters differed significantly between the three landscape contexts, after accounting for the effects of elevation (m), dry season rainfall (mm) and (log transformed) *shola* fragment area.

In addition to this, the diameter size class distribution (SCD) of *shola* tree species was examined by fitting a Weibull distribution and comparing the parameters across landscape contexts. This analysis was repeated for a subset of 12 dominant tree species. The seedling data (individuals < 0.5m height) was not used to construct the SCDs.

Differences in soil characteristics of *sholas* across the different landscape contexts was examined graphically using boxplots and tested using ANOVAs.

Field observations indicated that *Cestrum* presence was strongly related to distance from tea plantation edges. Therefore I modelled it as a function of distance to the closest tea plantation edge using a GLM with binomial error and logit link function. The results of this modelling was used to set a threshold distance from tea plantations, beyond which the probability of *Cestrum* occurrence fell to zero, so that subsequent modelling of the determinants of *Cestrum* abundance was free from the issue of zero-inflation (Martin et al. 2005). This threshold was then used to define a subset of the study plots within which *Cestrum* presence was likely based on their distance from a tea plantation edge (*n* = 54). This subset of the data was then used to model *Cestrum* abundance was as a function of bioclimatic and habitat variables. The models were compared using Akaike Information Criteria to identify the model that best predicted *Cestrum* abundance. Finally, a GLM with a Poisson error term was used to test whether *Cestrum* abundance within a plot was related to the number of *shola* species seedlings and shrubs in the plot.

Results

Variation in shola diversity, composition and structure across landscape context

Shola patches (≥ 2000m elevation) sampled in wattle and tea plantations showed similar species richness levels to those in grassland (Table 5.1, Figure 5.1). However the values for Simpson's Inverse Index, which is sensitive to dominance within plots, were lower for tea and wattle *sholas* compared to the grassland *sholas*, indicating a greater dominance and lower evenness in the *sholas* that are located in transformed matrix types (Table 5.1).

Table 5.1: Measures of species diversity in shola patches across grass, tea and wattle landscapes.

Index	Grass	Tea	Wattle
S_{est} (Mao-Tau estimator)	55	52	56
Fisher's alpha	8.56	8.09	8.77
Shannon -Weiner	3.13	3.05	3.06
Simpson's Inverse Index	16.29	14.71	13.59

The distribution of pairwise Morisita-Horn Index index values for plots in tea plantation and grassland *sholas* had higher mean (0.56) and median (0.59) values than the plots located in wattle *sholas* (mean = 0.44, median = 0.43). The former also showed a wider range of values than the latter (Figure 5.2). This indicates that there was lower turnover in species composition among wattle *sholas* compared to grassland and tea plantation *sholas* that occur at similar elevation and rainfall. There was also greater dominance by common species as this index is sensitive to abundances of the most common species.

Sholas in grasslands had the following dominant species (IVI > 10, listed in order of decreasing importance): *Cryptocarya lawsonii*, *Cinnamomum macrocarpum* Hook.f., *Litsea floribunda*, *Saprosma foetens*, *Symplocos macrophylla*, *Microtropis ramiflora*, *Symplocos foliosa*, *Cinnamomum wightii* Meisn.and *Litsea oleiodes*. *Sholas* in tea plantation had the following dominant species (IVI > 10, listed in order of decreasing importance): *Litsea wightiana*,

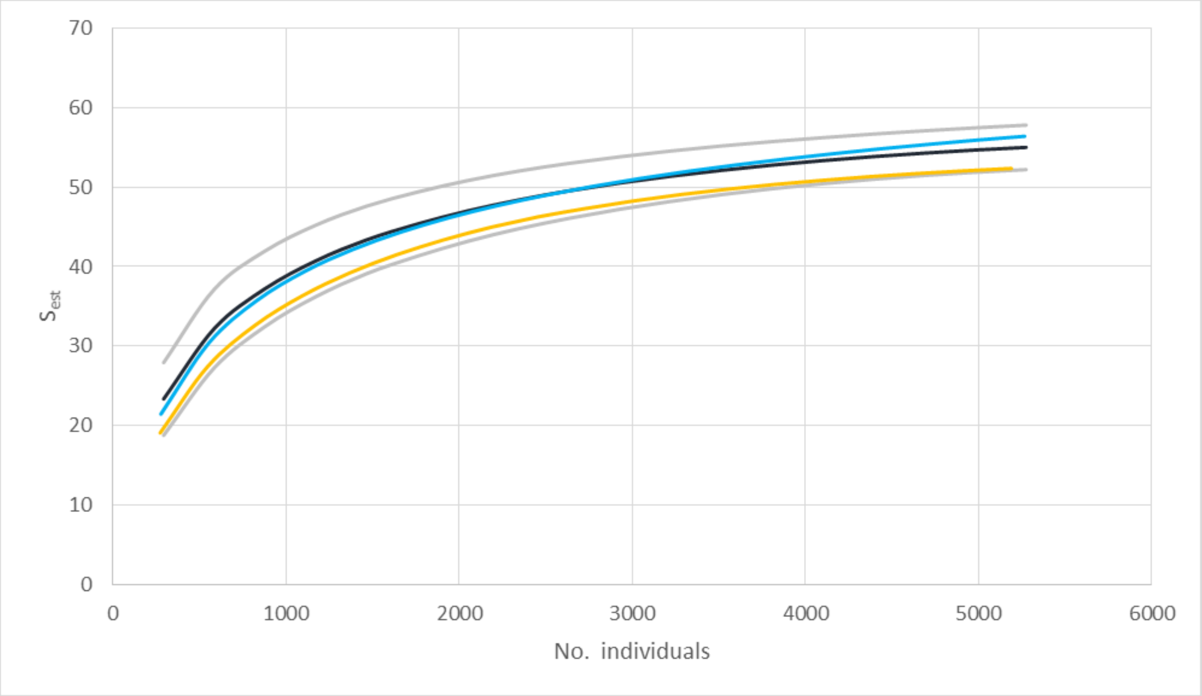

Figure 5.1: Rarefaction curves of S_{est} (Mao Tau) estimator of species richness in *sholas* across grassland (black line), tea (orange line) and wattle (light blue line) landscapes. Grey lines show 95% CI for grassland *shola* estimates.

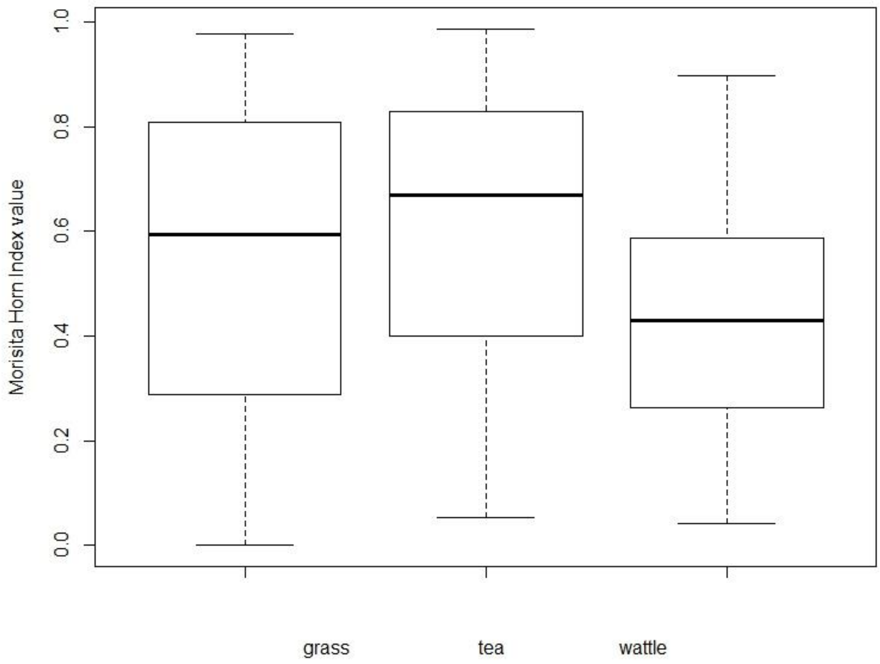

Figure 5.2: Boxplots showing the distribution of pair-wise Morisita-Horn values between plots in grassland *sholas* (*n* = 18), tea *sholas* (*n* = 22) and wattle *sholas* (*n* = 35)

Symplocos foliosa, *Neolitsea zeylanica* (Nees & T. Nees) Merr**.**, *Syzygium grande*, *Litsea oleiodes*, *Meliosma simplicifolia* and *Cinnamomum wightii*. *Sholas* in wattle plantations had the following dominant species (IVI > 10, listed in order of decreasing importance): *Symplocos foliosa*, *Syzygium calophyllifolium*, *Syzygium grande, Litsea wightiana, Cinnamomum wightii.* The set of dominant species differed across landscape context. *Symplocos foliosa* and *Litsea wightiana* are edge-tolerant, generalist and relatively fast-growing (average wood density for *Symplocos* = 0.49 g/cm^3 and *Litsea* = 0.42 g/cm^3; data compiled by J. Kanowski (2008) from (Ilic et al. 2000). These species were more dominant in wattle and tea *sholas* compared to those in grasslands. *Cryptocarya lawsonii* and *Cinnamomum macrocarpum*, which were mostly found towards the interior of fragments, dominated in grassland *sholas*. Two slow growing, edge-tolerant, generalist *Syzygium* sp. (wood density = 0.60 g/cm^3) were more dominant in tea and wattle plantation *sholas* compared to grassland *sholas*. *Psychotria* and *Lasianthus* species were far less dominant in the understorey of grassland and tea *sholas* than they were in the understorey of wattle *sholas*.

There were significant structural differences found between *sholas* in grasslands and those in tea and wattle plantations, even after accounting for the effect of elevation, dry season rainfall and *shola* fragment area (Table 5.2). Number of stems per plot showed a very slight but significant decrease with elevation (-0.0006 [0.0001], $P < 0.001$), a slight increase with dry season rainfall (0.004 [0.001], $P < 0.001$) and a stronger, significantly positive relationship with log of patch area (0.11 [0.004], $P < 0.001$) and was higher in grassland *sholas* compared to tea landscapes. Plot basal area (m^2/ha) was significantly positively related to log of *shola* fragment area (3.02 [1.32], $P < 0.05$) but was lower in grassland *sholas* compared to those in tea and wattle (Table 2). This was mainly driven by the presence of greater numbers of large trees (≥ 40cm dbh), especially in tea plantation *sholas* (Table 5.2). The number of individuals belonging to *Psychotria* and *Lasianthus* sp. in the understorey shrub layer of *sholas* increased slightly with elevation (0.003 [0.0002], $P < 0.001$) and dry quarter precipitation (0.018 [0.004], $P < 0.001$) and much more so with log fragment area (0.165 [0.01], $P < 0.001$).

Wattle *sholas* showed significantly higher numbers of *Psychotria* and *Lasianthus* sp. compared to grassland (Table 5.2) and tea *sholas* (0.98 [0.05], $P < 0.001$). This could be due to increased competition from other understorey species such as *Strobilanthes* sp. (not measured) and *Saprosma* sp. in the case of grassland *sholas*.
The number of dioecious individuals in the plot increased with size of *shola* fragment (0.039 [0.009], $P < 0.001$), and dry season precipitation (0.015 [0.002], $P < 0.001$), but was slightly negatively influenced by elevation (-0.003 [0.0002], $P < 0.001$). Interestingly, after accounting for *shola* fragment size, wattle and tea *shola* fragments had significantly higher numbers of dioecious individuals compared to grassland *sholas* (Table 5.2). Wattle *sholas* had a significantly lower number of dioecious individuals compared to tea *sholas* (-0.23 [0.03], $P <0.001$), indicating a possible positive effect on pollination and reproductive success for dioecious trees in a tea matrix.

Number of saplings was slightly negatively related to elevation (-0.0008 [0.0001], $P < 0.001$), but positively associated with dry quarter precipitation (0.015 [0.002], $P < 0.001$) and *shola* fragment area (0.11 [0.007], $P < 0.001$). Number of seedlings was significantly negatively associated with elevation (-0.003 [0.0002], $P < 0.001$) and positively with log fragment area (0.037 [0.011], $P < 0.001$). *Sholas* in tea plantations showed significantly lower sapling and seedling counts than grassland *sholas* (Table 5.2, Figure 5.3). The partial coefficient for the effect of a wattle matrix on seedling counts was non-significant (Table

5.2). However, wattle *sholas* had the lowest level of individuals in the sapling class (Table 5.2, Figure 5.3). This indicates a possible effect of a wattle matrix on establishment of *shola* saplings. Overall, regeneration levels appear to be decreased within *sholas* surrounded by altered landscape matrix.

Table 5.2: Results of GLM analysis comparing structural characteristics of *sholas* in tea and wattle landscapes to grassland *sholas*, after accounting for the effects of elevation, dry quarter precipitation and log of *shola* fragment area.

	Tea				**Wattle**			
Response	Slope	Std. error	z	*P*	Slope	Std. error	z	*P* <
No. stems	-0.075	0.02	-3.95	<0.001	-0.010	0.016	-0.59	>0.1
Plot basal area†	16.53	5.57	2.97	<0.01	11.54	4.975	2.32	<0.05
Mean dbh of plot†	2.33	1.22	1.91	<0.1	-0.93	1.09	-0.85	>0.1
No. large trees	0.465	0.15	3.18	<0.01	0.137	0.137	0.97	>0.1
No. seedlings	-0.64	0.06	-10.2	<0.001	-0.083	0.049	-1.68	<0.1
No. saplings	-0.365	0.03	-13.6	<0.001	-0.799	0.025	-30.9	<0.001
No. shrubs±	-0.058	0.07	-0.88	>0.1	0.941	0.052	18	<0.001
No. dioecious individuals	0.42	0.04	11.69	<0.001	0.209	0.034	6.11	<0.001

† t statistic used to test response level instead of z in GLMs with normal error term
± only individuals of dominant genera *Psychotria* and *Lasianthus* considered.

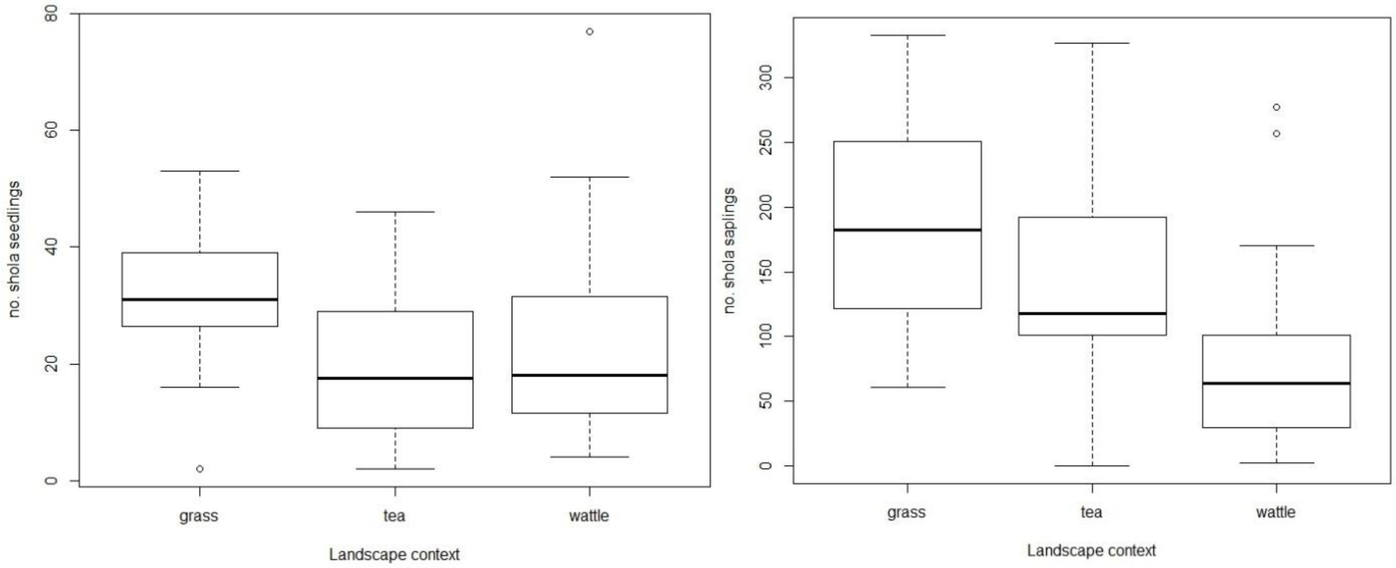

Figure 5.3: Boxplots showing differences in regeneration levels in *sholas* measured by number of seedlings and saplings across grass, tea and wattle landscapes.

Analysis of size class distributions across landscape context

The comparison of *shola* tree diameter size class distributions (SCDs) across landscape contexts shows that the SCDs of grassland and tea plantation *sholas* are very similar (Fig. 5.4). However *sholas* surrounded by wattle show fewer individuals in the smallest size class (0-5cm dbh) and a greater proportion of smaller trees (5-15cm dbh). The results of the GLM analysis on abundance of saplings above are supported by these SCDs. The SCDs do not include the seedling data.

Parameter estimates for the Weibull distributions fitted to individual species SCDs also reflect these differences (Figs 5.4 & 5.5, Appendix 5.1). Eight of the 12 species compared showed flatter inverse-J shaped SCDs in wattle landscapes (Appendix 5.1). These include both *shola* interior species such as *Litsea oleiodes* and *Cryptocarya lawsonii* as well as more edge-tolerant species such as *Litsea wightiana*, *Mahonia leschenaultii*, *Rapanea wightiana* (Wall. ex A. DC.) Mez, *Symplocos foliosa, Meliosma simplicifolia* and *Syzygium grande*. In the case of *M. leschenaultii*, a frost-adapted, endemic, *shola* edge species, the proportion of saplings in wattle *sholas* is much lower compared to tea and grassland *sholas* (Appendix 5.1). This species may therefore be negatively affected by altered conditions at the *shola*-wattle edge. *Syzygium calophyllifolium* and *Mictrotropis ramiflora* appear to have proportionally fewer individuals in the smaller size classes in grassland *sholas* compared to tea and wattle *sholas*, indicating better regeneration in these transformed landscapes (Appendix 5.1).

Differences in soil nutrient levels and texture in sholas across landscape contexts

Grassland *shola* soils had significantly higher levels of Al (F= 13.8, $P < 0.001$) and lower levels of Ca (F= 8.55, $P < 0.001$), Mg (F= 11.51, $P < 0.001$) and Cu (F= 3.99, $P < 0.05$) than *sholas* surrounded by tea and wattle plantations (Fig. 5.6). No significant difference was detected in the levels of total soil C and N, P, Fe, Mn, Zn or B across *sholas* in different landscape contexts (Fig 5.6), although wattle *sholas* appear to have slightly higher levels of percent total N (Fig 5.7). *Sholas* in tea plantations showed lower percentage of silt and higher percentage of sand than grassland and wattle *shola* soil (Fig. 5.8).

Factors related to Cestrum presence and abundance in sholas

The results of the GLM model of *Cestrum* presence using distance to tea edge showed that beyond 4km the probability of *Cestrum* occurring falls to near zero (Fig. 5.9). A set of 13 competing models for *Cestrum* abundance were tested in plots ≤ 4km from a tea plantation edge ($n = 54$). The best model, which receives practically all the support from the data, indicates that abundance is influenced by both bioclimatic (temperature seasonality and annual precipitation) and habitat factors i.e. distance to tea edge, distance to shola fragment edge and distance to stream (Table 5.3). The β coefficients [SE], for the predictors in this model indicate the effect they have on mean *Cestrum* abundance (on the log scale): the β for seasonality of temperature (0.0151 [0.0009]) indicates that *Cestrum* abundance is higher in areas with greater seasonality of temperature. It also decreases with mean annual precipitation (-0.004 [0.0005]). Abundance increases with distance from stream (0.0003 [0.0007]) and decreases with distance from the edge of the *shola* (-0.014 [0.002]) and from tea plantation edge (-0.0001 [0.0001]) (Fig. 5.10). The effect of distance to tea on abundance was dampened by the fact that one of the tea plantations sampled – Korakundah Estate – contains populations of *Cestrum* which have not yet spread into the *sholas*, mainly due to their organic ecologically-centred management practices. This observation indicates that improved management practices of tea estates can restrain the spread of *Cestrum* into *sholas*.

Possible effect of Cestrum invasion on regeneration of native shola species and shrub understorey

The number of seedlings in a plot was significantly negatively related to *Cestrum* abundance (-0.009 [0.002], $P < 0.001$). The number of *shola* saplings in a plot however did not show a significant relationship to *Cestrum* abundance (0.00006 [0.0007], $P > 0.1$).

The number of *Psychotria* and *Lasianthus* individuals in the plot was significantly negatively related to *Cestrum* abundance (-0.07 [0.005], $P < 0.001$), indicating possible negative competitive interactions with these dominant native shrub species.

