The disturbance-diversity relationship: integrating biodiversity conservation and resource management in anthropogenic landscapes
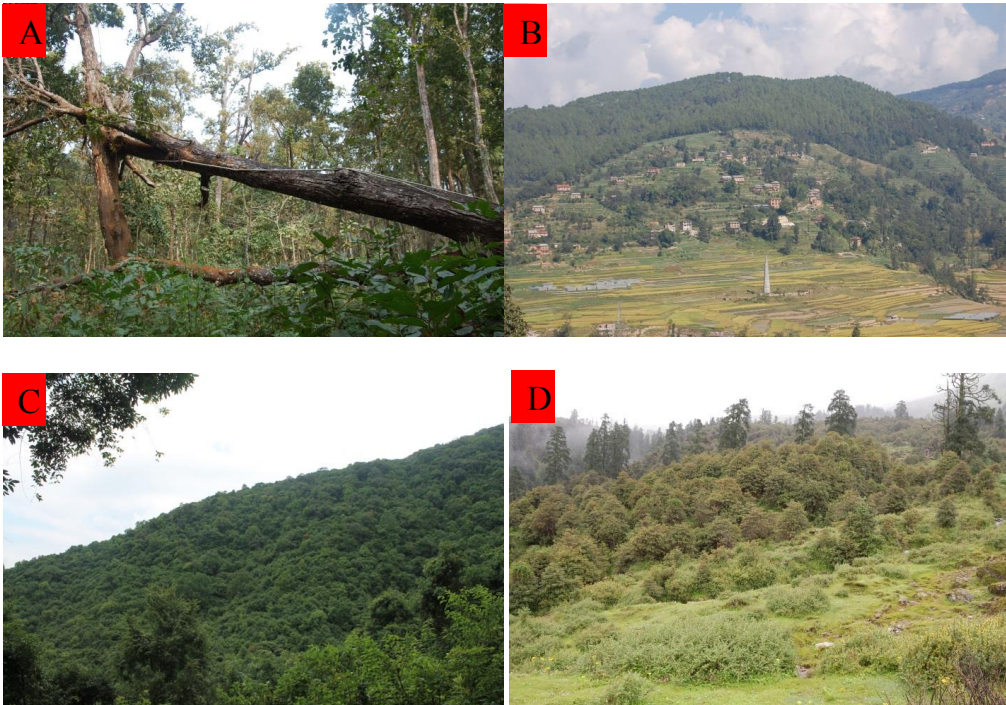
Lila Nath Sharma

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"Present and future threats arise both from increasing human activities and from withdrawal of the human activities that have shaped forests in the past"………………………………....Oliver Rackham (2008)

Photos of study sites and system: A) a fallen Sal tree forming a canopy gap in Sal forest of Chitwan, B) a typical agricultural landscape showing forest, cropfields and agroforests in midhills of Nepal, C) Oak forest of Phulchoki mountain, and D) an abandoned grassland encroached by shrubs and trees in Gorkha.

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Acknowledgements

Abstract

Disturbance, natural or anthropogenic, is ubiquitous to forest and grassland ecosystems across the globe. Many of these ecosystems have evolved alongside centuries old anthropogenic disturbance regimes. Understanding how disturbance impacts biodiversity and ecosystem service delivery is a topic of paramount importance as high biodiversity is likely to provide a wide array of ecosystem goods and services to an ever-growing human population. There is a general consensus that disturbance is an integral part of ecosystems and plays a role in shaping their diversity and function. It has been theorized that a certain threshold of disturbance plays a positive role in maintaining ecosystem diversity and health. However, the relationship between disturbance and diversity is contested on theoretical as well empirical grounds. The disturbance-diversity relationship is not as simple as theorized and appears somewhat elusive given the fact that impacts of disturbance are contingent on the attributes of the disturbance itself as well on the ecosystems exposed to disturbance. Empirical studies assessing impacts of disturbance, mainly anthropogenic, on diversity also do not show a general pattern; rather impacts can be considered as either positive or negative. In this context, this thesis synthesizes findings of four case studies dealing with impacts of human disturbance on floral diversity and composition at a local scale in specific ecosystems, with the aim of giving a perspective on how anthropogenic disturbance can be integrated at a landscape or regional level to manage resources at the intersection of societal and ecological concerns in a complex and dynamic socio-ecological system.

This thesis is anchored on four individual case studies from forests, grasslands and farmlands located at different elevations, ranging from tropical to subalpine climate, on the southern slopes and foot plains of the Himalaya in central Nepal. The study area comprises varying levels of anthropogenic disturbance from relatively little disturbed park area to visibly modified agroforests, and from government managed to privately owned resources. The main analyses include (i) a comparison of sites with different levels of disturbance and land-use to assess how natural and anthropogenic disturbance

impacts floristic composition and richness (Paper I and II), (ii) a comparison of time-gap vegetation data to assess the impacts of reduced disturbance (Paper III), and (iii) an analysis of vegetation and land-use change based on oral history and transect observations (Paper IV). A combination of quantitative and qualitative tools from vegetation and social sciences was used to collect and analyse the data. Vegetation data, mainly presence/absence and abundance of vascular plants collected in quadrats, are the main data for all study sites.

This synthesis demonstrates that anthropogenic disturbance and changes to it can have profound impacts on floral richness and composition, and these impacts are contingent to the type and intensity of disturbance and ecosystems exposed to these disturbances. It is found that canopy gap disturbance is important in subtropical and temperate forests as it promotes tree regeneration and species diversity. However, higher richness in gaps of intermediate size was not confirmed in the subtropical forest. It is demonstrated that a decline in anthropogenic disturbance – fire and grazing – in grasslands as a consequence of land abandonment allowed encroachment of shrubs and trees into the grasslands with a subsequent loss of grassland-dependent flora until the grasslands are eventually converted into closed-canopy forests. Cessation of anthropogenic disturbance in forest, mainly lopping and felling of trees for firewood and fodder, led to increased forest canopy and a decline in floral richness over a short time span of two decades. Changes in richness across the life-forms were not consistent with the overall decline: whereas herbaceous flora declined substantially, woody flora increased. In an agricultural landscape, farmlands were consistently richer than nearby naturally regenerated secondary forests in terms of tree species richness at different scales. Retention and planting of a variety of tree species in the farmlands in response to a shortage of forest resources and new conservation policies is a likely explanation for the higher richness found on farms.