Table 5.3: Results of model selection using GLMs with Poisson error to model *Cestrum* abundance in sholas as a function of bioclimatic and distance variables. Predictor codes: tmp.seas = temperature seasonality, ann.prec = mean annual precipitation, prec.cv = cv of precipitation, d.tea = distance to tea edge, d.stream = distance to nearest stream, d.edge = distance to nearest shola edge

S.no	Model	AIC	ΔAIC	Mod lik	AIC_Weight	df
1	tmp.seas+ann.prec+d.tea+d.edge+d.stream	668.69	0	~1	~1	6
2	tmp.seas+prec.cv+d.tea+d.edge+d.stream	707.52	38.83	~0	~0	6
3	tmp.seas+d.tea+d.edge+ d.stream	729.67	60.98	~0	~0	5
4	tmp.seas+ann.prec	918.93	250.24	~0	~0	3
5	tmp.seas	936.54	267.85	~0	~0	2
6	prec.cv+d.tea+d.edge+d.stream	952.71	284.02	~0	~0	5
7	ann.prec+d.tea+d.edge+ d.stream	1105.4	436.71	~0	~0	5
8	d.tea+d.edge+ d.stream	1107.7	439.01	~0	~0	4
9	prec.cv	1140	471.31	~0	~0	2
10	d.stream	1178.2	509.51	~0	~0	2
11	d.tea+ d.edge	1332.1	663.41	~0	~0	3
12	d.tea	1345	676.31	~0	~0	2
13	d.edge	1444	775.31	~0	~0	2
14	ann.prec	1509.2	840.51	~0	~0	2

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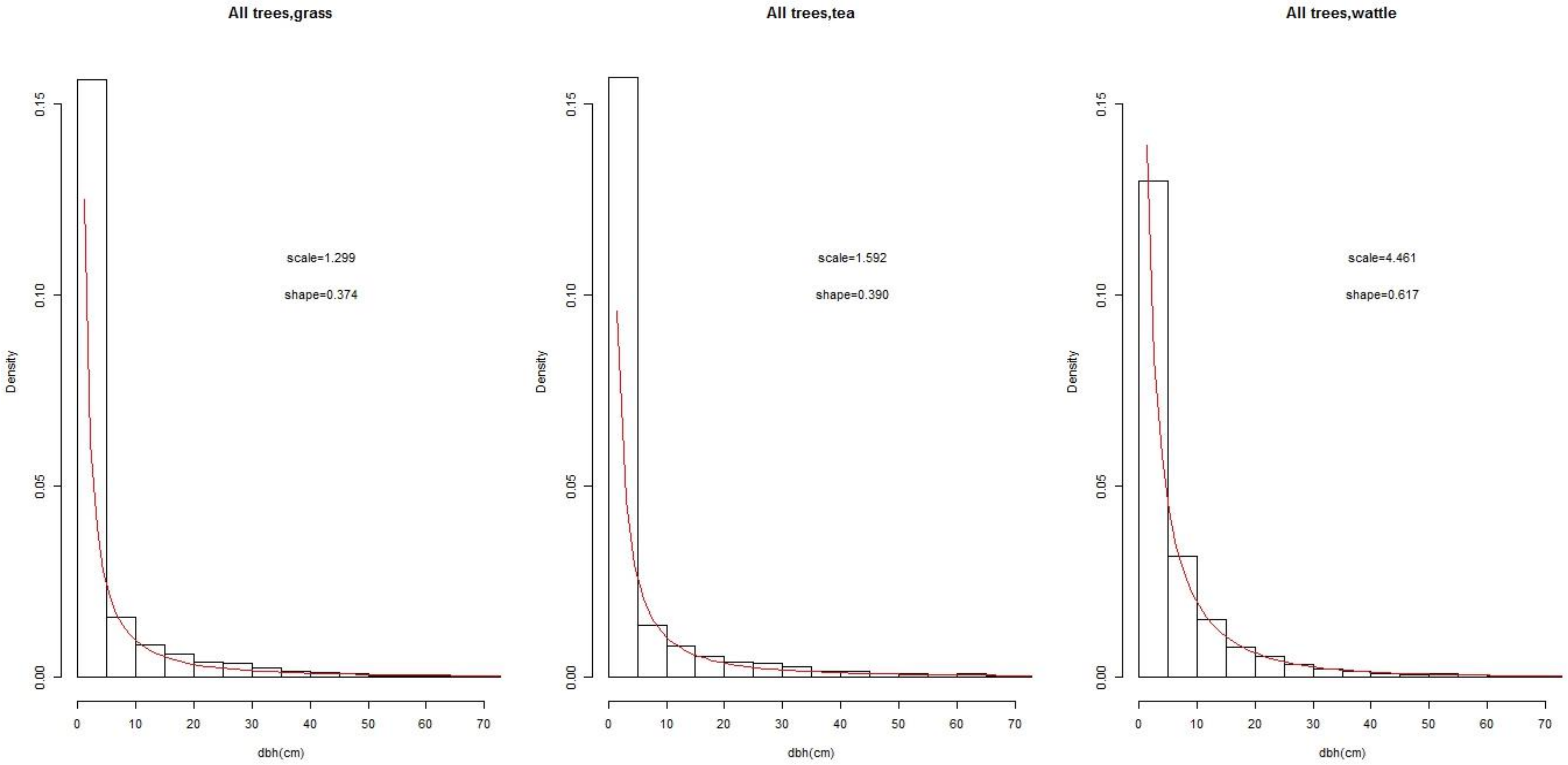

Figure 5.4: Shola tree diameter size class distributions across different landscape contexts with fitted Weibull distributions and their respective shape and scale parameter estimates

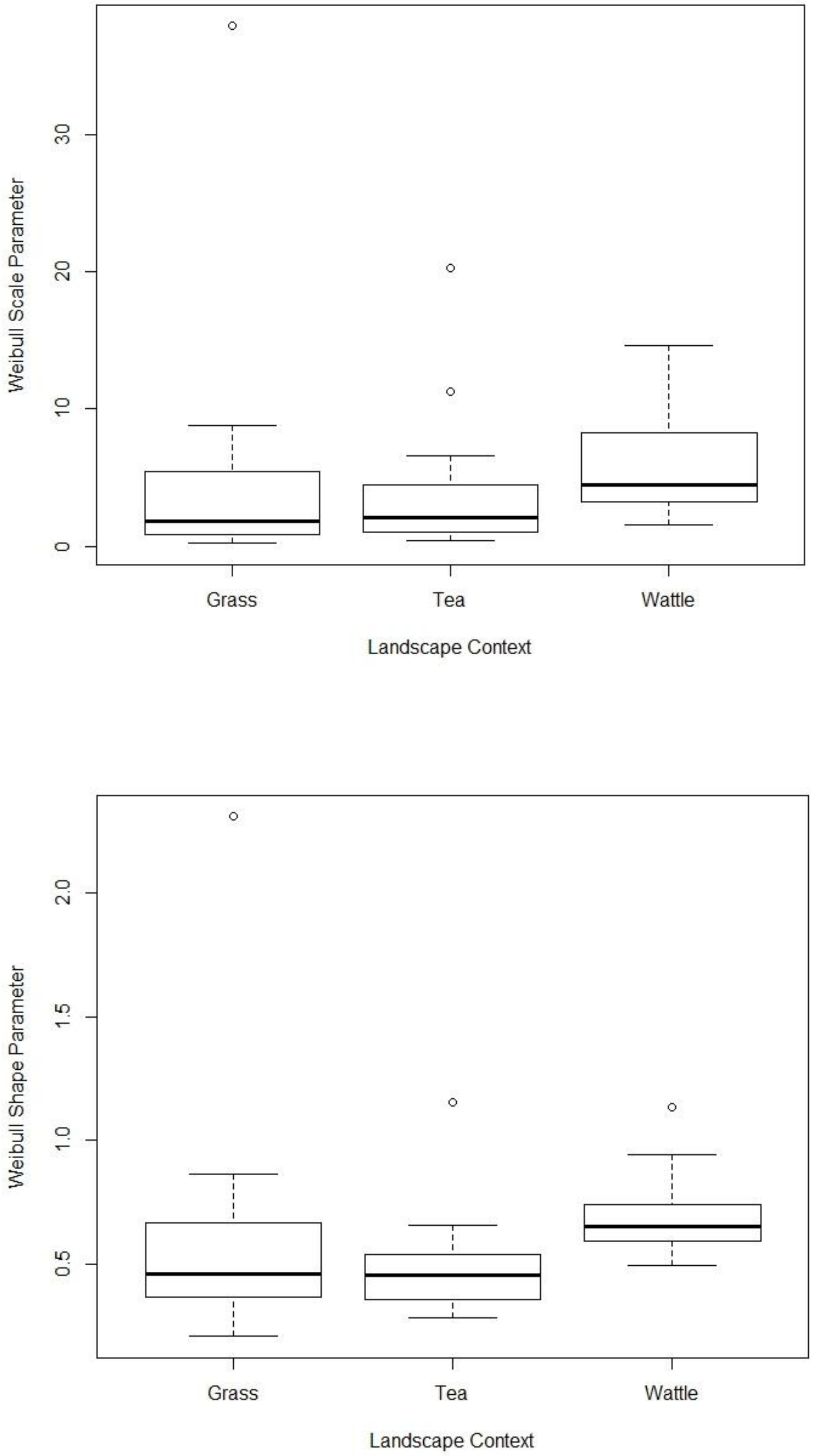

Figure 5.5: Boxplots of shape and scale parameter values of Weibull distributions fitted to diameter size class distributions for 12 dominant shola tree species across plots in grass, tea and wattle landscapes. Higher values for shape and scale parameters indicate flatter size class distributions.

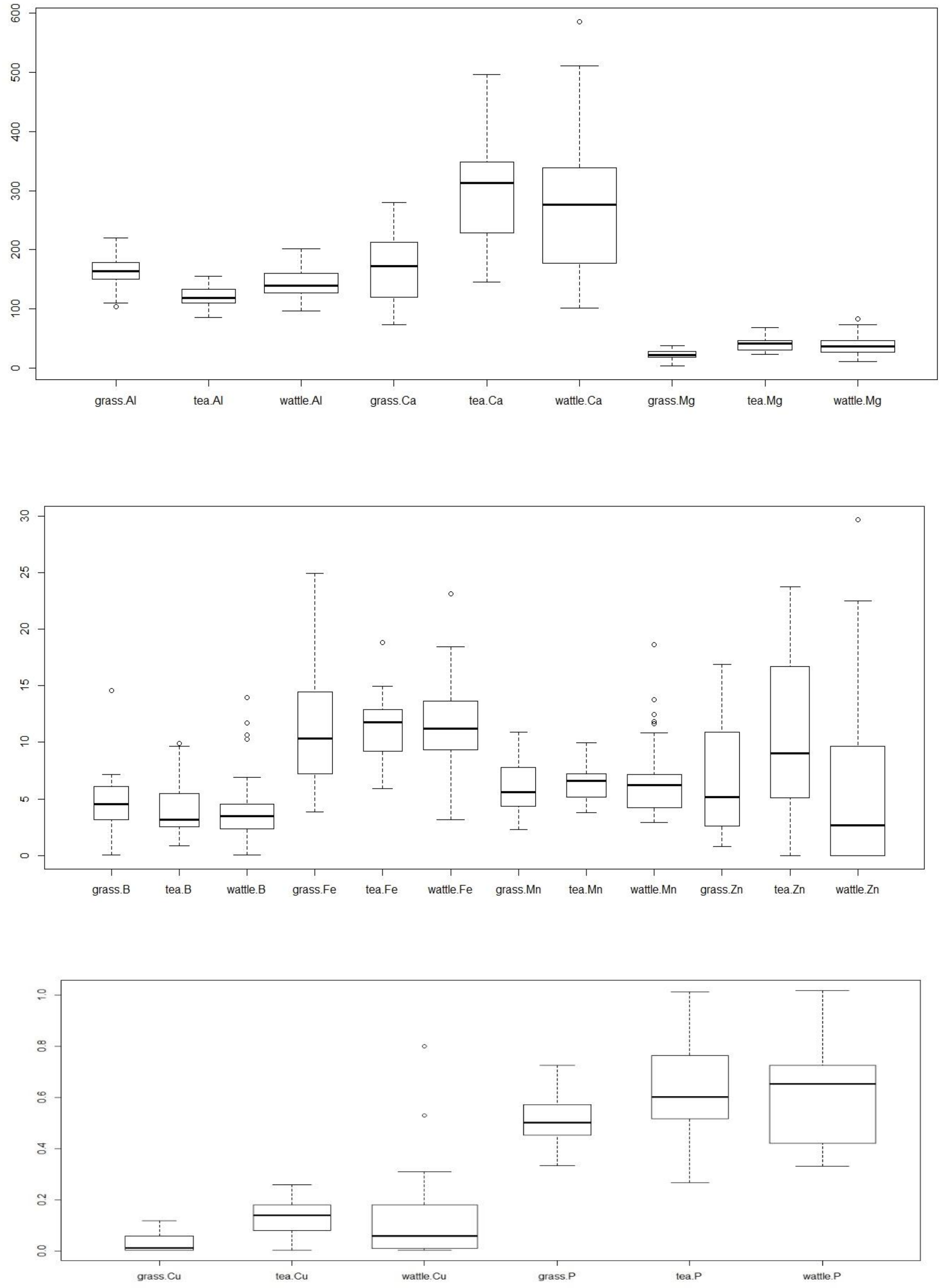

Figure 5.6: Boxplots showing *shola* soil macro and micro nutrient levels in ppm across different landscape contexts. Box widths scaled to reflect difference in sample size.

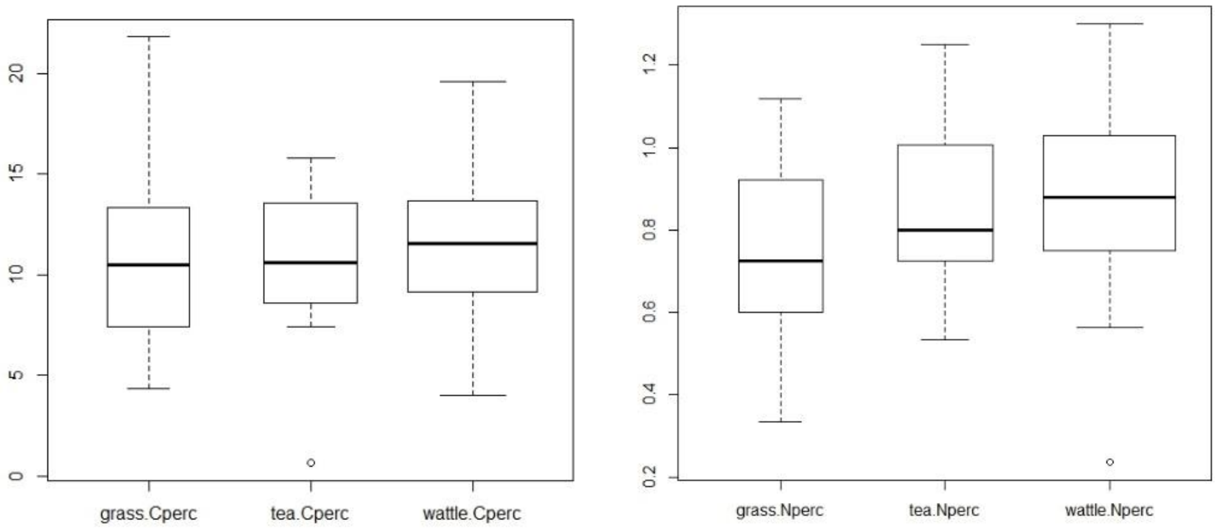

Figure 5.7: Differences in total C (right panel) and N (left panel) percentage in *shola* soils across grassland, tea and wattle landscapes.

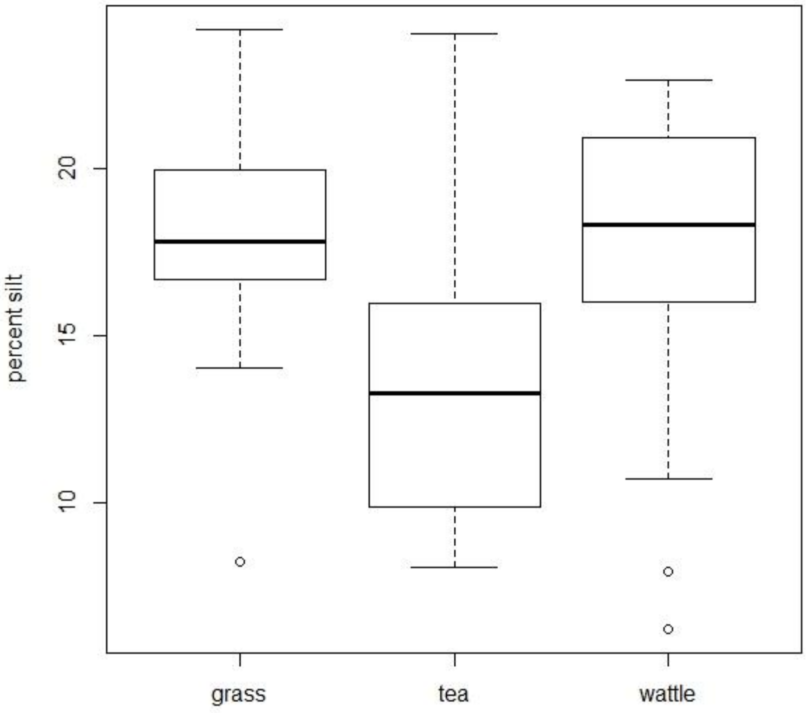

Figure 5.8: Differences in percentage silt in *shola* soils across grassland, tea and wattle landscape contexts

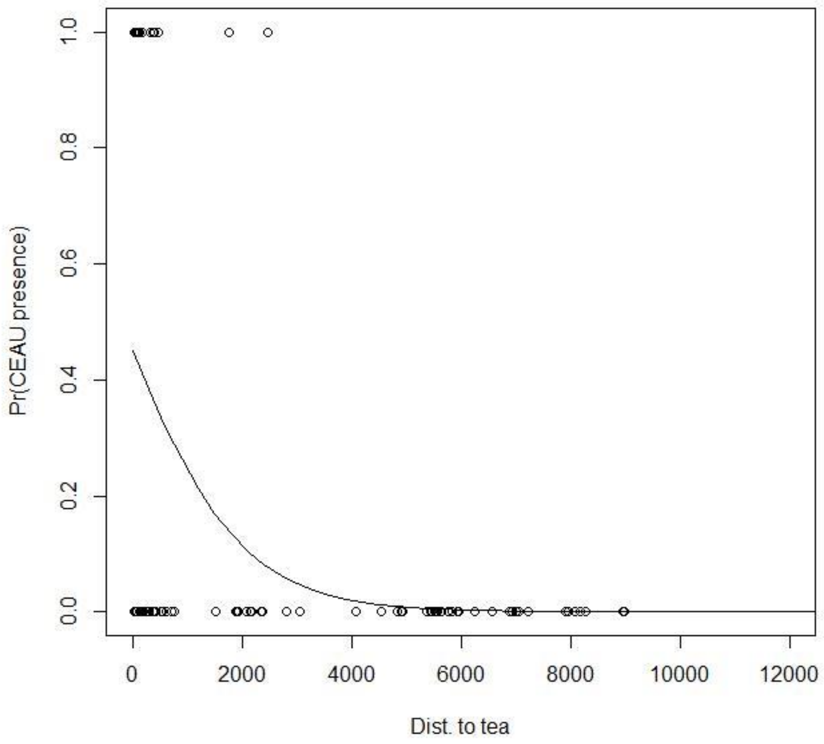

Figure 5.9: Probability of *Cestrum* presence modelled as a function of distance from tea plantation edge, using GLM with binomial error.

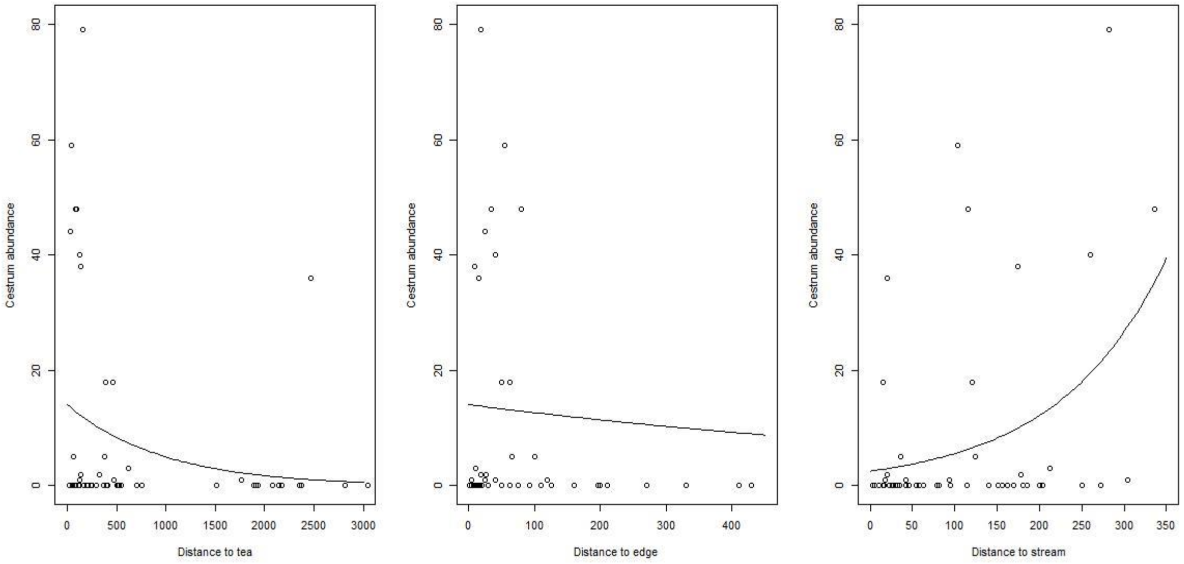

Figure 5.10: *Cestrum* abundance in *sholas* modelled as a function of distance to tea plantation edge, distance to nearest *shola* fragment edge and distance to stream, using GLMs with a Poisson error.

Discussion

There is substantial evidence of the ability of a human dominated matrix to enable persistence of tropical forest species in fragmented landscapes (Umapathy and Kumar 2000, Mudappa 2001, Bhagwat et al. 2005, Raman 2006, Perfecto and Vandermeer 2008). However the factors that enable this persistence are still poorly understood. Patterns of variation in community structure and composition across different matrix types in a naturally fragmented system could allow us to draw inferences about possible mechanisms through which the transformed matrix influences natural communities. Such inferences could then be formulated as competing hypotheses which can be further tested through field studies.

The results presented here indicate that conversion of natural grasslands to tea and wattle plantations in the Upper Nilgiri Plateau has affected both the structure and composition of *shola* plant communities. In terms of structural differences, there are a greater number of trees in smaller size classes (5-15 cm dbh) in wattle *sholas* compared to other landscape types and a significantly lower number of saplings (> 0.5m height and < 1cm dbh). Tea plantation *sholas* have significantly lower densities of dominant native shrub species and a significantly higher proportion of dioecious tree species. Past-logging and ongoing anthropogenic disturbance of tea estate *sholas* appears to have changed their structure compared to *sholas* in other landscape contexts. Both tea and wattle *sholas* show a reduction in seedling and sapling numbers compared to grassland *sholas*. In some tea estate *sholas* this maybe partly explained by the presence and higher abundances of *Cestrum* sp. which is an invasive exotic, that appears to repress *shola* tree regeneration. In terms of composition, *sholas* in tea and wattle plantations appear to be dominated to a greater extent by a smaller group of widespread, generalist species, both in the canopy and the understorey. This is also reflected in lower beta diversity levels among wattle *sholas*. However, overall species richness levels do not seem significantly different across landscape context. The soils of grassland *sholas* have lower concentrations of nutrients such as Calcium and Magnesium and higher concentrations of Aluminium, indicating greater acidity.

The conceptual framework for the domain of matrix effects on patch-dependent species presented by (Driscoll et al. 2013) provides a useful tool to organize patterns found in this study and draw inferences regarding possible mechanisms behind them. This framework posits three ‘core’ matrix effects: movement or dispersal, resource availability and abiotic environment of patches. These core effects are modified by five dimensions of matrix characteristics: spatial variability, spatial scale, temporal variability, temporal scale, and the ability of organisms to adapt to the matrix either genetically or through plasticity of traits and behaviour. For the sake of simplicity and because of the lack of information on some of these dimensions with regard to the study system, I focus primarily on the three ‘core’ matrix effects in the following discussion.

Altered patterns of pollen and seed movement

Abundance of dioecious individuals is likely to be a good indicator of whether matrix alteration has affected pollination processes, as most dioecious species are pollinated by insects such as small bees which have restricted movement between foraging sites (Bawa and Opler 1975, Bawa 1980). *Sholas* in altered matrix types did not show a decline in the number of dioecious species, in fact tea estate *sholas* showed the greatest number of such species. Therefore this study provides no evidence that occurrence or movement of pollinators has been negatively affected by matrix alteration. It may in fact even be enhanced in tea estates due to the presence of other plants that attract these pollinators.

A possible explanation for lower seedling and sapling counts in tea and wattle *sholas* could be reduced seed rain due to matrix effects on disperser movement behaviour. Most *shola* species are bird dispersed (Ganesh and Davidar 2001), however there are some such as *Syzygium* sp. which are also dispersed by mammals. One would expect the movement of avian dispersers to be strongly affected by matrix conversion from open grassland to wattle plantations (Sasal and Morales 2013, Morales et al. 2013). Avian frugivores tend to move through grassland rather rapidly, using shrub thickets or riparian strips for cover (*Personal observation*). In dense wattle stands their movement is likely to be slower and less direct, owing to the much higher availability of perches (Sasal and Morales 2013), greater cover from predators and reduced visibility. This altered movement is likely to result in reduced inter-patch seed rain among wattle *sholas* compared to their grassland counterparts (Morales et al. 2013). The wattle matrix could therefore act as a sink for *shola* seeds. The empirical (Hangsing 2012) and observational evidence (Bob Stewart & Tanya Balcar *Pers. comm.*) of substantial *shola* regeneration under mature wattle plantations support this. Further studies which directly measuring seed rain in the different landscape contexts are needed to test this hypothesis.

Another possible mechanism by which the matrix affects seed rain is through its influence on the composition of the disperser community (Raman 2006). Declines in abundance and diversity of frugivores have been found along a gradient of matrix types ranging from secondary forest, agroforests, exotic tree plantations, to agriculture and finally pasture (Gardner et al. 2009, Sekercioglu 2012). Vijayan and Gokula (2006) report overall bird species diversity and abundance to be highest in *shola* followed by grassland and lastly wattle plantation. They found the population density of the Nilgiri laughing thrush (*Trochalopteron cachinnans*) to be 79% lower in wattle plantations compared to undisturbed *shola* forest. This indicates wattle plantations would not increase the abundance of key endemic avian seed dispersers in the landscape (Zarri et al. 2008), despite their greater structural complexity and canopy connectivity. This is probably due to their impoverished floristic composition and lack of resources available for such species (Raman 2006). Tea plantations have been found to compare poorly with other matrix types such as coffee plantations in terms of rainforest bird communities (Raman 2006). The bird community in tea plantation landscapes is likely to be dominated by common, smaller birds from open scrub habitats, such as red-whiskered bulbuls (*Pycnonotus jocosus*) (Daniels et al. 1990, Sekercioglu 2012). Such species would selectively disperse smaller-seeded trees and shrubs. This may explain the increased dominance of species like *Litsea wightiana* and *Symplocos foliosa* in tea estate *sholas* compared to trees like *Cryptocarya lawsonii*, *Litsea oleoides* and *Litsea floribunda*, which have larger fruits and seeds. It would certainly explain the greater presence and abundance of *Cestrum* sp. in *sholas* closer to tea estate edges (Carleton and Owre 1975, *Personal observation*).

Altered matrix resource availability leading to spillover effects into shola fragments

As discussed above, movement of seeds and pollen is influenced by changes in matrix resource availability for frugivores and pollinators. A similar mechanism could affect rates of herbivory and seed predation within *sholas* in an altered matrix. Densities of wild herbivores such as sambar (*Rusa unicolor*) and gaur (*Bos gaurus*) appear to be higher in wattle and tea plantation landscapes compared to natural grasslands (*Personal observation*). Recent work indicates vertebrate herbivory levels play a critical role in determining seedling survival rates (Clark et al. 2012). Increased seedling herbivory leading to lowered survival rates could explain the lower sapling counts in wattle plantations.

Shanker (2001) found that the population density of *Rattus* sp. increased by a factor of 1.5 in old wattle plantations of the study area, compared to *sholas*. *Rattus* sp. was not found in grasslands but did occur in tea plantations at densities comparable to those of *shola* forests. Matrix conversion could therefore have led to altered resource availability for *Rattus* sp., potentially leading to increased seed predation and lowered seedling counts in wattle and tea plantation *sholas*.

Another way in which the altered matrix resource base affects the *shola* community is through a ‘spillover effect’ (Rand et al. 2006) of *Cestrum* sp. into tea plantation *sholas*. This appears to have had a negative impact on *shola* seedlings and native shrub species, which are highly endemic. *Cestrum* has established a growing population within open areas in tea estates and is dispersing into adjacent *sholas*, where it has formed dense thickets in the understorey. It should be noted however that not all tea estates that hold *Cestrum* populations have invaded *sholas*. Estate management appears to be an important determinant of invasion success. Apart from one or two seedlings in a couple of plots, none of the *sholas* sampled in Korakundah tea estate were invaded by *Cestrum*. This was the only estate sampled which is completely organic and has several ecologically-friendly management certifications. Their management policies actively attempt to reduce levels of anthropogenic disturbance in *sholas* within the estate (Pritam Dambekodi *Pers. Comm*). Therefore a combination of several interacting effects arising from the tea matrix seems to lead to actual invasion: establishment of large, fertile populations of *Cestrum* sp. in the matrix through resource provision, increased disturbance of the understorey through frequent human use of the *sholas* and increased propagule pressure effected through dispersal by common birds such as the red-whiskered bulbul.

Altered abiotic environment at the forest edge

The *shola*-grassland edge is characterized by short, sharp gradients in temperature, light and humidity (Bunyan 2009). Unlike lowland tropical forests, where edge effects can extend up to 100m into the forest (Laurance et al. 2011), *sholas* surrounded by grassland are thought to have shallower edges, on the order of tens of metres (Bunyan 2009). Smaller *shola* fragments (≤ 1ha) are influenced by the greater proximity of multiple edges and therefore do not demonstrate gradients in abiotic conditions that can be found in larger *shola* patches (Bunyan 2009). The abiotic environment of these smaller patches is therefore dominated by the pervasive edge. While *shola*-tea plantation edges should be more comparable to *shola*-grassland edges, conversion of the matrix from grassland to wattle plantation would result in a much greater 'softening' of edge conditions; lowered light availability, wind stress, diurnal temperature fluctuation and increased humidity (Ries et al. 2004). This could affect the regenerative and competitive abilities of certain edge-adapted species such as *Mahonia leschenaultii* and *Litsea wightiana*. Interestingly, the latter is the most dominant species in tea estate *sholas* but not in wattle plantation *sholas*. Conversely, the greater dominance of generalist endemics such as *Symplocos foliosa* and *Syzygium* sp. in wattle *sholas* - particularly in smaller fragments - could also indicate altered edge-related abiotic conditions favouring the growth of these species.

Finally, the higher density of small trees (5-15cm dbh) in wattle *sholas* compared to grassland and tea *sholas*, may be linked to specific *shola*-wattle edge conditions, such as increased soil Nitrogen availability (Le Maitre et al. 2011), enabling faster growth rates and therefore rapid transitions from sapling to small tree size classes (Condit et al. 1998). Unfortunately, the sampling scheme and type of data gathered here limits inferences regarding specific mechanisms. Further field studies are necessary to investigate the possible pathways through which altered edge environments influence the structure and composition of the *shola* plant community.

In conclusion, the patterns emerging from this study indicate definite structural and compositional differences in the *shola* tree and shrub community across the different landscape contexts. The results indicate that mitigation of negative effects of matrix conversion such as *Cestrum* invasion and reduced regeneration would require a management strategy in which the type of intervention is dependent on the landscape context of the *shola* fragments. Further, as conversion of grasslands to tea and wattle plantations appears to have altered successional trajectories and vegetation dynamics within *shola* fragments, long-term studies of *sholas* stratified by both fragment size and landscape context are urgently required in order to better conserve and manage these rare and biologically important habitats in the face of climate change. Such studies have provided critical insights into long-term effects of fragmentation on lowland tropical forests (Laurance et al. 2011), yet none exist for the equally important tropical montane forests in general and naturally fragmented habitats in particular.

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Chapter 6
Conclusion and Synthesis

The ecologically distinct and narrowly distributed upper montane (*shola*) forests in the Western Ghats are not as well studied as their lower elevation counterparts. Most studies on *sholas* are fairly restricted in spatial extent of sampling and inference, and generally do not attempt comparisons across different regions or within larger landscapes. Despite the great conservation significance of these forests, little is known about how patterns of tree and shrub species composition vary across space, how environmental factors such as climate, topography and soil affect tree and shrub community composition, and how widespread conversion of surrounding grasslands to tea and exotic tree plantations has affected plant communities. Additionally, the presence and distribution of transitional ecotones for this habitat type along elevation and rainfall gradients remain poorly studied.

The primary objective of this work was to understand the patterns of distribution and plant community composition of *shola* forests at different spatial scales. At the regional scale I attempted to understand the distribution of *shola* fragments within the grassland matrix in which they occur. At the landscape scale I studied variation in plant metacommunity composition across *shola* fragments and the environmental factors associated with this variation. I also investigated whether the structure, composition and regeneration of *sholas* have been affected by conversion of grassland to tea and wattle plantations. Several important insights have emerged from this study that provide a deeper understanding of the patterns and drivers of spatial heterogeneity in these forests. The findings of this work are relevant to ongoing conservation and management efforts and help define future research questions on this system.

Topographic and bioclimatic factors influencing vegetation pattern in shola-grassland mosaics

The distribution of *shola* forests at the regional scale in the central and southern Western Ghats is influenced by both topography and bioclimate as well as the interaction between the two. Elevation strongly influences the occurrence and distribution of *shola* fragments within the grassland mosaic. Above 2000m, the mosaic is dominated by grassland, with *shola* patches more likely to occur on northern aspects and in sites with concave land surface curvature, particularly along the sides of deep valleys. Below 2000m, relative topographic position (within a 300m neighbourhood), is an important predictor of vegetation pattern. Bioclimatic factors that influence *shola* forest and grassland distribution are: dry quarter precipitation, annual temperature range and the interaction between the two. The results indicate that the distribution of *shola* forest and grassland within these mosaics is influenced by complex interactions between topography and bioclimate and between topographic variables. The marked regional differences in the roles of various topographic and bioclimatic predictors across the range of the Western Ghats, indicates that the same pattern of grassland interspersed with forest patches, may be generated by different sets of processes across the region, depending on latitude and elevation. In particular, *shola* grasslands that occur above 2000m elevation differ in terms of their vegetation pattern and associated topographic and bioclimatic influences from mosaics that occur below 2000m.

Floristic composition of shola forests in the Upper Nilgiris

A total of 95 tree and shrub species occur in the *sholas* of the study area, with about 53% of them being endemic to the Western Ghats and Sri Lanka. While these forests are not as species-rich as middle and lower elevation evergreen forests in the Western Ghats (Pascal 1988, Ganesh et al. 1996, Ramesh et al. 2010, Jayakumar and Nair 2012), they hold a greater proportion of endemics (Jayakumar and Nair 2012). The majority of the tree and shrub genera in *sholas* have an Indo-Malayan affinity (Meher-Homji 1967, Suresh and Sukumar 1999), with a large proportion of endemics restricted to the central and southern Western Ghats, particularly within the shrub genera. Lauraceae is the most species rich family (19 species), followed by Rubiaceae (8 species) and Myrtaceae (6 species). Dominant tree genera include *Litsea*, *Cinnamomum*, *Syzygium* and *Symplocos*, while dominant shrub genera are *Psychotria* and *Lasianthus*. Above 1800m there is an increasing presence of Palaearctic components characterized by genera such as *Rhododendron*, *Ilex, Berberis* and *Mahonia*. Four dominant species associations were identified in the study area. Stem densities within these forests vary widely and are on average much higher than those in lower elevation evergreen forests (Ramesh et al. 2010). Average stand basal area fell within the range of values reported for *shola* forests in other parts of the Western Ghats.

Metacommunity pattern and response to the elevation gradient

The composition of *shola* tree and shrub communities is strongly influenced by elevation. The metacommunity pattern along the elevation gradient in the study area corresponds more closely to a Clementsian pattern rather than a Gleasonian one. Many species exhibit non-overlapping distributions, with significant turnover and clumping of species range boundaries. Turnover was the highest between 1900-2100m in the Upper Nilgiris. Basal area of Myrtaceae increased with elevation as did that of Symplocaceae, Magnoliaceae and Celastraceae. Taxa with temperate affinities such as Ericaceae and Berberidaceae also showed an increase with elevation, while Theaceae, Araliaceae, Oleaceae, Sapotaceae and Rutaceae showed the largest declines in basal area with elevation. Replacement of species by sister taxa along the elevation gradient was observed mainly in the genera *Litsea*, *Syzygium* and *Symplocos*. The nature of the floristic changes observed between 1800m and 2400m in the study area are consistent with transitions found in montane forests noted by previous in Sri Lanka (Werner 1995) and south east Asia (Ohsawa 1995, Ashton 2003). I therefore conclude that a transitional ecotone between lower and upper montane *shola* communities occurs between 1900 and 2100m in the study area. This zone appears to coincide with the elevation of cloud formation in many large, tropical mountains (Jarvis and Mulligan 2011). Metacommunity pattern in the study area is also correlated to the east-west precipitation gradient, but not as strongly as with elevation.

Influence of environment and dispersal on shola plant community composition

The observed turnover along the elevation gradient indicates that the *shola* metacommunity is largely structured by niche-based species sorting. However, the extent to which dispersal limitation plays a role in influencing community structure has not yet been investigated. I address this question by using variation partitioning to assess the relative influence of abiotic factors (i.e. climate, topography, soil and habitat) and biotic factors such as dispersal limitation on the spatial abundance patterns of *shola* tree and shrub species.

The results confirm strong spatial structuring of the *shola* plant community, driven mainly by spatial variation in environmental factors. Overall, the environmental and spatial predictors used were able to account for approximately half of the variation in species abundances across the study area. Most of this (~ 40%) was accounted for by environmental predictors, most of which were strongly spatially structured. However, a little less than 10% of the explained variation is accounted for by spatial predictors that represent dispersal processes and do not seem to be influenced by any unmeasured environmental factors. Among environmental predictors, bioclimate was the most influential in explaining variation in species abundances, particularly dry season precipitation and temperature seasonality (the latter being very strongly correlated with elevation), as well as their interaction. This demonstrates that in topographically heterogeneous terrain, variation in bioclimate over short spatial lags (5-10km) can cause high turnover in species composition. The next most influential set of environmental variables was related to habitat/historical factors - namely size of the shola fragment and whether the *shola* was surrounded by tea, wattle or grassland. Soil nutrient content was the next most important in explaining variation in species abundances. Finally, certain topographic predictors such as slope and topographic convergence index (TCI), emerged as having slight but significant effect on the abundances of some species.

Impacts of landcover change on shola tree and shrub communities

Conversion of the landscape matrix from natural grasslands to wattle and tea plantations has influenced the composition, stand structure and regeneration of *shola* tree and shrub species. While species richness levels are not significantly different across the three landscape contexts, *sholas* in tea and wattle plantations appear to be dominated to a greater extent by a smaller group of widespread, generalist species, both in the canopy and the understorey. This is reflected in lower beta diversity levels among wattle *sholas*. In terms of structural differences, *sholas* located within a matrix of wattle plantations have a greater number of trees in smaller size classes (5-15 cm dbh) compared to *sholas* in grasslands and tea plantations. They also have a significantly lower number of saplings (> 0.5m height and < 1cm dbh), indicating that recruitment to this size class is lower than in other *sholas*. Tea plantation *sholas* have significantly lower densities of dominant native shrub species and a higher proportion of dioecious tree species. Past-logging and ongoing anthropogenic disturbance of tea estate *sholas* appears to have changed their structure compared to *sholas* in other landscape contexts. Both tea and wattle *sholas* show a reduction in seedling and sapling numbers compared to grassland *sholas*. In some tea estate *sholas* this is partly explained by the presence and higher abundances of *Cestrum* sp., an invasive exotic that appears to repress *shola* tree regeneration. Finally, compared to wattle and tea *sholas*, soils of grassland *sholas* had lower concentrations of nutrients such as Calcium and Magnesium and higher concentrations of Aluminium – indicating greater acidity.

Further research is required to understand the mechanisms through which land cover change has impacted *shola* forests. These include; altered disturbance regimes, changes in seed predation, dispersal or herbivory, and changes in edge dynamics

Potential impacts of climate change on shola forests

The results support the primary importance of climatic factors such as variation in rainfall and temperature in determining the distribution and composition of *shola* forests, even at relatively small spatial scales (e.g. 5-10km). This in addition to the fragmented, mountain-top nature of this forest, make it extremely vulnerable to anthropogenic climate change (Foster 2001). Studies have found that under a future scenario of doubled CO_2 levels, the suitable climatic conditions for cloud forest growth could shift upslope by approximately 200-500m (Still et al. 1999, Foster 2001). This would lead to a major reduction of area under *shola* forests in the Western Ghats. *Shola* species assemblages, including several endemics, which currently occur above 2000m could go extinct.