This thesis demonstrates that anthropogenic disturbances associated with low intensity land-use practices of subsistence farming system help maintain floral richness and composition in human-modified landscapes at a local scale, which in turn contributes to the biodiversity and ecosystem services at a landscape and regional level. Alteration

of the traditional practices of management/disturbance can have notable consequences not only for species richness but also for landscape patterns and processes. Mimicking near-natural disturbance in forests and pastures and considering human disturbance as an integral ecosystem process contributes to maintain biodiversity and ecosystem function, and can be regarded as an amicable strategy to produce food with a minimal ecological footprint in landscapes where human disturbance is inevitable due to people's dependency on local natural resources.

Declaration

This thesis includes a synthesis, three published research articles and a manuscript. All papers, including the manuscript, are co-authored. An overview of the contributions of the co-authors in respective co-authored articles is given below.

Paper I:

Lila Nath Sharma: Study design, fieldwork, data analyses, writing, editing

John-Arvid Grytnes: data analyses, editing

Inger Elisabeth Måren: Co-writing, editing

Ole Reidar Vetaas: Co-writing, editing

Paper II:

Lila Nath Sharma: Study design, fieldwork, data analyses, writing, editing

Ole Reidar Vetaas: Study design, co-writing, editing

Paper III:

Lila Nath Sharma: Fieldwork, Data analyses, writing, editing

Ole Reidar Vetaas: Study design, editing

Paper IV:

Lila Nath Sharma: Field work, data analyses, writing, editing

Ole Reidar Vetaas: Editing

Ram Prasad Chaudhary: Editing

Inger Elisabeth Måren: Editing

List of publications

(They will be represented by the Roman numeral hereafter)

Sharma LN, Grytnes JA, Måren IE,Vetaas OR (2016) Do composition and richness of woody plants vary between gaps and closed canopy patches in subtropical forests? J. Veg Sci, Doi: 10.1111/jvs.12445 (paper I).

Sharma LN, Vetaas OR (2015) Does agroforestry conserve trees? A comparison of tree species diversity between farmland and forest in mid-hills of central Himalaya. Biodivers Conserv 24:2047–2061. DOI 10.1007/s10531-015-0927-3 (paper II).

Sharma LN, Vetaas OR (2016) Decline in anthropogenic disturbance in Himalayan montane forests have negative impacts in floral richness (DRAFT) (paper III).

Sharma LN, Vetaas OR, Chaudhary RP, Måren IE (2014) Pastoral abandonment, shrub proliferation and landscape changes: A case study from Gorkha, Nepal, Landsc Res, 39:1, 53-69, DOI: 10.1080/01426397.2013.773299 (paper IV)

Contents

Introduction

Biodiversity conservation is an overriding environmental concern of our time as species are being lost and biodiversity threatened at an unprecedented rate due to anthropogenic activities, mainly the conversion and destruction of forested habitats (Millennium Ecosystem Assessment, 2005; Baillie et al., 2004). A suite of conservation policies from local, national to international level is already in place to avert the impending crisis associated with biodiversity loss. Protected areas are an essential strategy for the conservation of biodiversity (Watson et al., 2016), and contribute tremendously to protect species and their habitats; the approach of strict conservation, however, has been confronted by some challenges in its efforts to achieve overall biodiversity conservation goals, especially in areas of high biodiversity and economically poor regions of the world, such as the tropics where deforestation rates are also high. People in these areas depend substantially on forest resources, which can become a source of conflict between the people and the management of protected areas (Sunderlin, 2005). In addition, a large number of species and important habitats are still beyond the geographical jurisdiction of protected areas, particularly in fertile human-dominated landscapes (Brooks et al., 2004; Chape et al., 2005; Rodrigues et al., 2004).

Primary forests or wilderness areas offer irreplaceable conservation opportunities (Barlow et al., 2007; Gibson et al., 2011). However, human domination of the Earth has transformed ecosystems and landscapes across all scales leaving very little area without any human footprint (Kareiva et al., 2007; Vitousek et al., 1997). The human factor, therefore, is an important driver that has long since shaped the world we live in (Boivin et al., 2016; Ellis et al., 2013). Evidence demonstrating the conservation opportunities of human-dominated landscapes, especially in areas beyond formal reserves, is increasing and species and ecosystems of considerable conservation importance have been identified (Bhagwat and Rutte, 2006; Bhagwat et al., 2008; Velle and Vandvik, 2014). It has been noted that conservation in human-dominated

landscapes, particularly in the fragmented forests and agricultural and cultural landscapes, serves a dual purpose by complementing the conservation goals of protected areas and by providing ecosystem goods and services for the livelihood of dependent people (Chazdon et al., 2009; Gardner et al., 2009). Recent shifts in the focus of forest management from production to multifunction reflect a strategy of conservation within a productive human-dominated landscape.

In our 'increasingly domesticated world' conservation of resources or biodiversity is at the intersection of a complex and coupled socio-ecological system, and conservation therefore needs to address social, economic, ecological and development related concerns to be successful (Newsham and Bhagwat, 2015; Kareiva and Marvier, 2011). People's dependency on forests and pastures for ecosystem goods and services are inevitable in rural areas throughout the world. Understanding the trade-offs between resource use/management and biodiversity/ecosystem function is crucial to harmonize conservation with resource use. Ecological theories can inform managers and conservationists on the trade-off between resource use and biodiversity conservation (Driscoll and Lindenmayer, 2012; Keddy, 2005). This thesis brings together four case studies to improve our understanding of the relationship between resource use expressed in terms of 'disturbance' and biodiversity conservation with a focus on plant species richness and composition in the low-intensity agricultural landscapes of central Nepal.

Disturbance as an ecosystem process

Our philosophical standpoint on 'how and what about' nature has influenced the principles and approaches of nature conservation and natural resource management. Classical views about nature, i.e. 'nature is in balance', 'nature is in equilibrium' and 'nature untouched is good' guided early ecological thinking and, most importantly, approaches of nature management (Marais, 2011). However, the 'nature in equilibrium' view has already been challenged owing to some processes inherent to every ecosystem. The process which curtails ecosystems achieving equilibrium or balance is 'disturbance' (Botkin, 1990; Connell, 1978). Accumulation of knowledge on the role of disturbance in shaping ecosystem function and services has challenged

the deep-rooted concepts pertinent to the equilibrium of nature. Disturbance has been considered as an inherent feature of ecosystems and it is acknowledged that some current forest and grassland ecosystems and species therein have evolved alongside some level of disturbance, which may be natural or anthropogenic (Bengtsson et al., 2000; Denslow, 1980; Turner, 2010). Recognizing the role of disturbance, it has been suggested that emulating 'nearly-natural' disturbance regimes in ecosystem management, mainly for forests, could synchronize conservation and production goals (Bengtsson et al., 2000; Franklin et al., 2002). High diversity and heterogeneity at different spatial scales may be attained by the careful and regular intervention of disturbances such as fire, grazing and harvesting (Fuhlendorf and Engle, 2001, 2004).