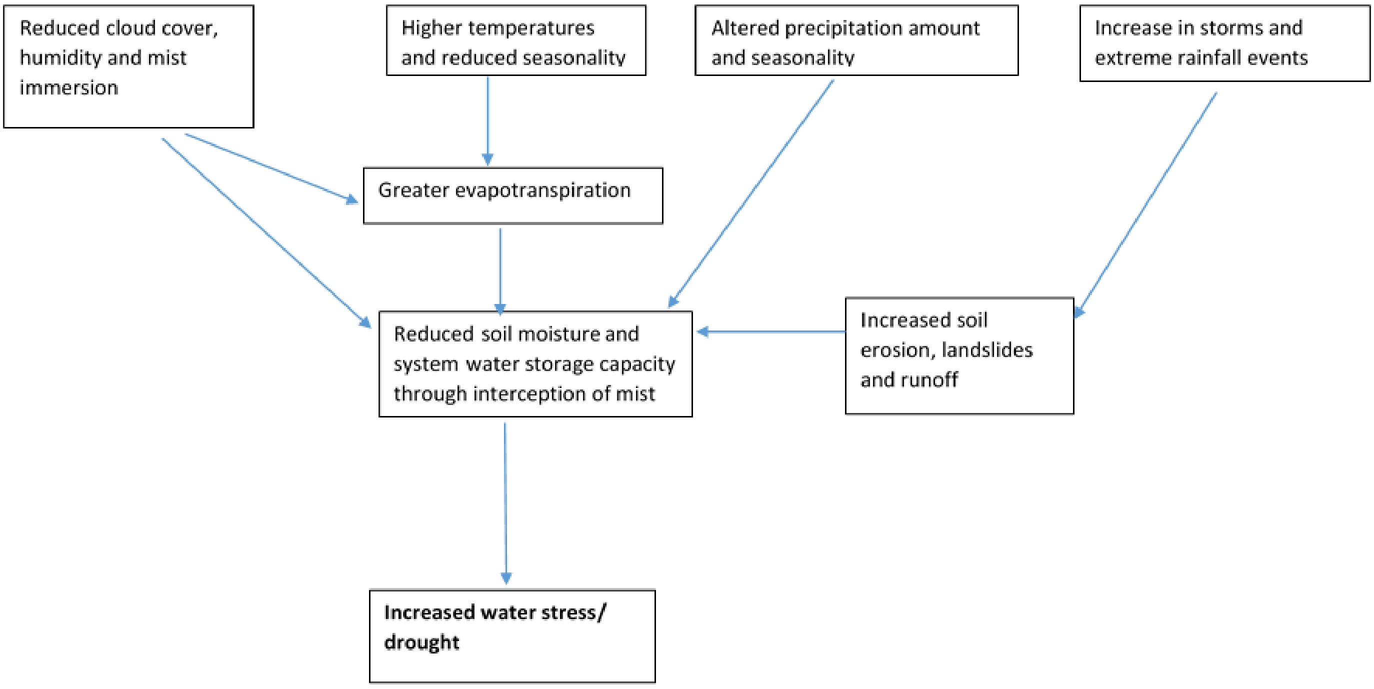

Figure 6.1: Potential mechanisms through which climate change may threaten montane cloud forest (*shola*) ecosystems. Based on Foster (2001).

The biggest threat to cloud forests from climate change consists of increased water stress and drought (Fig. 6.1), coupled with increased disturbance in the form of fire and hurricanes (Bawa and Markham 1995, Foster 2001, Oliveira et al. 2014). This could result from a number of possible changes including the lifting of the cloud base and associated reduction in mist immersion (Foster 2001), which would affect much of the flora, such as epiphytes and even trees and shrubs that are known to be very drought sensitive (Oliveira et al. 2014). Reduction in dry season precipitation and increase in extreme rainfall events would also lead to greater water stress and shifts in species compositions (Fig. 6.1). Higher temperatures combined with reduction in mist immersion would negatively impact *shola* trees and weaken their ability to compete with lower elevation species migrating upslope. This is confirmed by the results of previous modelling efforts looking at the impact of climate change on the cloud forest zone (Still et al. 1999, Foster 2001, 2010). Observational evidence from some sites support this. Pounds et al. (1999) document an increase in the number of mist-free days in Monte Verde since the 1970s. Other major impacts could include shifts in phenology which would disrupt existing plant-pollinator as well as plant-disperser networks and affect the reproductive success of *shola* species. The combined effects of increased disturbance and disruption of plant-animal networks would enhance the spread of exotic invasive species in this ecosystem (Foster 2001).

In light of the results of this work and future climate projections, one would expect to see major shifts in *shola* community composition and a reduction in species diversity (driven by the loss of narrow endemics) with climate change. These climatically-driven shifts should be most apparent within the transitional ecotone between lower and upper montane *shola* communities (Bawa and Markham 1995). Finally, studies that attempt to model projected range shifts for *shola* species must take into account the effects of local-scale topography on the distribution of *shola* fragments.

Emerging issues and implications for management

The *sholas* have persisted in a natural mosaic with grasslands over tens of thousands of years, expanding or retreating during previous episodes of climate change (Sukumar et al. 1995, Caner et al. 2007). Apart from high levels of endemism, this ecosystem provides critical hydrological services to millions of people in Tamil Nadu, Kerala and Karnataka (Nair and Khanduri 2001, Srivastava 2001). However, the present situation facing *sholas* is unprecedented in terms of combined stresses of rapid climate change and recent large scale habitat conversion and throws into question this ecosystem's ability to resist and adapt to current and future change.

In the last 70 years, this ecosystem has already undergone a major regime shift (Parrott and Meyer 2012) i.e. the conversion of thousands of hectares of natural grassland to exotic tree plantations (Prabhakar 1994). Results presented here provide evidence that successional trajectories and associated vegetation dynamics of *shola* fragments occurring within these altered matrix types have already been affected. This increases the level of complexity and uncertainty with regard to management of this system, making it increasingly difficult to predict the outcomes of any management intervention. Such levels of uncertainty require a management approach that is flexible and adaptive in nature, with a strong emphasis on monitoring (Filotas et al. 2014, Messier et al. 2015). Such an approach would require forest managers to build alternative scenarios that consider the likelihood of possible future states, given current conditions, predicted changes in climate and the scale and type of intervention planned (Filotas et al. 2014).

For instance, the current policy being enacted in Tamil Nadu is to clear fell existing exotic tree plantations with the objective of restoring the original *shola*-grassland mosaic habitat in their place (Proceedings of the Principal Chief Conservator of Forests, Chennai, dated 26/3/2014, Proc.No.WR1/7028/2014). Given climate-induced changes in disturbance regimes and the current levels of invasion by exotic species in remnant grasslands (Thomas and Palmer 2007) as well as in *sholas*, a possible outcome of such a large-scale, soil-disturbing intervention could be yet another regime shift in favour of woody alien invasives in clear-felled areas, further threatening *sholas* as well as remnant grasslands. It could also lead to the replacement of a relatively stable, though altered vegetation state (i.e. mature *Acacia* and *Eucalyptus* plantations) with an inherently unstable one (Scheffer and Carpenter 2003, Scheffer et al. 2012) – with attendant implications for biodiversity and ecosystem services. In short, the feasibility as well as suitability of restoration to an earlier state should first be evaluated relative to other possible scenarios and then pursued accordingly. At the very least, clear-felled areas should be monitored to assess the impact of this intervention before extending it to larger areas.

Linked to this is the need for an integrated, ecosystem-based approach for the *shola*-grassland mosaic as a whole, which fosters capacity for resilience and adaptation to climate change. This would entail examining effects of management practices that are currently being deployed at large spatial scales (hundreds of hectares), such as the clear-felling of exotic tree plantations or the planting of *shola* saplings in grasslands, to assess whether these actions enhance or reduce the *shola*-grassland ecosystem's capacity to persist in the face of climate change.

Specific management recommendations that emerge from this work include:

a) The *shola*-grassland mosaics that occur above 2000m elevation require a distinct set of management prescriptions and guidelines, as they differ in terms of vegetation pattern and associated topographic and bioclimatic factors.
b) Species composition of *sholas* are most strongly influenced by elevation, precipitation seasonality, fragment size and landscape context. Therefore these factors should be taken into consideration while deciding on management interventions for individual *shola* fragments.
c) As conversion of grasslands to tea and wattle plantations appears to have altered successional trajectories and vegetation dynamics within *shola* fragments, **long-term monitoring plots**, stratified by elevation, fragment size and landscape context, are required in order to better conserve & manage these habitats in the face of climate change.
d) Effects of climate change on *sholas*, such as upslope migration of lower elevation species, reduction in cloud immersion or changes in phenology should be most apparent at the transition zone between lower and upper montane *sholas*. Therefore, for the Nilgiris it is recommended that monitoring plots be established particularly within the 1900-2100m elevation zone with particular attention paid to monitoring epiphytic flora (Foster 2001).
e) Measures to monitor and control the spread of *Cestrum* sp. into *shola* fragments near tea plantations should be undertaken as this invasive appears to suppress regeneration of native tree and shrub species.

In summary, I find that both vegetation pattern within *shola*-grassland mosaics in general, and the *shola* tree and shrub metacommunity in particular, are strongly structured by the elevation gradient. Specifically, above approximately 2000m elevation, there appear to be shifts in both the distribution of forest and grassland within these mosaics, as well as high turnover in community composition within *shola* fragments. Whether this transition is being driven by the height of the cloud base (Grubb and Whitmore 1966, Foster 2001, Jarvis and Mulligan 2011) or by a temperature-related mechanism remains to be resolved. The answer to this is critical to determining how the system will respond to climate change. Spatially structured environmental variability, generated primarily by topographic heterogeneity, accounts for much of the variation in *shola* tree metacommunities. However, approximately half of the variation in tree and shrub communities remains unexplained by the environmental, historical and spatial predictors considered here. Finally, *sholas* located within a landscape matrix of grassland differ significantly in terms of structure, composition as well as regeneration levels from those located within an altered landscape matrix of tea plantations and wattle (*Acacia mearnsii*), indicating that landscape matrix conversion has affected the structure and dynamics of vegetation in *sholas*.

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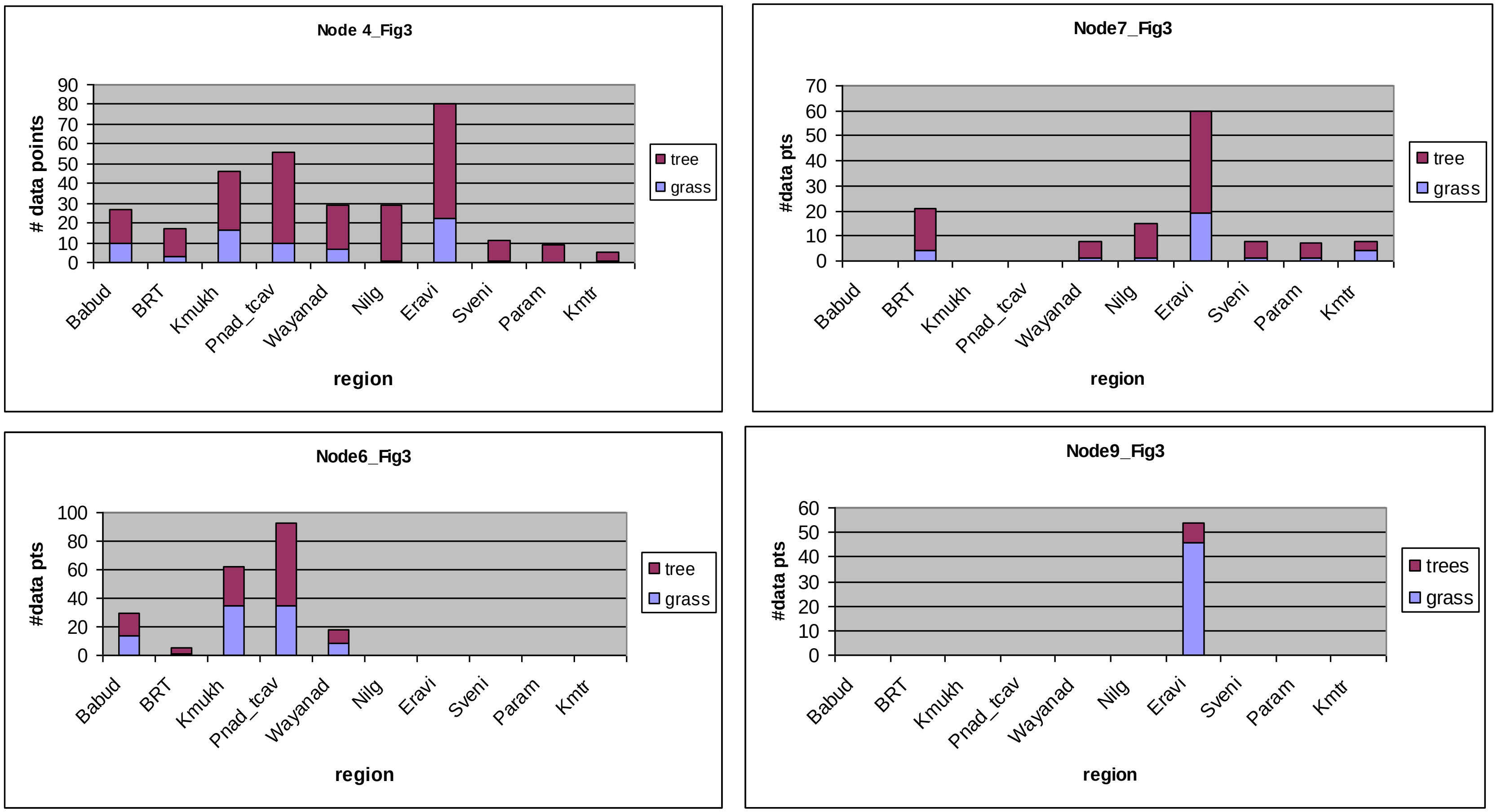
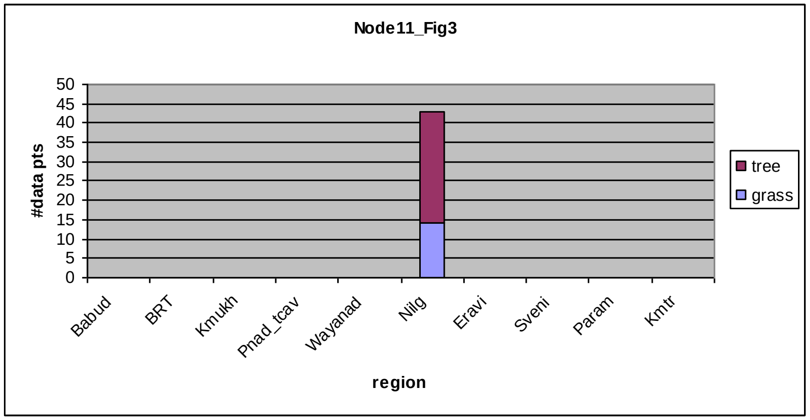
Appendix 2.1

Stacked barplots indicating regional identity and vegetation type of data points falling in terminal nodes of the classification tree in Figure 2.3

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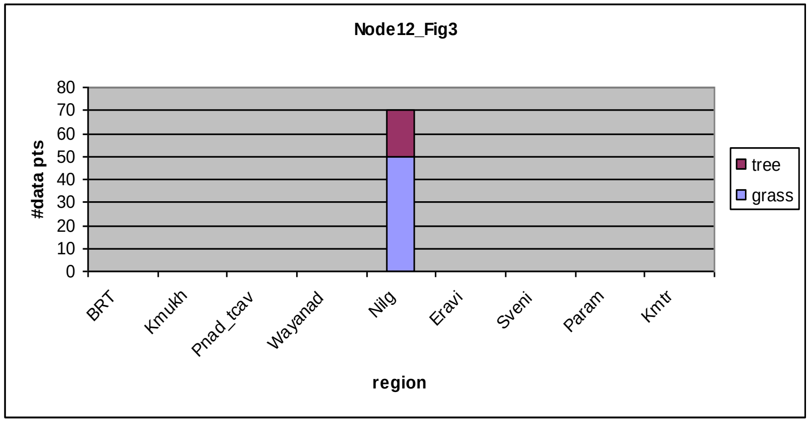
Eravi
Sveni
Param
Kmtr
region
tree
grass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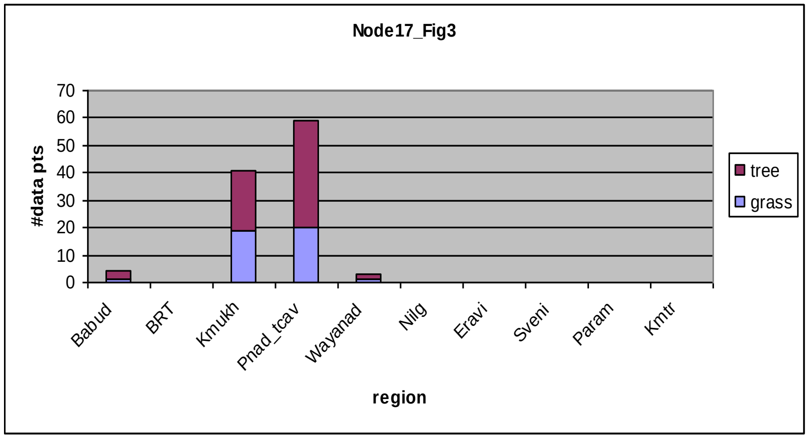
Param
Kmtr
region
tree
grass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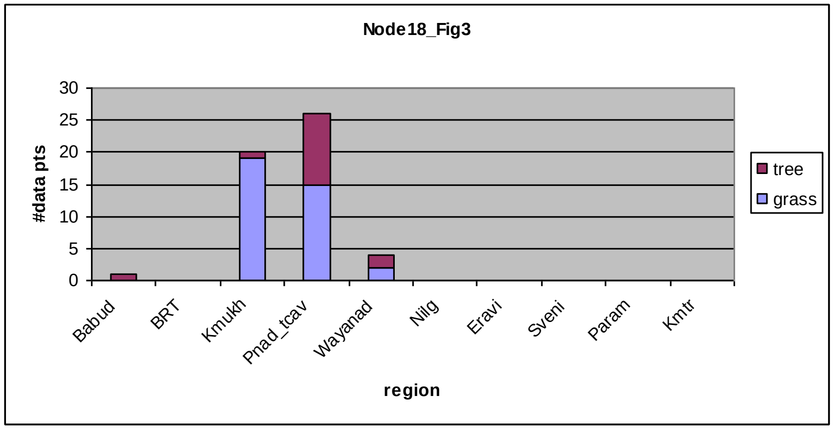
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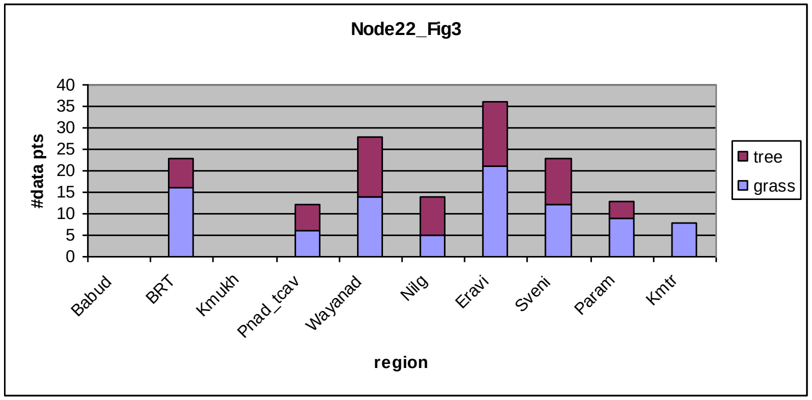
region
tree
grass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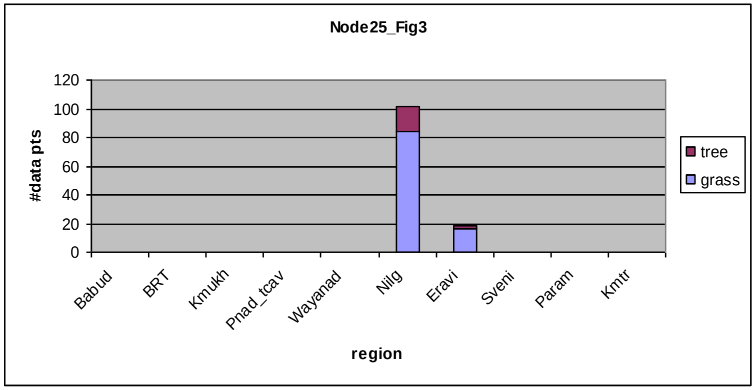
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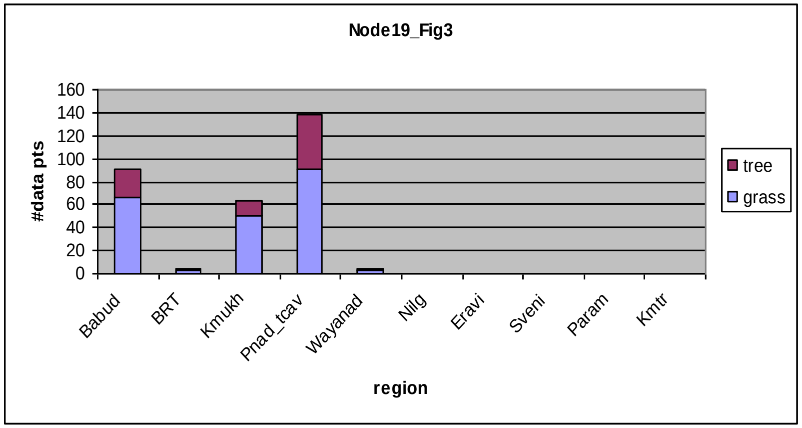
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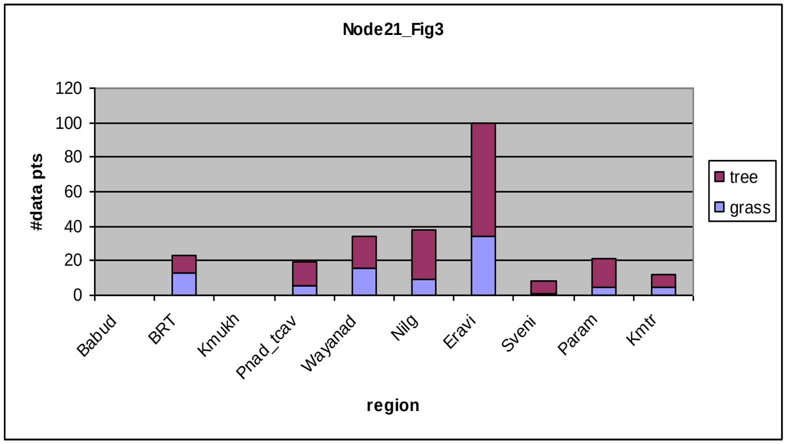
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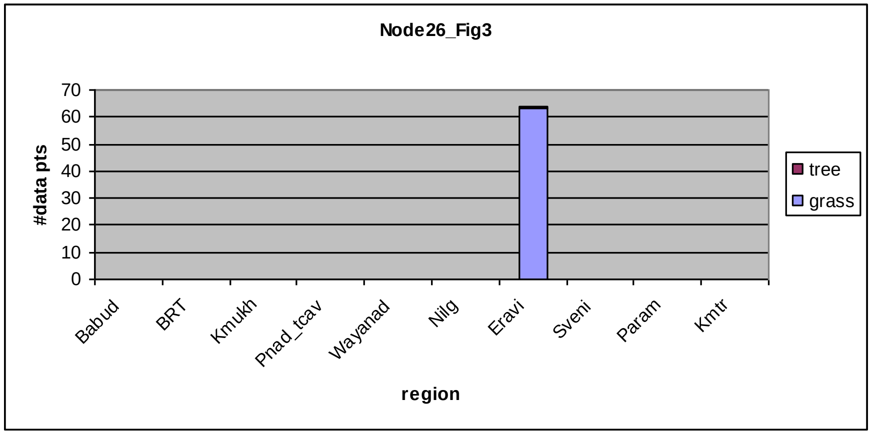
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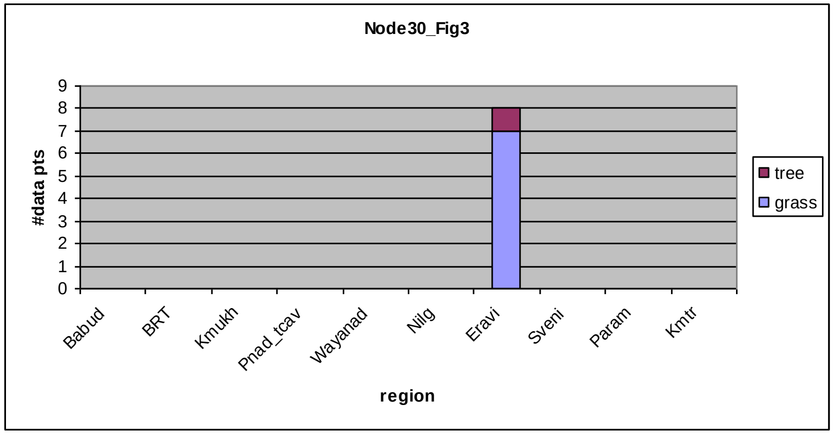
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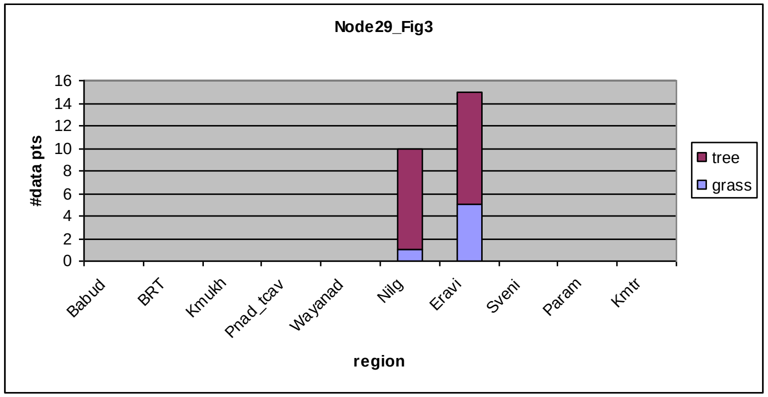
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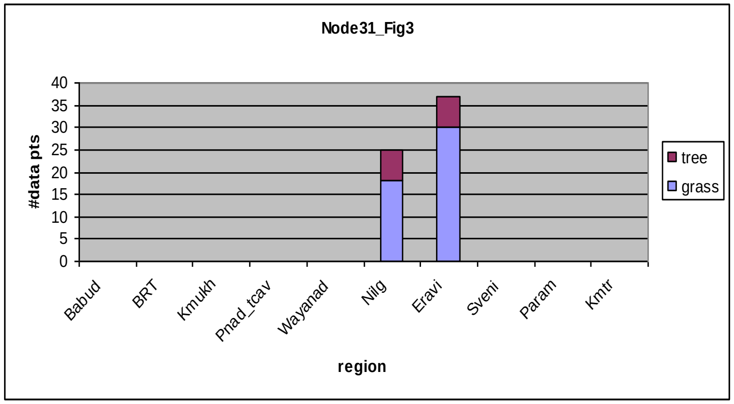
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grass