Disturbance, although laden with negative connotations in its literal meaning indicating a disruptive impact on an organism (Pickett et al., 2007), is actually an integral process to maintain a healthy functioning and structure of forest and grassland. Disturbance refers to a range of discrete events in ecosystems that leads to change in the configuration of physical or biological components of the ecosystem (White, 1979) and is common to all forest and grassland ecosystems. Disturbance may be natural or human caused, and may range from small to large in extent and intensity – from branch breaking to stand clearance, trampling to felling of trees, from burrowing to grazing or browsing by animals. A certain level of disturbance is essential to maintain the diversity and functioning of an ecosystem, but high disturbance, either natural or anthropogenic can impact forests and grasslands negatively (Connell, 1978; Grime, 1973). Human domination of the planet during the last one and half centuries has continued to clear and fragment forests for agro-pastoral activities. Increased human disturbance has altered ecosystems and biota across the globe and human activities in general continue to threaten biodiversity and ecosystem services (Millennium Ecosystem Assessment, 2005; Newbold et al., 2015).

Disturbance not only affects species and their habitats but also contributes to conserving species and ecosystem functioning. Disturbance theories posit that many ecosystems and species have evolved with disturbance and it is an integral process of

an ecosystem (Vandvik et al., 2014). Low-intensity disturbance in a forest is considered to be an ecosystem process and contributes to the conservation of flora, fauna and ecosystem service delivery (Siebert and Belsky, 2014). Rangelands in North America and elsewhere, or forest in the tropics or in boreal regions are adapted to different types and level of disturbances. For example, fire is a routine management intervention in many ecosystems to assure the continuation of ecosystem function and services. Species have adapted to the disturbance which is a regular ecosystem or landscape process (Vandvik et al., 2014). In subtropical forest, the dominant species *Shorea robusta* and associated species are well adapted to most recurring disturbances, i.e. fires and grazing (Troup, 1986; Wesche, 1996). In North America giant sequoia forest is dependent on fire for regeneration and suppression could alter the natural assemblages of forests (Parsons and DeBenedetti, 1979). Grasslands in North America converted to thickets and woodlands following a decline in herbivores and fire suppression (Van Auken, 2000).

The paradox of the disturbance-diversity relationship

There is a general consensus that some sort of disturbance is an integral ecosystem process and it plays a role in maintaining ecosystem diversity and heterogeneity, mainly in forests and grasslands (Turner, 2010). The Intermediate Disturbance Hypothesis (IDH; Connell, 1978; Grime, 1973) and forest gap-dynamics theory (Denslow, 1987; Yamamoto, 1992) attempt to formalize the relationship between disturbance on diversity using associated concepts like competitive exclusion, colonization, species coexistence, niche partitioning in time and space, etc. The IDH posits that diversity is maximum when disturbance is intermediate on the scale of frequency and intensity. The IDH logically assumes that no communities reach equilibrium as a result of disturbance and the likelihood of coexistence of species is highest at intermediate levels of disturbance. It builds on the idea that under low or no disturbance competitively superior species dominate other species and under high disturbance mortality obliterates intolerant species, implying that at both extremes of the disturbance continuum fewer species exist than could potentially occur. Similarly, forest canopy-gap dynamics theory asserts that canopy disturbance reduces the

competitively dominant species at local level from the forest creating resources and spaces for other species to grow and regenerate which would otherwise be suppressed below the closed-canopy. Canopy gaps are richer in resources and more heterogeneous in their microenvironment making them more conducive for species coexistence and hence maximize richness. It is also argued that canopy gaps of intermediate size and age are richer than large and old or small and young gaps. The basic tenet of the IDH and gap dynamics theories, therefore, is compatible with the diversity component of successional theory of plant community.

The diversity-disturbance relationship appears to be rather paradoxical given that the empirical evidence accrued so far can be considered as either positive or negative. The evidence for maximum richness at intermediate disturbance is not as robust as expected and IDH itself is contested on both theoretical and empirical grounds (Fox, 2013; Mackey and Currie, 2001). On the one hand, anthropogenic disturbance has imperilled biodiversity, threatened many species with extinction and we have witnessed the loss of species (Millennium Ecosystem Assessment, 2005, Martínez-Ramos, 2016). Deforestation and habitat fragmentation associated with agricultural expansion and intensification is the dominant driver of biodiversity loss during the last century (Foley et al., 2005; Ramankutty and Foley, 1999). On the other hand it has been found that a certain threshold of disturbance, including anthropogenic disturbance, has played a role in enhancing species coexistence and maintaining ecosystem health. Contrasting reports in recent publications mirror the chaos in disturbance-diversity relationships; two meta-analyses report that anthropogenic disturbance in general has negatively impacted biodiversity (Murphy and Romanuk, 2014; Newbold et al., 2015), while others argue that there is no net loss in plant species richness as a consequence of disturbance (Dornelas et al., 2014; Vellend et al., 2013). Similarly, another meta-analysis finds that managed forest has higher richness of plants including other taxa than those of the protected forests in Europe, and attributes the higher richness to the heterogeneity created by anthropogenic disturbances in managed forests (Paillett et al., 2010). Irrespective of contrasting reports on the outcome of disturbance on diversity in these reviews, they commonly

suggest that impacts of disturbance are idiosyncratic to the taxa, ecosystems and attributes of disturbance itself.

Analysing the disturbance-diversity relationship within the scope, content and scale as envisioned by the theories would improve our understanding on how disturbance influences biodiversity across the temporal and spatial scale. The variance in the disturbance-diversity relationship so far reported is partly related to issues of taxonomic group, scale of study and types of disturbances. For instance, analysing richness across ecosystem types, e.g. forests and grasslands, to assess the intermediate disturbance hypothesis is beyond its scope.

Production and conservation: is it possible in the same land-unit?

Enhanced food production to feed the booming human population is an important development goal of our time, but expansion and intensification of agriculture is ascribed as a serious threat to biodiversity conservation because forests become fragmented and destroyed, and species are threatened with extinction (Baillie et al., 2004; Foley et al., 2005; Koh and Wilcove, 2008; Sodhi et al., 2004). This threat is projected to magnify with increased food production (Laurance et al., 2014; Sala et al., 2000; Tilman et al., 2001). Reconciling food production and biodiversity conservation is, therefore, an important challenge we need to address (Phalan, 2011), a challenge that is particularly difficult in the tropics and subtropics where subsistence farming is common and food shortage is frequent (Laurance et al., 2014). Two distinct land-use strategies – land-sparing and land-sharing – have been proposed as ways to achieve the dual objectives simultaneously (Kremen, 2015; Phalan et al., 2011). The land-sparing strategy separates conservation and production into mutually exclusive land units such that there is intensive food production but with a smaller land footprint. The land-sharing strategy, or wildlife-friendly agriculture, advocates for production and conservation simultaneously in the same land unit necessitating a larger land footprint for production. Both strategies are contested as each of them has trade-offs between production, land-area footprint and biodiversity (Seppelt et al., 2016), and the sharing-sparing dichotomy is considered an oversimplification of the complexity associated with increased production without compromising biodiversity (Kremen, 2015).

Evidence supporting the role of farmland/agricultural lands in biodiversity conservation has been steadily accumulating with empirical studies. Farmland can support conservation by retaining and planting trees, which in turn can mitigate species loss from deforestation (Bhagwat et al., 2008; Tadesse et al., 2014), as well as providing landscape connectivity and alternative habitats for fauna (Fischer et al., 2010; Manning et al., 2006; Martin et al., 2012; Mulwa et al., 2012). The sharing strategy is confronted, for example, with the challenges associated with conservation of large mammals requiring larger and relatively less disturbed areas. Proponents of the sharing strategy admit that conservation in agricultural landscapes can complement the goals of protected areas but not substitute them.

Human-modified landscapes like the mid-hills of Nepal reflect a perfect picture of the sharing strategy where the dominant uses of land – forests, pastures and farmlands including settlement – form a mosaic. In the region, large swathes of forests were fragmented and converted to agricultural terraces several centuries ago and people's means of subsistence are so intricately connected with forests, pastures and agriculture that animal husbandry and forests are inseparable components of the subsistence livelihood of smallholder farmers. In such a multifunctional landscape, conservation interest is more on ecosystem services and biodiversity in general than on, for example, the flagship mammals. The trade-off among land-uses determines the fate of biodiversity in forests and farmlands. Determinants and states of biodiversity in the agricultural landscape can inform the ways in which biodiversity and food production can be synchronized.

Contextualizing resource use and conservation
Subsistence farming, a mainstay of livelihood in rural Nepal, is a three-pronged system consisting of agriculture, livestock and forests as crucial resource bases. In the agricultural landscape of Nepal particularly the midhills, forests, pastures and agroforests or farmlands are in mosaics. People's dependency on these resources for ecosystem goods and services is inevitable, and they are managing these resources since long, modifying the ecosystems and species, consequently resulting in a novel ecosystem (Hobbs et al. 2006). These resources, on which people depend for

livelihood, may look as a discrete unit but they are embedded in the complex and dynamic social-ecological systems (SES; Liu et al., 2001; and Liu et al., 2007). These resource units interact among each other and through human management as component of SES; the interaction indeed influences the outcomes of resource use (Ostrom, 2009) in terms of ecosystem services and health.
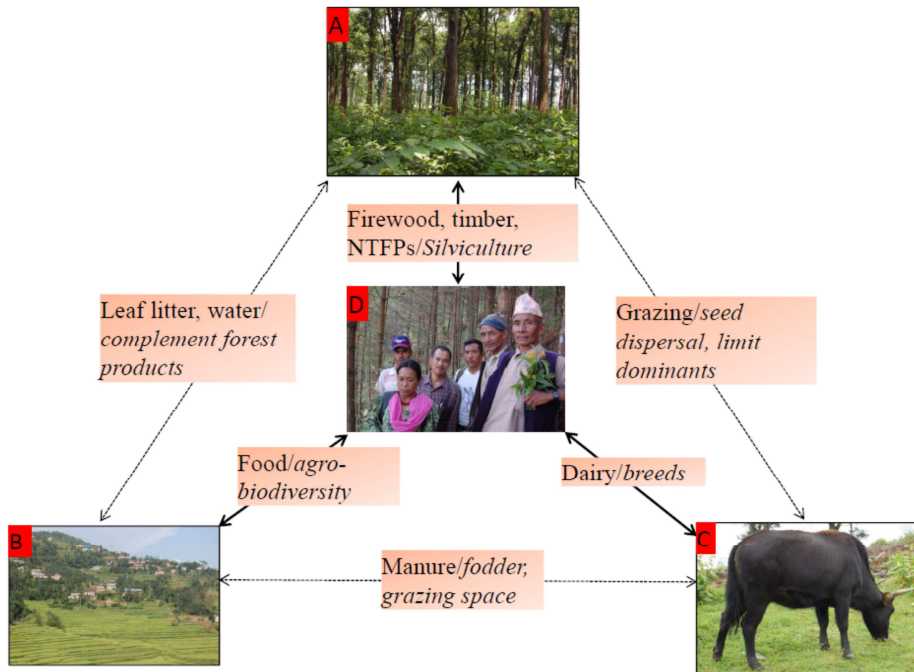
Figure 1: Conceptual framework depicting the linkages among the components (resource units) of subsistence farming systems – forests and pastures (A), agroforestry (B), and livestock (C). Local people (D) manage these resources for ecosystem goods and services and the nature and intensity of management determines the ecosystem health and the services they deliver. There is twofold interaction; interaction between resources and people and interaction among resource unit through human management. Italicized text represents reverse flow of goods and services of the plain text. Modified from Måren et al. (2014).

Viewing the biodiversity conservation in the human modified landscape with the lens of SES is important given the landscape context on which resource unit and their users are situated and the outcome of interaction between resource users and resource is dynamic and contingent to various social, economic and cultural factors. Forest,

pastures and agroforests are main resource units' people interact with them through management i. e. disturbance. The nature and intensity of interaction determines the structure, function and diversity of the resources. In this thesis, I do not analyse the complex and intertwined interactions of the social-ecological system rather consider the resources management and its ecological consequences to be part of complex and dynamic SES. This perspective guides the linkages of the individual case studies embedded herewith.