Appendix 3.1

Shola tree and shrub species from the central and southern Western Ghats

Genus	Species	ssp. / var.	Synonym	Family	Habit	Biogeog	Red List
Abelmoschus	*angulosus*				Shrub	Indo-Malay	
Acronychia	*pedunculata*		*Jambolifera pedunculata, A. barberi, A. laurifolia*	Rutaceae	Tree	Indo-Malay	
Actinodaphne	*bourdillonii*			Lauraceae	Tree	S.WG	
Actinodaphne	*bourneae*			Lauraceae	Tree	C. & S. WG	EN
Actinodaphne	*campanulata*			Lauraceae	Tree	C. & S. WG	VU
Actinodaphne	*lanata*			Lauraceae	Tree	C.WG	CR
Actinodaphne	*lawsonii*			Lauraceae	Tree	C. & S. WG	VU
Actinodaphne	*malabarica*		*A. hirsuta*	Lauraceae	Tree	S.WG	
Actinodaphne	*salicina*			Lauraceae	Tree	C. & S. WG	EN
Aglaia	*bourdillonii*			Meliaceae	Tree	C. & S. WG	
Agrostitachys	*indica*			Euphorbiaceae	Tree	Indo-Malay	
Allophylus	*rhomboidalis*			Sapindaceae			
Alseodaphne	*semecarpifolia*			Lauraceae	Tree	WGSL	
Alstonia	*venenata*			Apocynaceae	Tree	S. India	
Aphanamixis	*polystachya*			Meliaceae	Tree	Indo-Malay	
Apodytes	*dimidiata*		*A. beddomei, A. benthamiana*	Icacinaceae	Tree	Indo-Malay, Africa	
Apollonias	*arnottii*			Lauraceae	Tree	S.WG	
Antidesma	*menasu*		*A. montanum*	Euphorbiaceae	Tree	Indo-Malay	
Ardisia	*blatteri*			Myrsinaceae	Tree	S.WG	
Ardisia	*pauciflora*			Myrsinaceae	Tree	S. India, SL	
Ardisia	*rhomboidea*			Myrsinaceae	Shrub	C. & S. WG	
Ardisia	*sonchifolia*			Myrsinaceae	Shrub	C. & S. WG	EN
Atalantia	*wightii*		*A. ceylanica*	Rutaceae	Shrub	Indo-Malay	
Beilschmeida	*wightii*			Lauraceae	Tree	C. & S. WG	
Berberis	*tinctoria*			Berberidaceae	Shrub	India, Himalaya	
Bhesa	*indica*			Celastraceae	Tree	Indo-Malay	
Bischofia	*javanica*			Euphorbiaceae	Tree	Indo-Malay	
Breynia	*retusa*		*Sauropus elegantissimus*	Euphorbiaceae	Shrub	Indo-China, Himalaya, SL	CR
Bridelia	*retusa*			Euphorbiaceae	Tree	Indo-Malay	
Cajanus	*trinervius*			Leguminosae	Shrub	S. India, SL	
Calamus	*gamblei*			Arecaceae	Shrub	WG	
Callicarpa	*tomentosa*		*C. lanata*	Verbenaceae	Tree	S. India, SL	
Calophyllum	*polyanthum*			Clusiaceae	Tree	Indo-Malay	
Canthium	*dicoccum*	var. umbellatum	*Plectronia didyma, Psydrax umbellata*	Rubiaceae	Tree	Indo-Malay, China	
Canthium	*neilgherrense*			Rubiaceae	Tree	C. & S. WG	VU
Canthium	*travancoricum*		*Plectronia travancorica*	Rubiaceae	Tree	C. & S. WG	

Genus	**Species**	**ssp. / var.**	**Synonym**	**Family**	**Habit**	**Biogeog**	**Red List**
Casearia	*ovata*		*C. esculenta*	Flacourtiaceae	Tree	WGSL	
Casearia	*thwaitesii*		*C. coriacea*	Flacourtiaceae	Tree	WGSL	
Casearia	*zeylanica*			Flacourtiaceae	Tree	Indo-Malay	
Cassine	*paniculata*		*Elaeodendron paniculatum*	Celastraceae	Tree	S.WG	
Celtis	*phillipensis*			Ulmaceae	Tree	Indo-China, SL	
Celtis	*tetrandra*			Ulmaceae	Tree	Indo-Malay	
Celtis	*timorensis*			Ulmaceae	Tree	Indo-Malay	
Chionanthus	*linocieroides*		*Olea linocieroides*	Oleaceae	Tree	S.WG	
Chionanthus	*malabarica*		*C. mala-elengi*	Oleaceae	Tree	S. India	
Chionanthus	*ramiflorus*			Oleaceae	Tree	Indo-Malay	
Chrysophyllum	*roxburghii*		*C. lanceolatum*	Oleaceae	Tree	Indo-Malay	
Cinnamomum	*macrocarpum*		*C. iners*	Lauraceae	Tree	C. & S. WG	
Cinnamomum	*malabathrum*			Lauraceae	Tree	WG	
Cinnamomum	*perrottetii*			Lauraceae	Tree	C. & S. WG	VU
Cinnamomum	*riparium*			Lauraceae	Tree	C. & S. WG	VU
Cinnamomum	*sulphuratum*			Lauraceae	Tree	C. & S. WG	
Cinnamomum	*verum*			Lauraceae	Tree	WGSL	
Cinnamomum	*walaiwarense*			Lauraceae	Tree	S.WG	
Cinnamomum	*wightii*			Lauraceae	Tree	C. & S. WG	
Cipadessa	*baccifera*		*Melia baccifera*	Meliaceae	Shrub	Indo-Malay	
Cissampelopsis	*walkeri*			Asteraceae	Tree	S. India, SL	
Clerodendrum	*viscosum*		*C. infortunatum*	Verbenaceae	Shrub	Indo-Malay	
Cotoneaster	*buxifolius*			Rosaceae	Shrub	WG	
Crotalaria	*barbata*			Leguminosae	Shrub	C. & S. WG	
Crotalaria	*calycina*			Leguminosae	Shrub	Paleotropics	
Crotalaria	*formosa*			Leguminosae	Shrub	S.WG	
Crotalaria	*madurensis*			Leguminosae	Shrub	WG	
Crotalaria	*notonii*			Leguminosae	Shrub	India	
Crotalaria	*semperflorens*			Leguminosae	Shrub	Indo-Malay	
Croton	*laccifer*			Euphorbiaceae	Tree	S. India, SL	
Cryptocarya	*bourdillonii*		*C. wightiana*	Lauraceae	Tree	S. India	
Cryptocarya	*lawsonii*			Lauraceae	Tree	C. & S. WG	
Cryptocarya	*neilgherrensis*		*C. stocksii*	Lauraceae	Tree	S. India	
Daphniphyllum	*glaucescens*		*D. lancifolium*	Daphniphyllaceae	Tree	Indo-Malay, E. Asia	
Daphniphyllum	*neilgherrense*			Daphniphyllaceae	Tree	Indo-Malay	
Debregeasia	*longifolia*		*D. velutina*	Urticaceae	Shrub	Indo-Malay	
Dendrophthoe	*memecylifolia*			Loranthaceae	Hemi-parasite	WG	
Dendrophthoe	*neelgherrensis*			Loranthaceae	Hemi-parasite	S. India, SL	
Dendrophthoe	*trigona*			Loranthaceae	Hemi-parasite	WG	
Desmodium	*ferrugineum*			Leguminosae	Shrub	S. India, SL	
Dodonea	*viscosa*			Sapindaceae	Shrub	Pantropical	

Genus	Species	ssp. / var.	Synonym	Family	Habit	Biogeog	Red List
Drypetes	*elata*		*Hemicyclia elata*	Euphorbiaceae	Tree	C. & S. WG	
Drypetes	*wightii*		*Hemicyclia wightii*	Euphorbiaceae	Tree	C. & S. WG	
Elaeocarpus	*munronii*		*Monocera munronii*	Elaeocarpaceae	Tree	C. & S. WG	
Elaeocarpus	*recurvatus*		*E. ferrugineous*	Elaeocarpaceae	Tree	C. & S. WG	
Elaeocarpus	*serratus*			Elaeocarpaceae	Tree	Indo-Malay	
Elaeocarpus	*tuberculatus*			Elaeocarpaceae	Tree	Indo-Malay	
Elaeocarpus	*variabilis*		*E. glandulosus, E. oblongus*	Elaeocarpaceae	Tree	WG	
Erythroxylum	*moonii*		*E. acuminatum*	Erythroxylaceae	Tree	WGSL	
Eugenia	*roxburghii*		*E. bracteata*	Myrtaceae		S. India, SL	
Euonymus	*angulatus*			Celastraceae	Tree	C. & S. WG	VU
Euonymus	*crenulatus*			Celastraceae	Tree	C. & S. WG	
Euonymus	*dichotomus*			Celastraceae	Tree	C. & S. WG	
Euonymus	*indicus*			Celastraceae	Tree	WG	
Euonymus	*serratifolius*			Celastraceae	Shrub	C. & S. WG	EN
Eurya	*nitida*		*E. japonica*	Theaceae	Tree	Indo-Malay, China	
Excoecaria	*oppositifolia*	var. crenulata	*E. robusta*	Euphorbiaceae	Tree	S. India, SL	
Fagraea	*ceilanica*		*F. obovata*	Loganiaceae	Tree	Indo-Malay	
Ficus	*drupacea*		*F. mysorensis*	Moraceae	Tree	Indo-Malay	
Flaucourtia	*indica*			Flacourtiaceae	Tree	Paleotropics	
Flaucourtia	*montana*			Flacourtiaceae	Tree	WG	
Garcinia	*cowa*			Clusiaceae	Tree	Indo-Malay	
Garcinia	*gummi-gutta*		*G. cambogia*	Clusiaceae	Tree	WGSL	
Gaultheria	*fragrantissima*			Ericaceae	Shrub	Indo-Malay	
Glochidion	*ellipticum*		*G. malabaricum*	Euphorbiaceae	Tree	C. & S. WG	
Glochidion	*heyneanum*		*G. velutinum*	Euphorbiaceae	Tree	Indo-China, Himalaya	
Glochidion	*neilgherrense*		*G. candolleanum*	Euphorbiaceae	Tree	WGSL	
Gomphandra	*coriacea*			Icacinaceae	Tree	WGSL	
Goniothalamus	*wightii*			Annonaceae	Tree	S.WG	
Gordonia	*obtusa*			Theaceae	Tree	WGSL	
Gnidia	*glauca*		*Lasiosiphon erioephalus*	Thymelaeceae	Tree	India, SL, Africa	
Hedyotis	*articularis*		*Olendlandia articularis*	Rubiaceae	Shrub	C. & S. WG	
Hedyotis	*buxifolia*			Rubiaceae	Shrub	S.WG	
Hedyotis	*hirsutissima*			Rubiaceae	Shrub	C. & S. WG	
Hedyotis	*leschenaultiana*	var. leschenaultiana	*H. stylosa*	Rubiaceae	Shrub	C. & S. WG	
Hedyotis	*swertioides*			Rubiaceae	Shrub	C. & S. WG	
Helixanthera	*intermedia*			Loranthaceae	Hemi-parasite	C. & S. WG	
Helixanthera	*obtusata*			Loranthaceae	Hemi-parasite	C. & S. WG	

Genus	**Species**	**ssp. / var.**	**Synonym**	**Family**	**Habit**	**Biogeog**	**Red List**
Heritiera	*papilio*			Sterculiaceae	Tree	India	
Holigarna	*nigra*			Anacardiaceae	Tree	C. & S. WG	
Hydnocarpus	*alpina*			Flacourtiaceae	Tree	S. India, SL	
Hypericum	*japonicum*			Hypericaceae	Shrub	Indo-Malay, Australia, New Zealand, E. Asia	
Hypericum	*mysurense*			Hypericaceae	Shrub	Indo-Malay	
Ilex	*denticulata*			Aquifoliaceae	Tree	Indo-China, SL	
Ilex	*gardneriana*			Aquifoliaceae	Tree	C. & S. WG	CR
Ilex	*walkeri*			Aquifoliaceae	Tree	India, SL	
Ilex	*wightiana*			Aquifoliaceae	Tree	S. India, SL	
Ixora	*notoniana*			Rubiaceae	Shrub	WG	
Isonandra	*lanceolata*			Sapotaceae	Tree	S. India, SL	
Isonandra	*perrottetiana*		*I. candolleana*	Sapotaceae	Tree	C. & S. WG	
Isonandra	*montana*			Sapotaceae	Tree	S. India, SL	
Jasminum	*cuspidatum*			Oleaceae	Shrub	S. India, SL	
Lasianthus	*acuminatus*		*L. coffeoides*	Rubiaceae	Shrub	WG	
Lasianthus	*blumeanus*			Rubiaceae	Shrub	S.WG	
Lasianthus	*ciliatus*			Rubiaceae	Shrub	C. & S. WG	VU
Lasianthus	*venulosus*			Rubiaceae	Shrub	C. & S. WG	
Leucus	*lanceifolia*			Lamiaceae	Tree	S. India	
Ligustrum	*lucidum*		*L. roxburghii*	Oleaceae	Tree	E. Asia	
Ligustrum	*perrottetii*		*L. neilgherrense*	Oleaceae	Tree	WG	
Ligustrum	*robustrum*			Oleaceae		S. India	
Litsea	*bourdillonii*			Lauraceae	Tree	WG	
Litsea	*deccanensis*			Lauraceae	Tree	S. India, SL	
Litsea	*floribunda*			Lauraceae	Tree	WG	
Litsea	*glabrata*			Lauraceae	Tree	C. & S. WG	
Litsea	*ghatica*			Lauraceae	Tree	WG	
Litsea	*ligustrina*		*L. quinqueflora*	Lauraceae	Tree	S. India	VU
LItsea	*myristicaefolia*			Lauraceae	Tree	Indo-Malay	
Litsea	*mysorensis*			Lauraceae	Tree	C. & S. WG	
Litsea	*oleiodes*			Lauraceae	Tree	S. India	
Litsea	*stocksii*	var. glabrata		Lauraceae	Tree	WG	
Litsea	*wightiana*	var. wightiana		Lauraceae	Tree	WG	
Lobelia	*leschenaultiana*			Lobeliaceae	Shrub	India, SL	
Lonicera	*ligustrina*			Caprifoliaceae	Shrub	Indo-China, Himalaya	
Macaranga	*indica*			Euphorbiaceae	Tree	India, SL	
Macrosolen	*parasiticus*			Loranthaceae	Shrub	S. India, SL	
Maesa	*Indica*		*M. perrottetiana*	Myrsinaceae	Tree	Indo-Malay	
Mahonia	*leschenaultii*		*Berberis nepalensis, B. leschenaultii*	Berberidaceae	Shrub	C. & S. WG	

Genus	Species	ssp. / var.	Synonym	Family	Habit	Biogeog	Red List
Mallotus	*phillipensis*			Euphorbiaceae	Tree	Indo-Malay, Australia	
Mallotus	*tetracoccus*		*M. albus*	Euphorbiaceae	Tree	Indo-China, Himalaya, SL	
Mastixia	*arborea*		*Bursinopetalum arboreum*	Cornaceae	Tree	C. & S. WG	
Melicope	*lunu-ankenda*		*Euodia lunu-ankenda*	Rutaceae	Tree	Indo-Malay	
Memecylon	*flavescens*			Melastomataceae	Tree	C. & S. WG	EN
Memecylon	*randerianum*		*M. malabaricum, M. amplexicaule*	Melastomataceae	Tree	C. & S. WG	
Memecylon	*sisparense*			Melastomataceae	Tree	C. & S. WG	CR
Memecylon	*umbellatum*		*M. edule*	Melastomataceae	Tree	S. India, SL	
Meliosma	*simplicifolia*	ssp. pungens	*M. wightii*	Sabiaceae	Tree	Indo-Malay, China	
Meliosma	*pinnata*	ssp. barbulata	*Meliosma arnottiana*	Sabiaceae	Tree	Indo-Malay, China	
Michelia	*nilagirica*			Magnoliaceae	Tree	WG	
Microtropis	*microcarpa*			Celastraceae	Tree	C. & S. WG	
Microtropis	*ovalifolia*			Celastraceae	Tree	C. & S. WG	
Microtropis	*ramiflora*			Celastraceae	Tree	S. India, SL	
Microtropis	*stocksii*			Celastraceae	Tree	WG	
Mitragyna	*parvifolia*			Rubiaceae	Tree	Indo-Malay	
Myristica	*dactyloides*			Myristicaceae	Tree	S. India, SL	
Neolitsea	*cassia*			Lauraceae	Tree	Indo-Malay	
Neolitsea	*fischeri*			Lauraceae	Tree	S.WG	VU
Neolitsea	*foliosa*		*N. umbrosa*	Lauraceae	Tree	S. India	
Neolitsea	*zeylanica*			Lauraceae	Tree	Indo-Malay	
Neolitsea	*scrobiculata*			Lauraceae	Tree	C. & S. WG	
Nothopegia	*beddomei*			Anacardiaceae	Tree	S. India, SL	
Nothopegia	*heyneana*	var. heyneana	*N. colebrookiana*	Anacardiaceae	Tree	S. India	
Nothopodytes	*nimmoniana*		*N. foetida*	Icacinaceae	Tree	Indo-Malay	
Olea	*paniculata*		*O. glandulifera*	Oleaceae	Tree	India, Himalaya	
Osbeckia	*aspera*			Melastomataceae	Shrub	S. India, SL	
Osbeckia	*cupularis*			Melastomataceae	Shrub	C. & S. WG	
Osbeckia	*gracilis*			Melastomataceae	Shrub	C. & S. WG	
Osbeckia	*reticulata*			Melastomataceae	Shrub	C. & S. WG	
Pavetta	*blanda*			Rubiaceae	Tree	S. India, SL	
Pavetta	*breviflora*			Rubiaceae	Tree	C. & S. WG	
Persea	*macrantha*		*Machilus macrantha*	Lauraceae	Tree	S. India, SL	
Phoebe	*lanceolata*			Lauraceae	Tree	Indo-Malay	
Phoebe	*paniculata*			Lauraceae	Tree	India, Burma	
Phoebe	*wightii*			Lauraceae	Tree	India, Burma	
Photinia	*intergrifolia*	vars. sublanceolata	*P. notoniana*	Rosaceae	Tree	India, SL	