Objectives

This synthesis aims to contribute to our understanding on how floral biodiversity conservation can be harmonized with human use of resources in a landscape consisting of human-modified, semi-natural to natural ecosystems where human disturbance in the ecosystems in the forms of resource harvesting and management is inevitable. Specific objectives of this synthesis are:

1. Canopy disturbance is a dominant natural disturbance in forest ecosystems. The addition of human disturbance in the form of tree felling and lopping makes canopy disturbance more common and frequent. I specifically evaluate whether canopy gap disturbance contributes to the maintenance of floral diversity in subtropical and temperate forests.

2. Human use of natural resources is an integral component of complex socio-ecological systems. Anthropogenic impacts are subjected to changes in the socio-economic conditions of dependent populations, markets and policies affecting them. I evaluate whether fluctuation in the disturbance regime – mainly the withdrawal of age-old disturbance – influences vegetation structure and richness of grasslands and forests.

3. A large portion of land has been modified in the mid-hills of Nepal, as elsewhere in the world. Recent conservation discourse argues over the role of these landscapes in conserving biodiversity. I analyse whether biodiversity can be conserved in such human-modified and dominated landscapes.

Himalayan vegetation, land-use and disturbance regimes

Vegetation

The position of Nepal in the Himalaya at the cross-roads of floristic realms and provinces, coupled with its heterogeneous physiography makes it rich in biodiversity. Palearctic and oriental floristic realms converge in the Himalaya, linking the boreal and Indo-Malayan floral regions. Nepal lies at the confluence of the (i) Sino-Japanese, (ii) South East Asiatic, (iii) Indian, (iv) Sudano-Zambian, (iv) Irano-Turranian, and (vi) Central Asiatic floristic provinces (Department of Forests, 2010). The Nepalese flora is mainly dominated by elements from the Central Asiatic and Sino-Japanese floristic provinces. Several species occurring in Nepal are either endemic to the east or west Himalaya. Based on the Himalayan floristic element, Nepal can be divided into three longitudinal subdivisions, namely Western, Central and Eastern (Banerji, 1963). Western Nepal is dominated by west Himalayan flora and Eastern by the east Himalayan element, while Central Nepal has an overlap of the two. Nevertheless species from eastern or western Himalaya can be found across the whole of Nepal (Stainton 1972).

Climate and vegetation of the Himalaya and Nepal are largely determined by elevational gradients from south to north, and a rainfall gradient from east to west. Nepal covers the elevational gradient of the Himalaya within a short physical distance: clear physiographic and elevational profiles ranging from lowland of 100 meter above sea level (masl) to the snow-capped high mountains reaching above 8000 masl are evident when moving from south to north. This elevational gradient creates tropical to nival bioclimatic zones. The moisture gradient of the Himalaya is rather subtle while moving from east to west in Nepal.

Nepal harbours high diversity of ecosystems, vegetation types and species richness, including ca 6500 species of flowering plants of which ca 300 are endemic. Dobremez (1976) identified a total of 189 ecosystem types and 75 vegetation types. Stainton (1972) recognized 35 types of forest and vegetation. Similarly Department of Forests

(2010) classified Nepal's vegetation into 38 types, which is basically a synthesis of the previous works by Dobremez (1976) and Stainton (1972). All the classification schemes have a similar basis and largely correspond to the elevational gradient and, to some extent, the east-west moisture gradient coupled with floristic components from the east or west Himalaya. The main feature of vegetation in the Himalaya is a vertical zonation with elevation corresponding to the temperature gradient. One can see clear elevational profiles of vegetation while moving from south to the north; dense tropical forest in the south is replaced by subtropical forest and so forth. Alpine vegetation occupies the high mountains to the north (Table 1).

Land-use and disturbance regimes

Himalayan vegetation is intricately connected with the livelihood and culture of people. Since long ago, people have used the forests, plant resources and ecosystem services of the region. Palynological analysis has revealed that the original vegetation has been substantially altered and human impact on the vegetation has a very long history (Miehe et al., 2009; Schlutz and Zech, 2004). The existing vegetation is the outcome of a long interaction of ecological processes and human disturbance in terms of grazing, burning and forest harvesting. Throughout Nepal, forest is fragmented with only a few large blocks of forest in protected areas on the southern plain and high mountains.

Forests and grasslands in Nepal are typically subjected to human disturbance of varying intensity and frequency. Forests in the Himalaya are widely used for timber, fodder, firewood and non-timber forest products (NTFPs). Accessible forests are also used for grazing and browsing livestock by settled villagers as well as transhumance herders, especially in the high mountains (Metz, 1994). On the southern plain of the country, large tracts of forest were cleared to make paddy fields during the second half of the last century following the eradication of malaria and subsequent migration of people from the mountains to the plains. Sal (*Shorea robusta*) is a dominant and high-value species that has been protected but instances of illegal felling are common where forest department has poor vigilance. In the subtropical zone, one sees a mosaic of settlements, agricultural fields and patches of forests: large tracts of forest are rare in

this region. People have lived in the mid-hills for millennia and forest fragmentation has a similarly long history. Population level in the region is believed to have peaked during the middle of last century. People mainly practice agroforestry and grow trees on private land in order to complement forest resource demand and as a response to shortage of forest products (Carter and Gilmour, 1989). Original forest has been converted into terraces and settlements. Now many of the forest patches in this region are under management as community forests (See Acharya, 2002) – a programme in which forest is managed by local users through a formal and forest-specific institution. In the temperate and subalpine zones, population density is low and forest cover is higher compared to the subtropical and tropical regions. Forest is fragmented in this zone too, by pastures and crop fields. People practice both sedentary agriculture and migratory herding and use forests and semi-natural grasslands for livestock grazing. Grasslands above the tree lines are also used by people for sheep and cattle grazing (Metz, 1994; Schmidt-Vogt, 1990).

During the last four decades people gradually migrated from many marginal mountains areas to the southern plains and cities in the mid-hills, and left pastures with a low stock density or entirely abandoned. In general, human disturbance in terms of burning, grazing and harvesting is declining in the temperate and subalpine pastures and forests. In the mid-hills disturbance is also declining due to forest conservation initiatives along with increased environmental awareness among the public.

Large-scale catastrophic natural disturbances are relatively rare in Nepal, but more local-scale natural disturbances such as floods and river scouring in the plains and land and mudslides on hilly slopes are common. Wind-throw and natural death of trees are obvious natural disturbances in the forests. Anthropogenic disturbance is mainly tree harvesting, fire, grazing and browsing and NTFPs collection (Miehe et al., 2015). This disturbance is related to the high dependence of rural people on biomass for energy. The dependency of agro-pastoral production on forest resources is another underlying cause of disturbance on these ecosystems. Details of the major disturbances in forest and grassland ecosystems in Nepal are given below.

Table 1: Main forest types and dominant species in different bioclimatic zones of Nepal (adapted from Stainton (1972), Dobremez (1976) and Department of forest (2010); E-occurring in eastern Nepal only and W-occurring in western Nepal only.

	Ecological zones	Main Forests/vegetation types	Common/dominant tree species
1	Tropical zone < 1000m (Terai, dun valleys and lower slopes of Siwalik)	Sal forest, Tropical deciduous riverine forest, Tropical evergreen forest (E), Terminalia forest, Grasslands on flood plain	*Shorea robusta, Dillenia species, Mallotus phillipensis, Terminalia species, Duabanga sonneratiodes, Adina cordifolia*
2	Subtropical zone(1000-2000masl) (parts of Siwalik and lower parts of Mahabharata)	Subtropical evergreen forest (E), Subtropical riverine forest, *Schima-Castanopsis* forest, Chir pine forest	*Ostodes paniculata, Eugena tetragona, Schima wallichhi, Castanopsis species, Lagerstroemia parviflora, Quercus glauca, Lyonia ovalifolia, Myrica esculenta, Alnus nepalensis, Myrsine capitellata, Fraxinus floribunda, Toona ciliata*
3	Temperate zone (2000-3000 masl) Parts of Mahabrarat and lesser Himalaya	Cedar forest (W), Cypress forest (W), Lower temperate oak forest, Mixed rhododendron forest, spruce forest, Oak-rhododendron forest, Fir-hemlock-oak forest, Deciduous walnut-maple-alder forest, East Himalayan oak laurel forest (E)	*Quercus incana, Q. lanata, Q. lamellosa, Symplocos ramossisima, Aesculus species, Acer campbelli, A. pectinatum, Abies pindrow, Tsuga dumosa, Magnolia campbelli, Rhododendron arboreum, Lindera pulcherrima*
4	Subalpine zone (3000-4000masl)	Blue pine forest, Birch-rhododendron forest, Fir forest, Larch forest, Subalpine oak forest	*R arboreum, R. barbatum, Q. semecarpifolia, Abies spectabilis, Pinus wallichii, Larix himalaica*
5	Alpine zone (4000-5000 masl)	Alpine meadows, Dry alpine scrub, Moist alpine scrub	*R. setosum, R. anthopogon, R. nivale, Juniperus recurva, J. indica, J. communis*
6	Outer valleys/arid zone	Juniper forest, Alpine steppe, *Caragana* shrubland	*Juniperus indica, Cupressus tolrulosa, Caragana species, Lonicera spinosa, R. anthopogon, Rosa sericia, Ribes species*

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1. Biomass harvesting: Timber, firewood, fodder and wild edible/medicinal plants are important resources that people harvest from the forest. Trees are felled and lopped for timber, firewood and charcoal which are a major disturbances creating gaps in forests. Fuelwood is the major source of energy for kitchens in rural areas and more than 70% of people use firewood for cooking. NTFP harvesting, including some high-value medicinal plants, is common in high-elevation grasslands. Fodder collection is common in forests throughout the country. Trampling along the trails is usually higher in the forests.

2. Grazing: Livestock husbandry is an important component of subsistence farming in Nepal. In most of the areas people graze their cattle, goats and sheep in nearby forests, grasslands and fallow lands. In the temperate and subalpine regions, forest and pastures are used by transhumance herders as summer pastures. In recent decades transhumance grazing has declined and community forests have also imposed regulations on forest grazing.

3. Burning: Deliberate as well as accidental fire in forests and grasslands is another form of disturbance. People use fire in forest and grasslands to encourage a more luxuriant growth of grass and forbs which are more palatable to livestock. Forest fire is a common phenomenon during the dry season (late march to early may) and has played a role in altering forest composition and regeneration (Schmidt-Vogt, 1990; Wesche, 1996).

4. Shifting cultivation: Shifting cultivation used to be a dominant form of land-use on the hilly slopes of subtropical and lower temperate regions in the Himalaya until the middle of last century. With the migration of people to the lowlands, shifting cultivation has declined substantially but a few farmers still practice it.

5. Invasive species: Degraded forests mainly in the Terai and mid-hills have been invaded by non-native species. *Mikania micrantha*, *Lantana camara*, *Parthenium hysterophorous*, *Eupatorium odoratum* and *Ageratum conyzoides* are the major invasive species in forests and fallowlands; *Imperata cylindrica,* a naturalized exotic species, is common in dry places and grasslands.

Study areas

This dissertation is a synthesis of four case studies from different physiographical regions of Nepal, covering different elevational profiles and vegetation types from lower subtropical forest in the south to subalpine vegetation in the north (Figure 2). A brief introduction to the physiography, climate and disturbance is presented below. Disturbance impact class of respective study system is taken from Miehe et al. (2015).
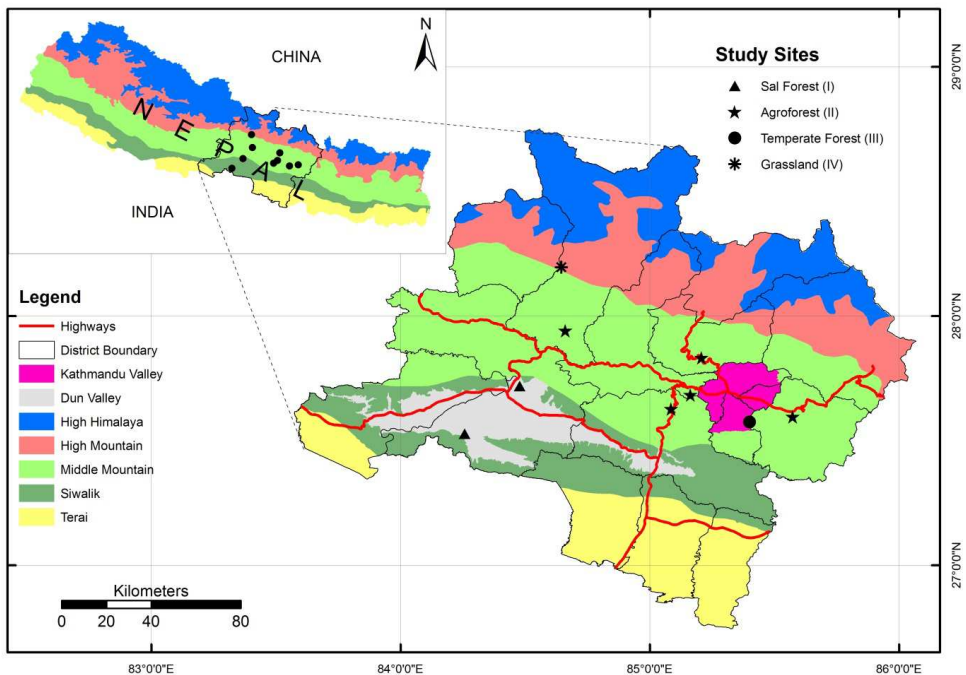
Figure 2: Map of central Nepal showing specific study sites in the different physiographical regions. Numbers in parenthesis by the study sites indicate the relevant paper for that particular system.