Genus	Species	ssp. / var.	Synonym	Family	Habit	Biogeog	Red List
Pittosporum	*dasycaulon*			Pittosporaceae	Tree	C. & S. WG	
Pittosporum	*neelgherrense*			Pittosporaceae	Tree	WG	
Pittosporum	*tetraspermum*			Pittosporaceae	Tree	S. India, SL	
Polygala	*arillata*			Polygalaceae	Shrub	Indo-Malay, China	
Prinsepia	*utilis*			Rosaceae	Shrub	India, Himalaya	
Prunus	*ceylanica*			Rosaceae	Tree	Indo-Malay	EN
Psychotria	*nilgiriensis*	var. astephana	*P. congesta*	Rubiaceae	Shrub	C. & S. WG	EN
Psychotria	*sohmeri*		*P. elongata*	Rubiaceae	Shrub	S. India, SL	
Psychotria	*truncata*			Rubiaceae	Shrub	WG	
Rapanea	*capitellata*			Myrsinaceae	Tree	India, Himalaya	
Rapanea	*daphnoides*			Myrsinaceae	Shrub	C. & S. WG	
Rapanea	*thwaitesii*			Myrsinaceae	Tree	S.WG	
Rapanea	*wightiana*	*Myrsine wightiana*		Myrsinaceae	Tree	S. India, SL	
Rauvolfia	*verticillata*	*R. densiflora*		Apocynaceae	Shrub	Indo-malay	
Rhododendron	*arboreum*	nilagiricum		Ericaceae	Tree	C. & S. WG	
Rhodomyrtus	*tomentosa*			Myrtaceae	Tree	Indo-Malay, China	
Rubus	*ellipticus*			Rosaceae	Shrub	Indo-Malay	
Rubus	*fairholmianus*			Rosaceae	Shrub	Indo-Malay	
Rubus	*niveus*	*R. mysorensis*		Rosaceae	Shrub	Indo-Malay, China	
Rubus	*racemosus*			Rosaceae	Shrub	C. & S. WG	
Rubus	*rugosus*	var. sub-lanceolata		Rosaceae	Shrub	Indo-Malay	
Saprosma	*foetens*	*ssp. ceylanicum*		Rubiaceae	Shrub	C. & S. WG	
Saprosma	*fragrans*			Rubiaceae	Shrub	C. & S. WG	VU
Sarcococca	*saligna*			Buxaceae	Tree	Indo-Malay	
Schefflera	*capitata*			Araliaceae	Tree	WG	
Schefflera	*racemosa*			Araliaceae	Tree	C. & S. WG	
Schefflera	*rostrata*			Araliaceae	Tree	C. & S. WG	
Schefflera	*wallichiana*		*Paratropia wallichiana*	Araliaceae	Tree	S. India, SL	
Scolopia	*crenata*		*Phoberos crenata*	Flacourtiaceae	Tree	Indo-Malay	
Semecarpus	*travancorica*			Anacardiaceae	Tree	S.WG	
Strobilanthes	*decurrens*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*foliosa*			Acanthaceae	Shrub	S. India	
Strobilanthes	*gracilis*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*heyneanus*			Acanthaceae	Shrub	India, SL	
Strobilanthes	*homotropa*			Acanthaceae	Shrub		
Strobilanthes	*integrifolius*			Acanthaceae	Shrub	WG	
Strobilanthes	*isophylla*			Acanthaceae	Shrub	India	
Strobilanthes	*kunthianus*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*lanatus*			Acanthaceae	Shrub	C. & S. WG	

Genus	Species	ssp. / var.	Synonym	Family	Habit	Biogeog	Red List
Strobilanthes	*lawsonii*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*lurida*			Acanthaceae	Shrub		
Strobilanthes	*micranthus*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*neilgherrensis*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*neoasper*			Acanthaceae	Shrub	WG	
Strobilanthes	*papillosus*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*wightianus*			Acanthaceae	Shrub	C. & S. WG	
Strobilanthes	*zenkerianus*			Acanthaceae	Shrub	C. & S. WG	
Solanum	*denticulatum*			Solanaceae	Shrub	S. India	
Solanum	*erianthum*			Solanaceae	Shrub	Indo-Malay, Australia	
Symplocos	*anamallayana*			Symplocaceae	Tree	S.WG	EN
Symplocos	*cochinchinensis*	ssp. laurina	*S. spicata*	Symplocaceae	Tree	Indo-Malay	
Symplocos	*foliosa*			Symplocaceae	Tree	C. & S. WG	
Symplocos	*macrocarpa*		*S. kanarana*	Symplocaceae	Tree	S.WG	VU
Symplocos	*macrophylla*	ssp. *macrophylla*	*S. gardneriana*	Symplocaceae	Tree	India, SL	
Symplocos	*macrophylla*	ssp. *microphylla*		Symplocaceae	Tree	C.WG	
Symplocos	*macrophylla*	ssp. *rosea*		Symplocaceae	Tree	C. & S. WG	
Symplocos	*monatha*			Symplocaceae	Shrub		
Symplocos	*obtusa*			Symplocaceae	Tree	S. India, SL	
Symplocos	*pendula*		*S. sessilis*	Symplocaceae	Tree	Indo-Malay	
Symplocos	*racemosa*		*S. beddomei*	Symplocaceae	Tree	Indo-China	
Syzygium	*calophyllifolium*			Myrtaceae	Tree	WGSL	
Syzygium	*caryophyllatum*		*S. caryophyllaeum, Myrtus caryophyllata*	Myrtaceae	Tree	WGSL	EN
Syzygium	*cumini*			Myrtaceae	Tree	Indo-Malay	
Syzygium	*densiflorum*		*S.arnottianum*	Myrtaceae	Tree	C. & S. WG	VU
Syzygium	*hemisphericum*			Myrtaceae	Tree	S. India, SL	
Syzygium	*lanceolatum*		*S. wightianum*	Myrtaceae	Tree	S. India, SL	
Syzygium	*grande*		*S. tamilnadensis. S. montanum*	Myrtaceae	Tree	C. & S. WG	
Tarenna	*asiatica*		*Rondeletia asiatica*	Rubiaceae	Shrub	C. & S. WG	
Taxillus	*recurvus*			Loranthaceae	Hemi-parasite	WG	
Ternstroemia	*gymnanthera*		*T. japonica*	Theaceae	Tree	Indo-Malay, China	
Trema	*orientalis*		*Celtis orientalis*	Ulmaceae	Tree	Paleotropics, Australia	
Trichilia	*connaroides*		*Zanthoxylum connaroides*	Meliaceae	Tree	Indo-Malay	
Tricalysia	*apiocarpa*		*Dicospermum apiocarpum*	Rubiaceae	Tree	WG	CR
Turpinia	*cochinchinensis*		*T. nepalensis*	Staphylaceae	Tree	Indo-Malay, China	

Genus	Species	ssp. / var.	Synonym	Family	Habit	Biogeog	Red List
Vaccinium	*leschenaultii*			Vacciniaceae	Tree	India, Burma, SL	
Vaccinium	*neilgherrense*			Vacciniaceae	Tree	C. & S. WG	
Vernonia	*arborea*		*V. monosis*	Asteraceae	Tree	Indo-Malay	
Vernonia	*bourneana*			Asteraceae	Tree	C. & S. WG	
Viburnum	*coriaceum*		*V. capitellatum*	Caprifoliaceae	Tree	Indo-Malay	
Viburnum	*cylindricum*			Caprifoliaceae	Tree	Indo-Malay	
Viburnum	*erubescens*			Caprifoliaceae	Tree	India, SL	
Viburnum	*hebanthum*			Caprifoliaceae	Tree	C. & S. WG	
Viburnum	*punctatum*		*V. acuminatum*	Caprifoliaceae	Tree	Indo-Malay	
Wendlandia	*thyrsoidea*		*W. notoniana*	Rubiaceae	Tree	S. India, SL	
Xantolis	*tomentosa*		*Sideroxylum tomentosum*	Sapotaceae	Tree	Indo-Malay	
Xenacanthus	*pulneynensis*			Acanthaceae	Shrub	S. India	
Zizyphus	*jujuba*			Rhamnaceae	Shrub	C. Asia, China	

List compiled from the following sources:

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Appendix 3.2

Shola tree and shrub species of the Western Upper Nilgiris Plateau above 1800m

Species	ssp. / var.	Synonym	Family	Endemic	Habit
Actinodaphne wightiana (Kuntze) Noltie		*A. hirsute, A. malabarica*	Lauraceae	Y	Tree
Actinodaphe bourdillonii Gamble			Lauraceae	Y	Tree
Acronychia pedunculata (L.) Miq.			Rutaceae	N	Tree
Apodytes dimidiata Meyer ex Arn.		*A. beddomei*, *A. benthamiana*	Icacinaceae	N	Tree
Beilschmeida wightii Benth. ex Hook. f.			Lauraceae	Y	Tree
Berberis tinctoria Lesch.			Berberidaceae	N	Shrub
Canthium dicoccum (Gaertn.) Teys. & Binn.	var. umbellatum (Wt.) Sant. & Merch.	*Plectronia didyma, Psydrax umbellata*	Rubiaceae	N	Tree
Casearia sp.			Flacourtiaceae		Tree
Casearia thwaitesii Briq.		*C. coriacea*	Flacourtiaceae	N	Tree
Celtis tetrandra Roxb.			Ulmaceae	N	Tree
Cestrum aurantiacum Lindl.			Solanaceae	N	Shrub
Cinnamomum macrocarpum Hook.f.		*C. iners*	Lauraceae	Y	Tree
Cinnamomum malabatrum (Burm.f.) J.Presl		*C. iners*	Lauraceae	Y	Tree
Cinnamomum riparium Gamble			Lauraceae	Y	Tree
Cinnamomum sulphuratum Nees			Lauraceae	Y	Tree
Cinnamomum verum J.Presl			Lauraceae	N	Tree
Cinnamomum walaiwarense Kosterm.			Lauraceae	Y	Tree
Cinnamomum wightii Meissn.			Lauraceae	Y	Tree
Cissampelopsis walkeri (Arn.) C.Jeffrey & Y.L.Chen			Asteraceae	N	Tree
Crotalaria semperflorens Vent.			Papilionaceae	N	Shrub
Cryptocarya lawsonii Gamble			Lauraceae	Y	Tree
Cryptocarya neilgherrensis Meisner			Lauraceae	Y	Tree
Daphniphyllum neilgherrense (Wt.) Rosenth.			Daphniphyllaceae	N	Tree
Elaeocarpus munronii Mast.			Elaeocarpaceae	Y	Tree
Elaeocarpus recurvatus Corner		*E. ferrugineus*	Elaeocarpaceae	Y	Tree
Elaeocarpus variablis Zmarzty		*E. glandulosus, E. oblongus*	Elaeocarpaceae	Y	Tree
Euonymus crenulatus Wall.			Celastraceae	Y	Tree
Eurya nitida Korth.			Theaceae	N	Tree
Gaultheria fragrantissima Wall.			Ericaceae	Y	Shrub
Glochidion heyneanum Wight		*G. velutinum*	Euphorbiaceae	N	Tree
Glochidion neilgherrense Wight		*G. candolleanum*	Euphorbiaceae	Y	Tree
Gomphandra coriacea Wight			Icacinaceae	N	Tree
Gordonia obtusa Wall. ex Wight			Theaceae	Y	Tree
Hedyotis articularis R.Br. ex G.Don		*Olendlandia articularis*	Rubiaceae	Y	Shrub
Ilex denticulata Wall. ex Wight			Aquifoliaceae	N	Tree

Species	ssp/var	Synonym	Family	Endemic	Habit
Ilex wightiana Wall. ex Wight			Aquifoliaceae	N	Tree
Isonandra lanceolata Wight			Sapotaceae	N	Tree
Isonandra perrottetiana A.DC.		*Isonandra candolleana*	Sapotaceae	Y	Tree
Isonandra montana (Thw.) Gamble			Sapotaceae	Y	Tree
Lasianthus venulosus Wight			Rubiaceae	Y	Shrub
Leucas lanceaefolia Desf.			Lamiaceae	N	Shrub
Lonicera ligustrina Wall.			Caprifoliaceae	N	Shrub
Litsea floribunda Gamble			Lauraceae	Y	Tree
Litsea oleiodes Hook.f.			Lauraceae	Y	Tree
Litsea stocksii (Meisner) Hook. f.	var. glabrata		Lauraceae	Y	Tree
Litsea wightiana (Nees) Hook. f.	var. wightiana		Lauraceae	Y	Tree
Maesa indica (Roxb.) A.DC.			Myrsinaceae	N	Tree
Mahonia leschenaultia (Wall. ex Wight & Arn.) Takeda		*Berberis nepalensis, B. leschenaultii*	Berberidaceae	Y	Tree
Melicope lunu-ankenda (Gaertn.) Hartley		*Euodia lunu-ankenda*	Rutaceae	N	Tree
Memecylon randerianum SM & MR Almeida		*M. malabaricum, M. amplexicaule*	Melastomataceae	Y	Tree
Meliosma simplicifolia (Roxb.) Walp.	pungens		Sabiaceae	N	Tree
Meliosma pinnata (Roxb.) Maxim.	barbulata	*M. arnottiana*	Sabiaceae	N	Tree
Michelia nilagirica Zenk.			Magnoliaceae	Y	Tree
Microtropis sp.			Celastraceae		Tree
Microtropis microcarpa Wight			Celastraceae	Y	Tree
Microtropis ramiflora Wight			Celastraceae	N	Tree
Neolitsea zeylanica (Nees & T. Nees) Merr.			Lauraceae	N	Tree
Neolitsea scrobiculata (Meisner) Gamble			Lauraceae	Y	Tree
Nothapodytes nimmoniana (J.Graham) Mabb.			Icacinaceae	N	Tree
Olea paniculata R.Br.			Oleaceae	N	Tree
Pavetta breviflora DC.			Rubiaceae	Y	Tree
Phoebe paniculata (Nees) Nees		*P. wightii*	Lauraceae	N	Tree
Photinia intergrifolia Lindl.	vars. sublanceolata & serratifolia	*P. notoniana*	Rosaceae	Y	Tree
Pittosporum dasycaulon Miq.			Pittosporaceae	Y	Tree
Pittosporum tetraspermum Wight & Arn.			Pittosporaceae	N	Tree
Prunus ceylanica (Wight) Miq.			Rosaceae	N	Tree
Psychotria nilgiriensis Deb & M.G. Gangop.		*P.congesta*	Rubiaceae	Y	Shrub
Rapanea wightiana (Wall. ex A. DC.) Mez		*Myrsine wightiana*	Myrsinaceae	N	Tree
Rhododendron arboreum Smith	nilagiricum (Zenk.)		Ericaceae	Y	Tree
Rhodomyrtus tomentosa (Aiton) Hassk.			Myrtaceae	Y	Shrub

Species	**ssp/var**	**Synonym**	**Family**	**Endemic**	**Habit**
Saprosma ceylanicum (Gardner) Bedd.		*S. foetens* ssp. *ceylanicum*	Rubiaceae	Y	Tree
Saprosma fragrans (Bedd.) Bedd			Rubiaceae	N	Shrub
Sarcococca saligna (D.Don) Muell.-Arg.		*S. pruniformis*	Buxaceae	N	Tree
Schefflera capitata (Wight & Arn.) Harms		*Paratropia capitata*	Araliaceae	Y	Tree
Scolopia crenata (Wt. & Arn.) Clos		*Phoberos crenata*	Flacourtiaceae	N	Tree
Strobilanthes sp.			Acanthaceae		Shrub
Strobilanthes wightianus			Acanthaceae	Y	Shrub
Strobilanthes neilgherrensis			Acanthaceae	Y	Shrub
Strobilanthes neoasper			Acanthaceae	Y	Shrub
Solanum denticulatum Blume			Solanaceae	N	Shrub
Symplocos macrophylla Wall. ex DC	ssp. *microphylla*	*S. gardneriana*	Symplocaceae	Y	Tree
Symplocos cochinchinensis (Lour.) S. Moore	ssp. *laurina*	*S. spicata*	Symplocaceae	N	Tree
Symplocos foliosa Wight			Symplocaceae	Y	Tree
Symplocos obtusa Wall. ex G. Don			Symplocaceae	Y	Tree
Syzygium cumini (L.) Skeels		*S. jambolanum*	Myrtaceae	N	Tree
Syzygium wightianum Wall. ex Wight & Arn.		*S. lanceolatum*	Myrtaceae	Y	Tree
Syzygium densiflorum Wall. ex Wight & Arn.		*S.arnottianum*	Myrtaceae	Y	Tree
Syzygium grande (Wight) Walp.		*S. tamilnadensis*	Myrtaceae	Y	Tree
Syzygium calophyllifolium (Wight) Walp.		*Eugenia calophyllifolia*	Myrtaceae	Y	Tree
Tarenna asiatica (L.) Kuntze ex K.Schum.		*Rondeletia asiatica*	Rubiaceae	Y	Shrub
Ternstroemia gymnanthera (Wight & Arn.) Sprague			Theaceae	N	Tree
Trichilia connaroides (W.& A.) Bentv.		*Zanthoxylum connaroides*	Meliaceae	N	Tree
Turpinia cochinchinensis (Lour.) Merr.		*T. nepalensis*	Staphylaceae	N	Tree
Vaccinium leschenaultia Wight			Vacciniaceae	N	Tree
Viburnum hebanthum Wight & Arn.			Caprifoliaceae	Y	Tree
Xantolis tomentosa (Roxb.) Raf.		*Sideroxylon tomentosum*	Sapotaceae	N	Tree

Appendix 4.1

Protocol for analysis of soil texture

Samples were sieved using a 2mm mesh, large particles were ground before placing through the sieve. Organic matter and rock fragments were separated and weighed and the colour and consistency of each sample noted. Forty grams of soil from each of the subsamples from each plot was then combined and mixed thoroughly to give a combined sample for the plot. Of this, 40g was weighed and placed in food grade plastic texture containers. Hundred ml of 5% solution of Sodium Hexametaphosphate (NaHMP) solution was added to each container and shaken. An additional container in which 100 ml of NaHMP solution but no soil was also prepared to serve as the blank. The closed containers were placed overnight on a mechanical shaker set to slow-medium speed and left there to shake overnight for a minimum of 12 hours.

After this, the soil solution was transferred from the texture containers to 1L graduated glass cylinders, which were then filled up to the 1L mark (lower meniscus) with distilled water stored at room temperature i.e. final solution of soil, NaHMP and water together made up 1L in volume. The blank solution was treated in the same way as the soil solution. The contents of each cylinder were then mixed using a plunger (10 short strokes followed by 10 long strokes), after which the plunger was removed, a hydrometer was placed in the cylinder and the start time noted. Hydrometer readings (upper meniscus; added 1 to these readings at the time of texture calculations) were taken at 30 sec, 40sec, and 1 minute from start. This procedure was repeated for all the cylinders. After this the solution in each cylinder was allowed to settle for a period of 2 hours from the start time and a final hydrometer reading was taken for each cylinder. As water temperature affects specific density readings of soil solution, I corrected for this by adding 0.4g/L to the hydrometer reading for every degree above 20°C or subtracting 0.4 g/L for every degree below 20°C.

Ten grams of each soil sample was weighed and placed separately into paper bags (wt. 1.35g) and left overnight in a 105°C oven. Samples were removed after 24 hours and reweighed to assess gravimetric soil moisture content.

Percent sand, silt and clay was calculated using the following formulae:
% sand = (original conc. – corrected 40sec reading)/ (original conc.)
% clay = (corrected 2 hr reading/original conc.)*100
% silt = 100%- (% sand+ % clay)
Where, original conc. of the soil solution = (air dried soil weight/ (1+GWC))/1000mL.
corrected hydrometer readings => soil reading – blank reading g/L

Appendix 4.2

Results of soil texture and nutrients analysis for vegetation plots

The results of this texture analysis show that most of the plots had soil texture that varied from loamy sand to sandy loam the mean sand content was 75.13% ± 5.67, mean silt content was 16.75% ± 4.34 and mean clay content was 8.11% ± 2.95 (Fig. 1). The color of the samples varied greatly from light brown to very dark brown (almost black). There was also high organic matter content consisting of small roots or leaf and bark fragments in the samples.