1. **Sal forest**: Impacts of canopy disturbance on woody plant richness and composition was studied in two old-growth Sal (*Shorea robusta*) forest stands in Chitwan district, a dun valley. One of the forests was protected as part of the core area of Chitwan national park, and another forest was used by local people. Sal is a high-value timber

species forming gregarious stands, mainly distributed within the Indian subcontinent, south of the main Himalayan range. A large area of Sal forest was cleared following malaria eradication and the hill-Terai migration that started in 1950s. However, large blocks of forest still remain as islands in the populated areas. In the Sal forest, canopy gaps are created naturally as well as by human disturbance and gaps and non-gap areas exist as a mosaic. Sal forest in Chitwan can be categorized as evidently disturbed forest (impact class II).

2. **Mid-hills of central Nepal**: Tree diversity in forest and farmland of the mid-hills of central Nepal between an elevation of 1000 and 1800 masl were juxtaposed to see whether farmlands contribute to the conservation of tree species. The mid-hills is a broad belt between the Terai and the high Himalaya (Mahat et al., 1986) and it includes the slopes and valleys of the Mahabharat range and the lesser Himalaya or midlands (Uprety, 1999). Elevation zones in this region cross the transition from a subtropical to warm temperate climate. There is high human population in this elevation zone. Agriculture, animal husbandry and forestry are integral parts of the subsistence farming system – a dominant and traditional livelihood option, practiced by people living in this ecozone. People depend significantly on forests for firewood, timber, non-timber forest products, fodder for domestic animals, and manure (leaf litter) for crop-fields (Mahat et al., 1986). Trees in farmland, along with other ecosystem services, help fulfil demand for forest products, especially fodder and firewood. People have converted forest into terraces and planted trees mainly for fodder. The agroforestry of the mid-hills can be considered as replaced and degraded vegetation (impact class V), while the forest patches can be considered as strongly disturbed (impact class III) or widely replaced (impact class IV).

3. **Temperate forests at Phulchoki Mountain**: Changes in plant species richness were assessed between 1993 and 2013 in oak forest in the temperate region of central Nepal. The study area is located on Phulchoki Mountain in the south of Kathmandu valley, the highest mountain in the Mahabharat range, rising from 1600 to 2700 masl. Until the mid-1990s, Phulchoki forest was an open-access forest and people used to harvest firewood, fodder and timber. It was also used by people to graze domestic

animals. Forest canopy was very disturbed due to the lopping of oak trees for fodder (Vetaas, 1997). In the mid-1990s the lower parts of Phulchoki were handed over to local communities to become a community-managed forest, and this move has helped to protect the entire forest of the Phulchoki Mountain. It might have been strongly disturbed vegetation (impact class III) during 1990s but currently can be considered as evidently disturbed vegetation (impact class II) due to observable disturbance legacies.

4. **Temperate and subalpine grassland in Gorkha District**: Changes in temperate and subalpine pastures were assessed in north-western Gorkha in central Nepal. Eighteen grassland patches located between 2700 and 3900 masl were analysed. Grasslands below the forest limit were the outcome of forest clearance centuries back. People practising sedentary agriculture at lower elevations use these grasslands as summer pastures to graze cattle, goats and sheep. These pastures are gradually being abandoned, leaving them with low stock density and an overall decline in anthropogenic disturbances. The vegetation can be considered as replaced and degraded (impact class V).

Methods

Impacts of disturbance on diversity in natural/semi-natural ecosystems have mainly been assessed by two different but interrelated approaches. The first approach seeks the spatial pattern of diversity along the disturbance gradient or between the sites with different levels of disturbance. Many forests and grasslands which are subjected to different levels of management/use/disturbance are compared to assess impacts of disturbance on floral diversity. The second approach compares the temporal changes in diversity as consequences of disturbance or changes in management interventions in ecosystems. Studies on which this thesis builds compare the changes in plant richness or composition or both between and within sites.

The choice of approaches and methods to assess impacts of disturbance on floral richness and composition depends on the system to be analysed and the type of disturbance pertaining to the individual case studies. The main approach to studying the disturbance-diversity relationship included comparison of vegetation data between sites with different disturbance levels and land-use types, time-gap vegetation data spanned by differences in management and assessing recent vegetation change via the medium of oral history and interviews.

Vegetation sampling

Vegetation sampling was the main tool to gather quantitative data on the state of species composition, richness and changes in these measures over time and space. Only vascular plants were considered in the case studies.

Two Sal forest stands, one protected and one unprotected were sampled in the dun valley of Chitwan district. Vegetation data were collected from a total of 128 plots of 0.01ha each (10m*10m) laid out in gaps and under closed canopy of the forests. All the woody species present in the plots were recorded and tree species were counted as seedlings and saplings defined based on height and girth (Paper I). Tree richness data of forests and agroforests (farmlands) were collected in the mid-hills. Farmlands are very heterogeneous in terms of distribution of trees; trees may be clumped or widely

spaced. To capture the heterogeneity of farmlands the study opted to sample big plots of 350m*100m in the farmland and the same approach was taken in the forests (Paper II). Sixty-five plots of 10m*10m were used to resurvey the study area of Vetaas (1997) on Puhlchoki Mountain (Paper III). All vascular plants were recorded in each plot.

Interviews and key informant interviews

Herders were interviewed to explore land-use, grazing and fire management in temperate and subalpine grasslands of the Gorkha district. Past livestock population was also approximated by using interviews and group discussions (Paper IV). People in the mid-hills were also interviewed to discover the agroforestry practices, purposes of growing trees, local use of trees and forest management history in several locations of the mid-hills. Group discussions were organized to confirm and cross-validate the results of interviews.