Soil carbon and nitrogen:

Soil carbon and nitrogen was measured using a C/H/N analyzer (LECO). The analyzer uses combustion at very high temperatures to break down the soil into simple compounds which are then measured by infrared spectroscopy. Approximately 10g of soil from each plot was first ground to pass through a fine mesh sieve (0.25mm). Only approximately 0.15g of this was used for the LECO analysis. Each batch of samples was processed along with a blank as well as a set of known soil standards to calibrate the readings.

The results show that the average percent carbon in the samples was 11.27% ± 3.68 and the average percent nitrogen was 0.86 ± 0.22 (Fig. 2).

Soil cations:

Concentration of ten soil nutrients were measured in the lab from Mehlich III extracts using an ICP-OES (Thermo Fischer iCAP 6000). Figure 3 shows the range of concentrations for each of the cations measured across the plots. Results for K are not shown owing to problems with ICP results for some of the plots.

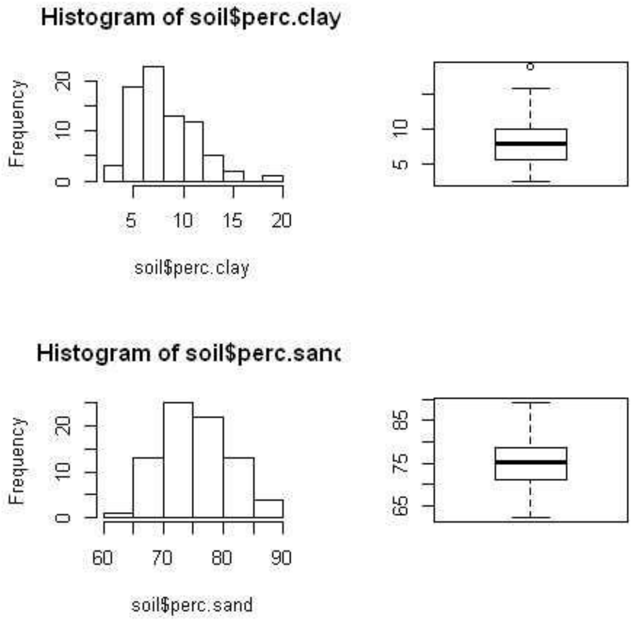


Figure 1: Histograms and boxplots of percent sand and clay for vegetation plots

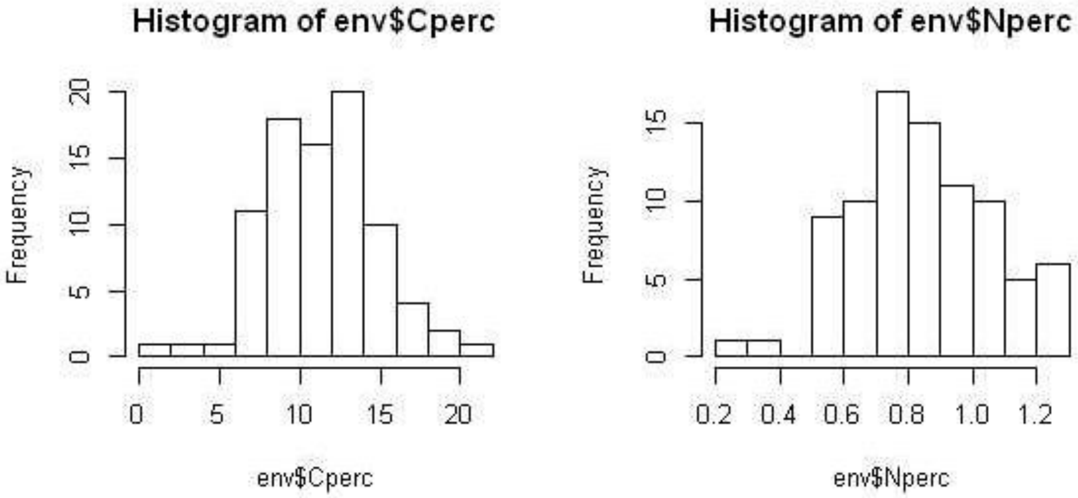
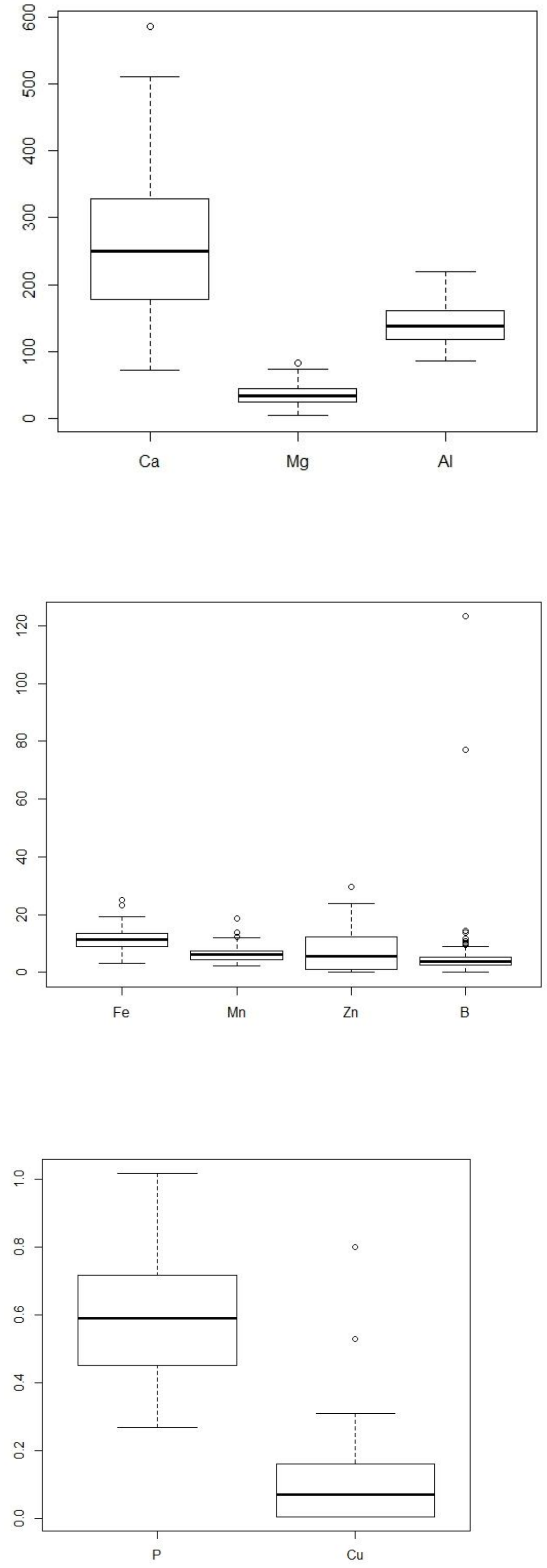


Figure 2: Histograms of percent Carbon and Nitrogen in soils of vegetation plots

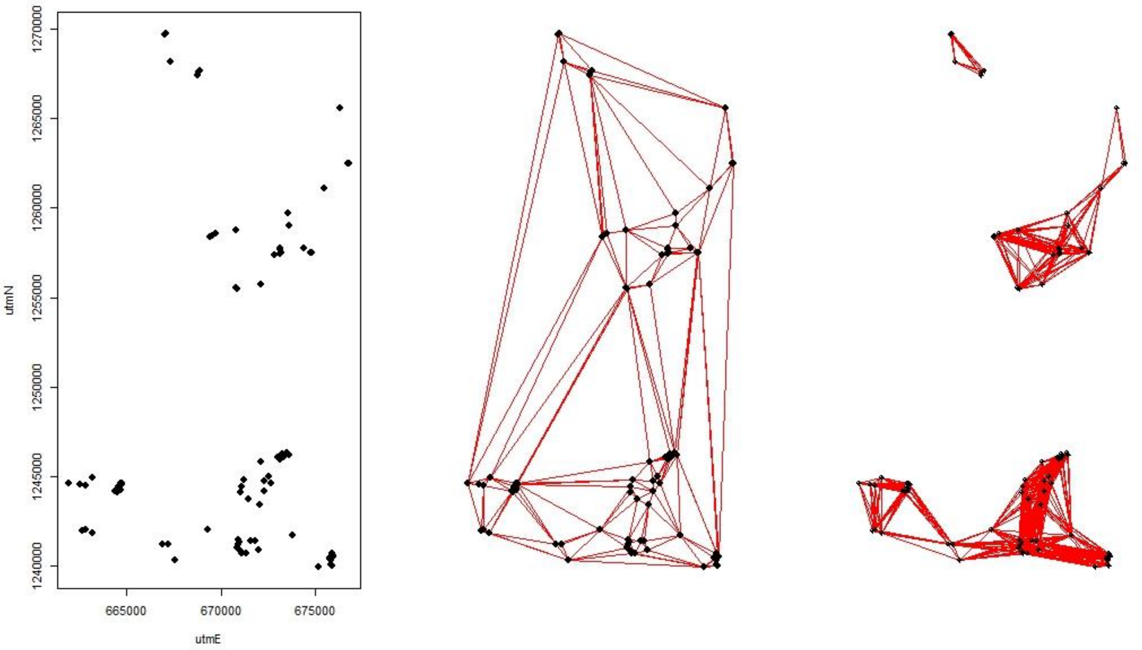
Figure 3: Boxplots of soil cation concentrations across vegetation plots. X axis is in units

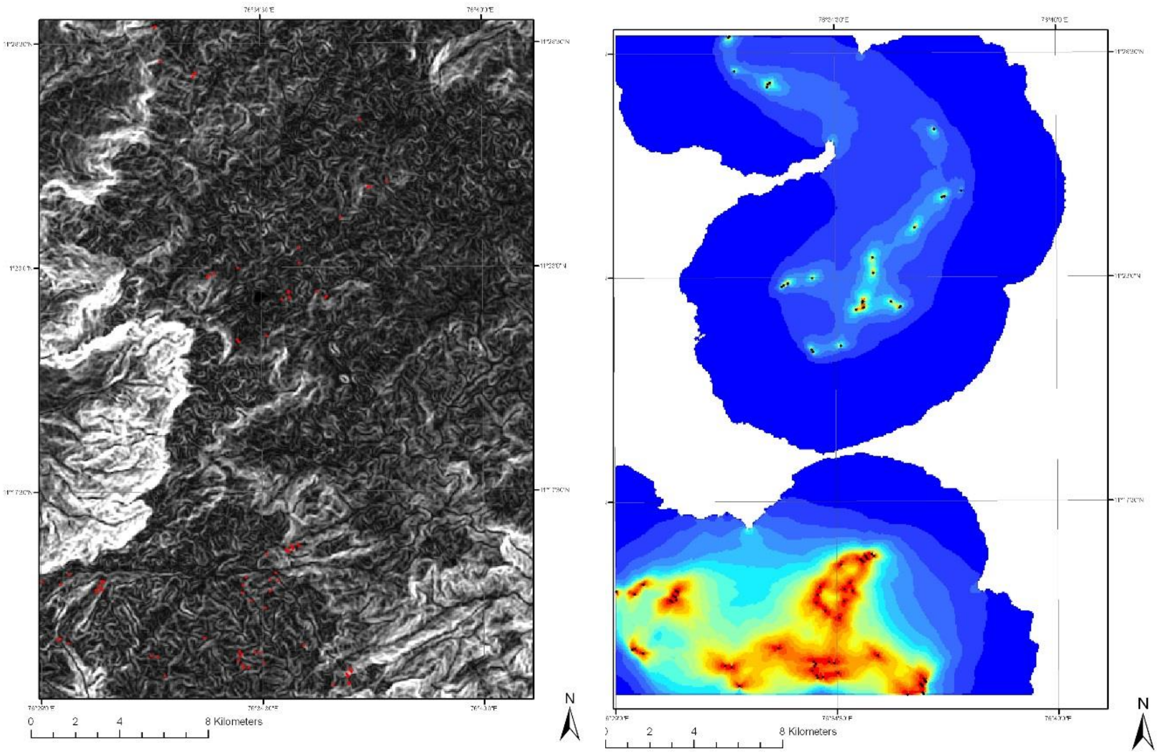


Appendix 4.3

Illustration of models used to test alternative spatial hypotheses

Alternative spatial models used for deriving MEMs: left panel shows plot distribution map with UTM coordinates, centre panel shows links between plots based on Delauney triangulation and right panel shows links based on a 4.8km threshold.



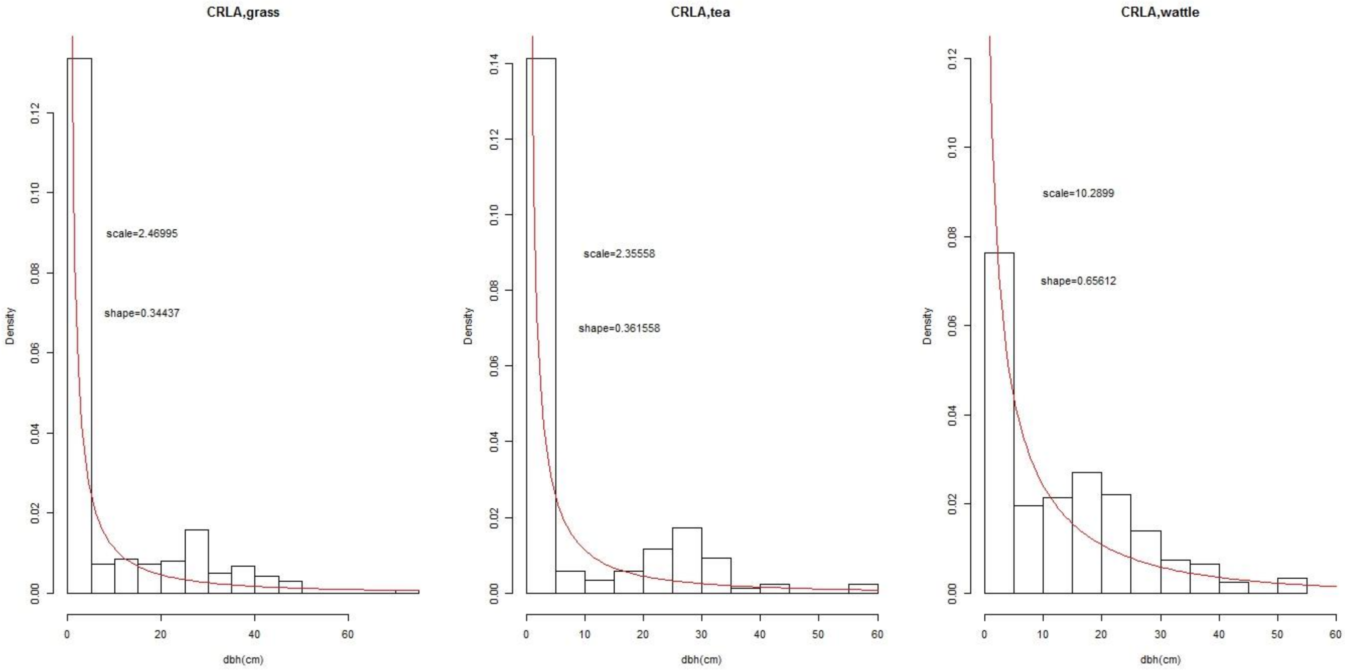


Right panel shows slope map for the study area with vegetation plots marked in red. Left panel shows cumulative current flow between sample points calculated using slope as a resistance surface (McRae et al. 2008a). The warmer colours indicate higher current flow or connectivity between plots

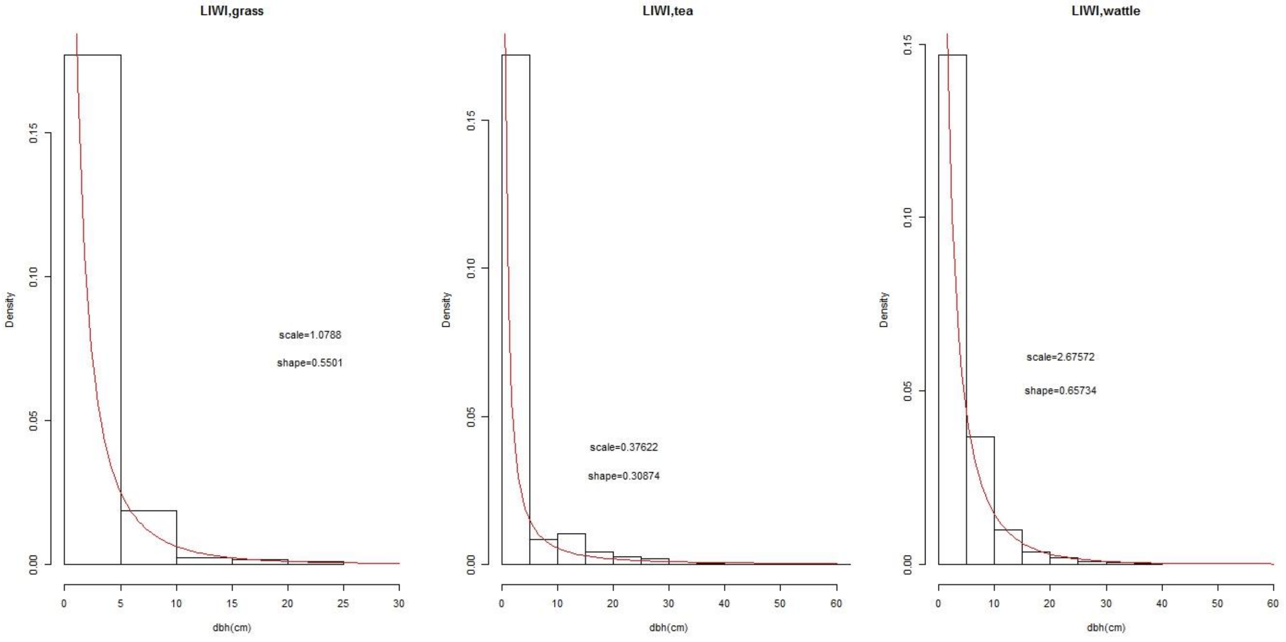
Appendix 5.1

Size class distributions across landscape contexts for common *shola* tree species

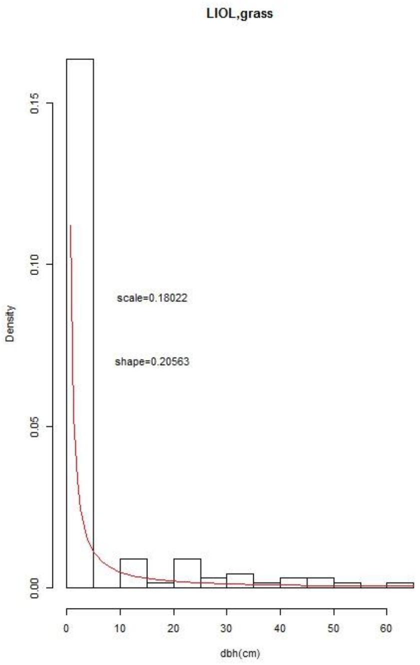
Cryptocarya lawsonii

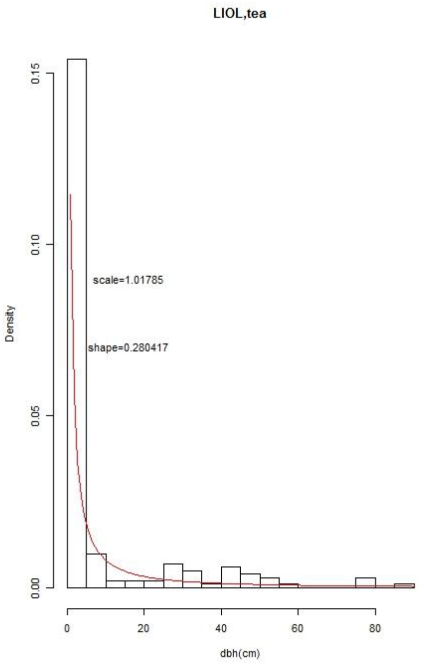


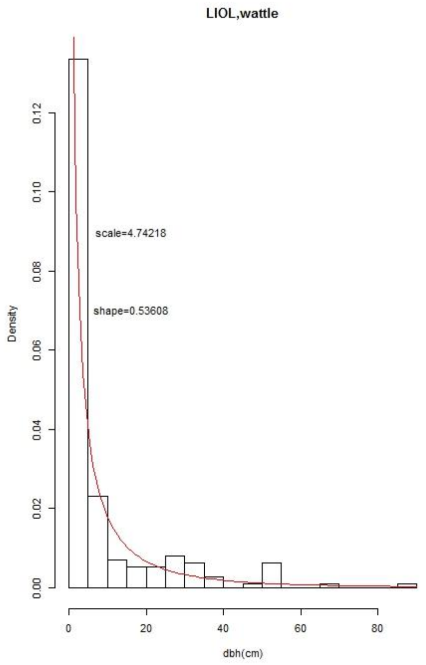
Litsea wightiana



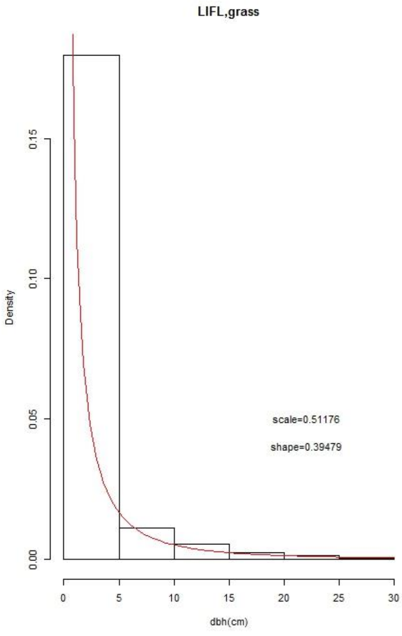
Litsea oleiodes

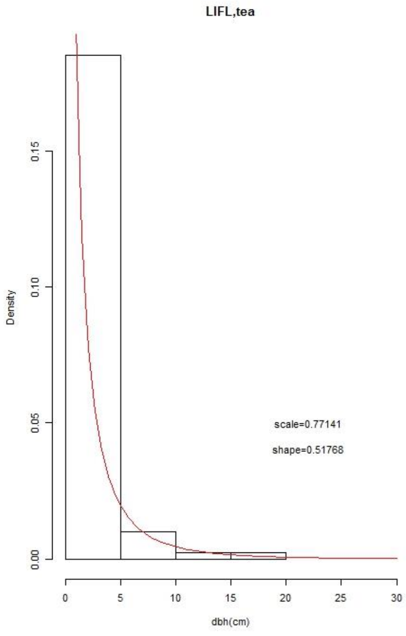


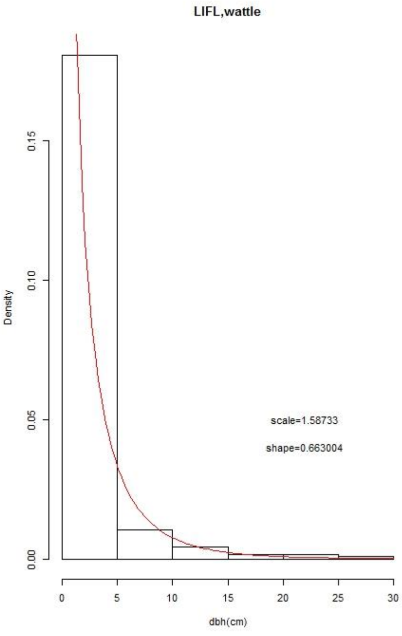




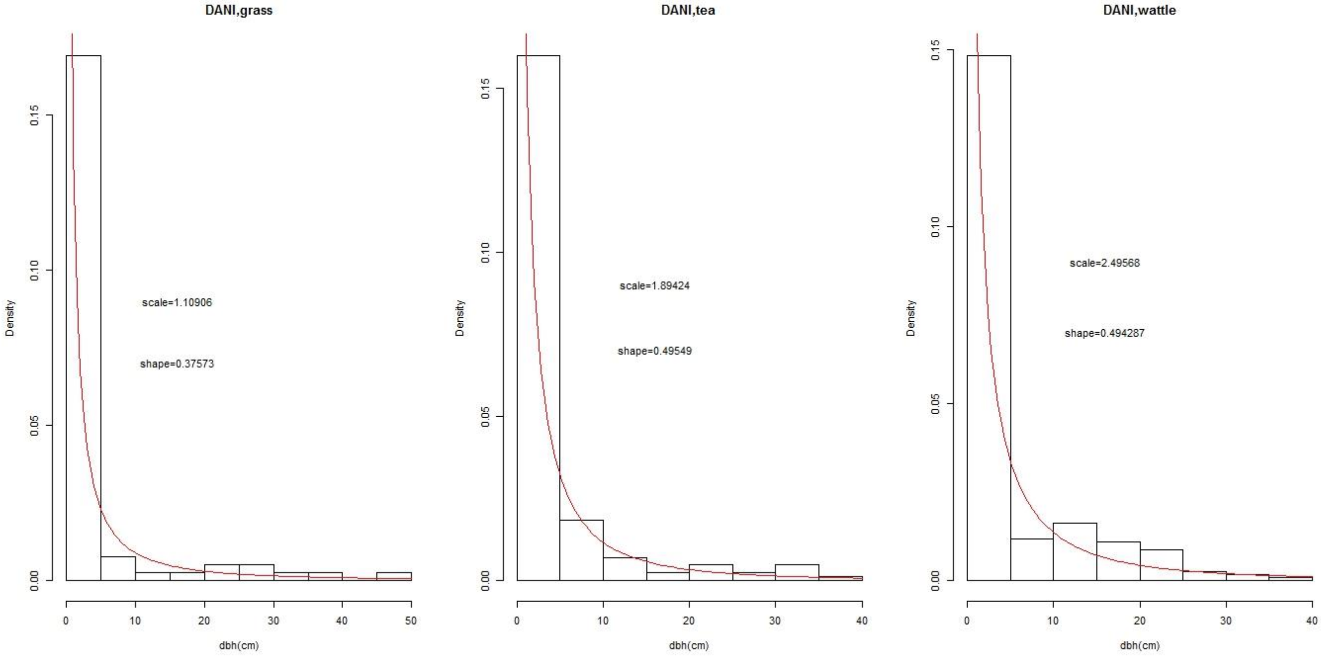
Litsea floribunda



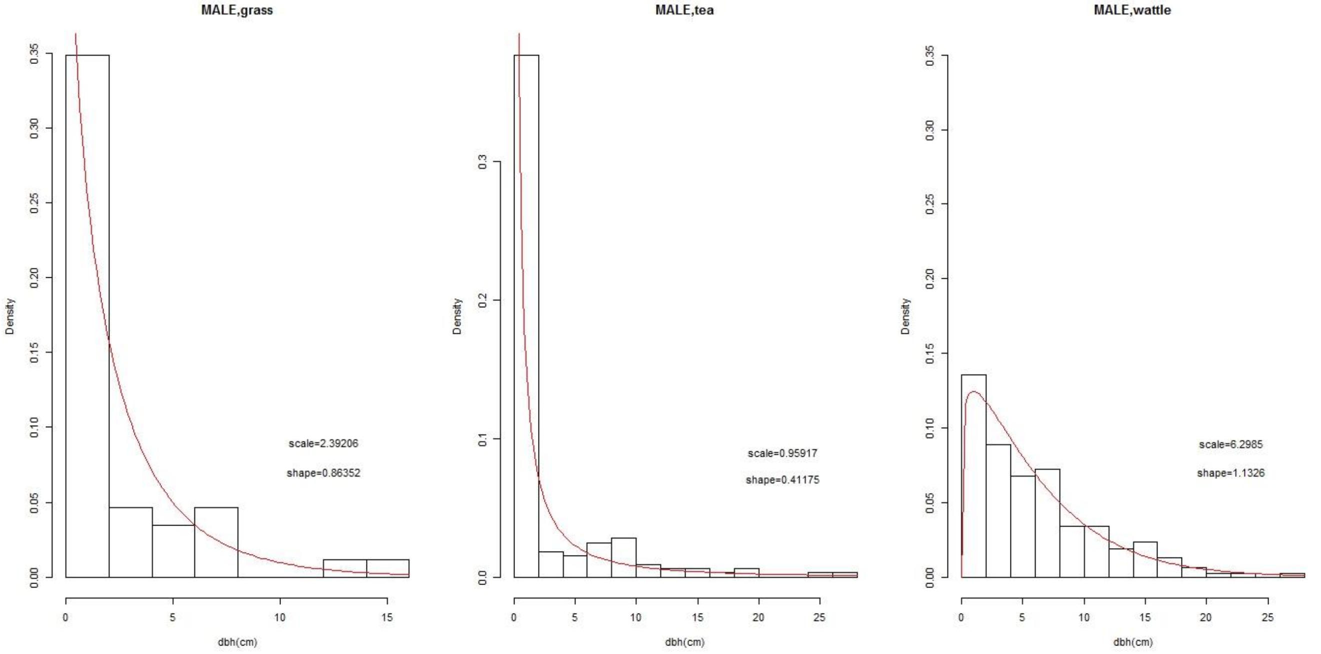




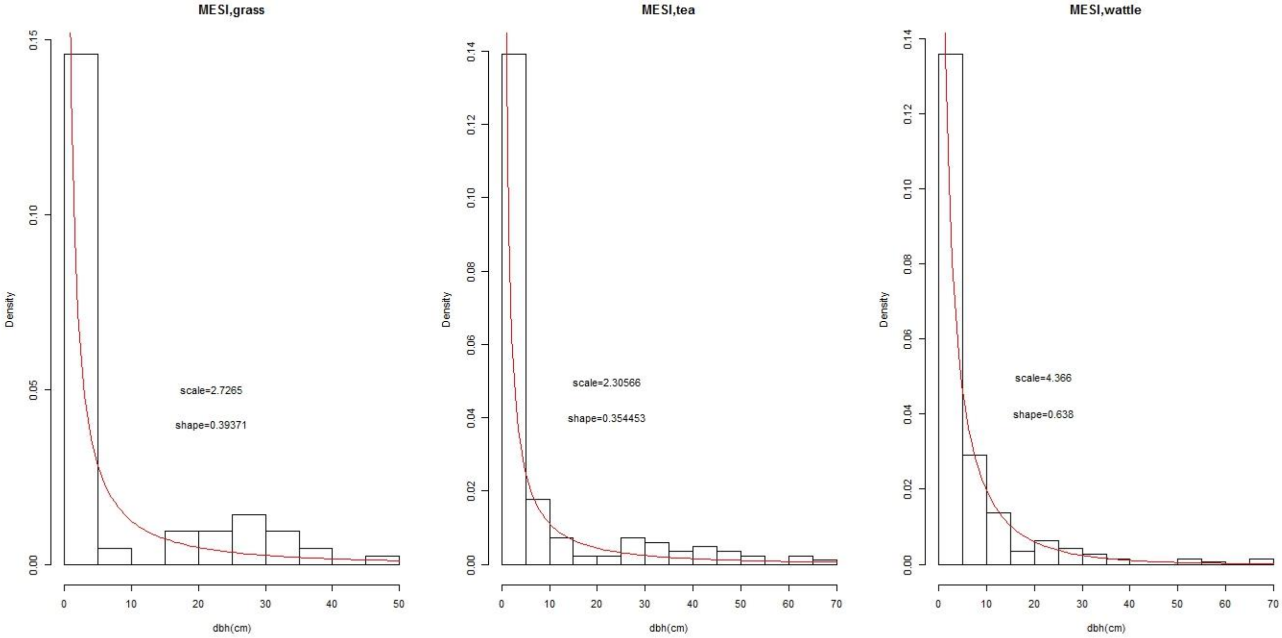
Daphniphyllum neilgherrense



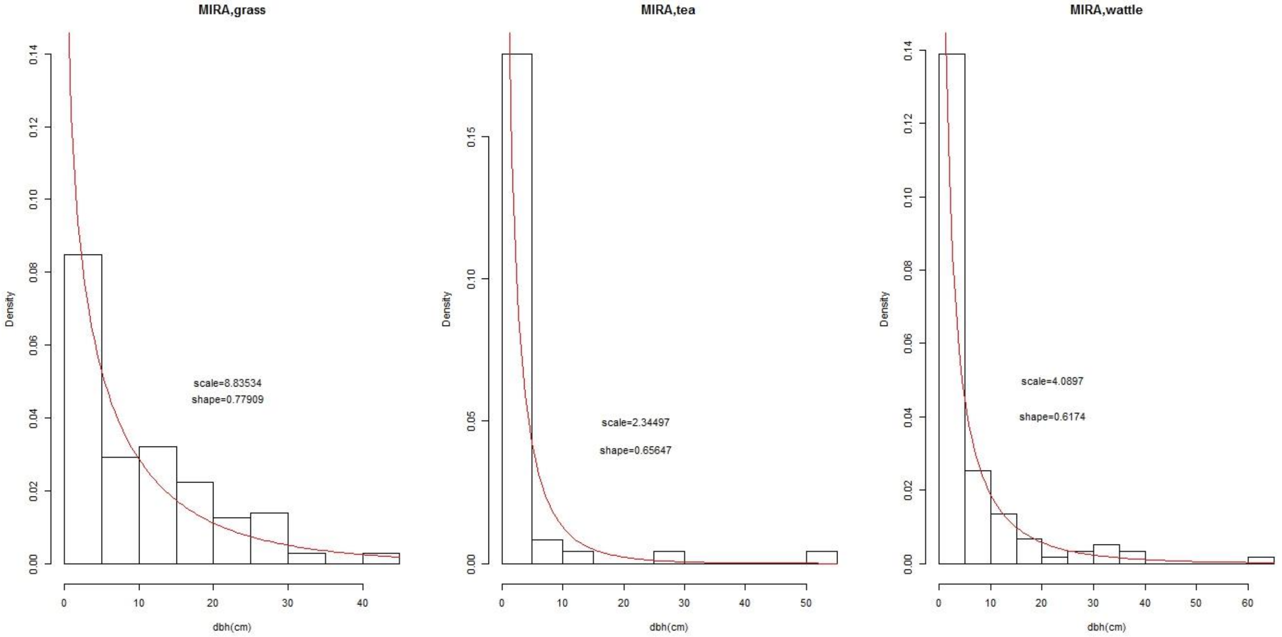
Mahonia leschenaultii



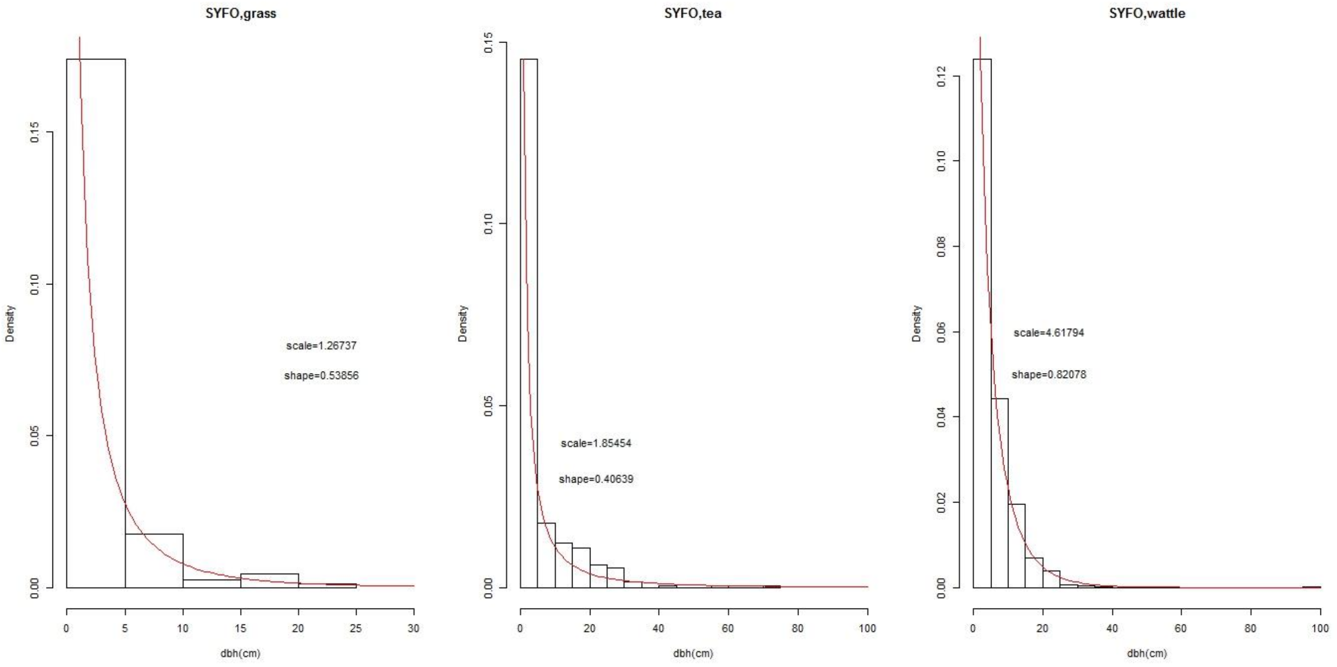
Meliosma simplicifolia



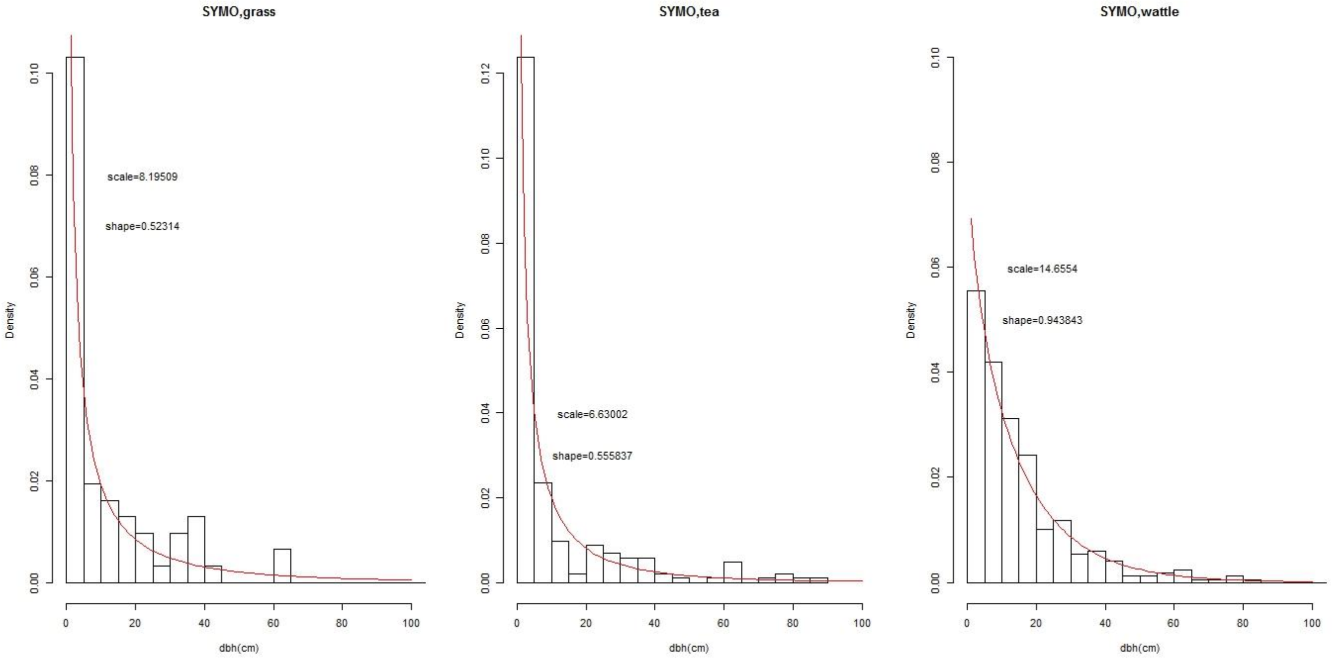
Microtropis ramiflora



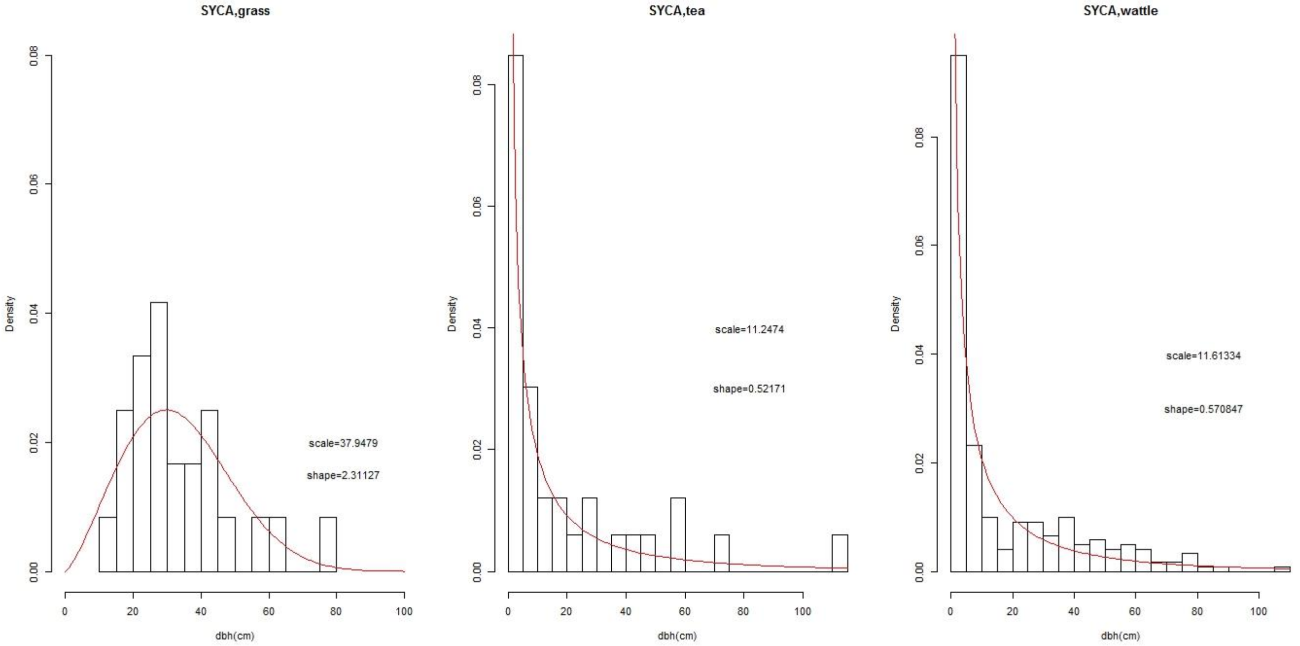
Symplocos foliosa



Syzygium montanum



Syzygium calophyllifolium



Rapanea wightiana