Plant identification and nomenclature

Plant species were mostly identified in the field using Polunin and Stainton (1984), Storrs and Storrs (1998), and Press et al. (2000). Taxonomic harmonization was done using Grierson and Long (1983–2001). Specimens of known and common plants were not collected but they were photographed. Deciduous trees and trees without reproductive materials were identified based on a combination of characters such as bark structure, branching pattern, and translation from local names. Specimens from unknown fertile trees were collected and identified with help from taxonomists at the Central Department of Botany, Tribhuvan University and the National Herbarium and Plant Laboratories (KATH). Nomenclature of Press et al. (2000) was followed in all the individual studies.

Data analysis

Descriptive statistics have been used to compare and visualize the results. Detrended Correspondence Analysis (DCA), an ordination analysis, was performed to demonstrate compositional similarities/differences among plots that can be categorized into discrete groups, for example gaps or closed-canopy (Paper I), and farmlands or

forests (Paper II). DCA, an indirect gradient analysis, is suitable for displaying floristic gradients and composition (Lepš & Šmilauer, 2003). Constrained ordinations were used to test the differences in the species composition between vegetation plots of different categories as in DCA. A *t*-test and ANOVA were used to compare the differences in means and variance in species richness. Taxon richness was also assessed with a rarefaction species accumulation curve when required (Paper I). Simple linear regression and a generalized linear model (GLM) were used to analyse the relationship between species richness/abundances and explanatory variables (elevation, canopy cover, gap size, disturbance classes etc.). The choice of regression method was based on the distribution of the response variable.

Results and discussion

Canopy disturbance: an important process to maintain species diversity in forests

Forests are exposed to different types of disturbances: canopy disturbance is ubiquitous to forest ecosystems across the globe and it is part of the natural disturbance regime. Canopy gap formation may be caused by the natural death of a tree(s) or by external process such as fire, pest outbreak and wind-throw. Canopy disturbance, natural or anthropogenic, has similar consequences for forests: a gap formed by natural death of old trees or by felling initiates the same processes in the forest. Gaps are richer in resources, most importantly light, and heterogeneous in microenvironment, making gaps an environment conducive for growth and the coexistence of plant species (Denslow, 1987; Canham et al., 1990). Gaps are therefore expected to have more species than their closed-canopy counterparts (Connell, 1978; Denslow, 1987). Moreover, it is evident that the growth of juveniles suppressed by the shade is released following gap formation. Forest containing patches of open areas will have more species than an even-aged and homogenous canopy forest. Therefore, emulation of near-natural disturbance has been gaining recognition in forest management in an attempt to harmonize biodiversity conservation and forest production. In this context, two case studies each from subtropical and temperate forests have been used to illustrate the role of canopy disturbance in forest floral richness.

In the subtropical *Shorea robusta* forest, composition and richness of total woody species and trees as seedlings and saplings were compared between two habitats (gaps and closed-canopy) (Paper I). Gaps and closed canopy plots were similar in terms of richness and composition of total woody species and seedlings but the differences between the habitats for these measures were apparent for saplings. This similarity in richness is counterintuitive to the notion and prediction of disturbance theories (Connell, 1978; Denslow, 1987), and some individual studies which have found gap richness to be higher than non-gaps (Busing and White, 1997; Hubbell et al., 1999; Schnitzer and Carson, 2001). Moreover, this study did not find any change in species

richness along the gap size gradient, neither the composition of seedlings and saplings varied between the gaps of bigger and smaller size. This refutes the prediction that species richness correlates with gap size (Connell, 1978; Denslow, 1980). Unlike total woody and seedling richness, however, sapling richness and composition was markedly different between gap and closed-canopy plots.

The similarity in richness and composition of woody species and seedlings between gaps and closed-canopy may be related to more than one driver (Paper I). The source of variation in richness and composition between gaps and closed-canopy patches in a forest is dispersal limitation, and obviously light availability. Compositional analysis of seedlings between the habitats clearly reveals that dispersal limitation is not a factor in the Sal forest. Most of the species of the forests are animal dispersed (Datta and Rawat, 2008), and herbivores have likely prevented any dispersal limitations and helped homogenize the seedlings throughout the forest (Holmes and Webster, 2011; Rooney, 2009). Homogeneity in seedlings and total woody species is also explained by the ability of forest species to survive as slow-growing individuals in the shaded understorey. Even gap-dependent species can survive under shade for a few to several years. Those individuals which survive in the shade grow vigorously when a gap is formed by canopy disturbance (Stan and Daniels, 2010; Altman et al., 2016). High diversity and density of saplings in gaps is consistent with this generalization. Individuals survive in low light and grow in high light, implying that there is a survival-growth trade-off and this trade-off best explains the similarity in woody species and seedlings as well as differences in saplings between gaps and non-gaps. Survival-growth trade-offs are mechanisms that maintain diversity in forests where gap and non-gap phases are in a shifting mosaic (Gravel et al., 2010; Wright, 2002).

In the gaps there was correlation of higher sapling richness with higher density of saplings; higher regeneration density is attributed as a likely cause of higher richness in the canopy gaps (Denslow, 1995; Hubbell et al., 1999). In the Sal forest, the species accumulation curve, which compares richness against the number of individuals, showed that sapling richness at a site was a function of stem density, while at another site it was independent of density. Irrespective of gap richness be a function of stem

density or not, gaps had more species in the sapling stage and many of them were not present as saplings in their corresponding closed-canopy site. From this we infer that canopy gaps enhance tree diversity by maximizing the seedling to sapling transition. Gaps are therefore sites for growth and allow the higher abundance of some light-demanding species, for example, *Shorea robusta*, *Terminalia alata*, *Litsea monopetalla* and *Mallotus phillipensis*. These species (except *L. monopetalla*) are also known for their fire tolerance. Fire along-with light might, therefore, have acted as a filter in the seedling to sapling transition (Paper I).

An earlier study of a temperate forest in Nepal documented higher species richness at an intermediate level of disturbance (Vetaas, 1997). This finding is consistent with the tenet of the intermediate disturbance hypothesis which posits that higher richness at an intermediate level of disturbance is expected due to the multispecies coexistence resulting from the trade-off between competitive exclusion and mortality from environmental stress. Recent resampling revealed that i) plot richness (alpha-richness) declined and ii) partly-open plots had more species than plots under the closed-canopy (Paper III). Previously open-access forest was subjected to canopy disturbance but was now under a new management regime which consequently reduced disturbance such as lopping and felling in the forest. The disturbance decline was followed by a decline in plant species richness in general but the decline across plant life forms was not consistent.

The two case studies on canopy disturbance clearly showed that canopy disturbance associated with anthropogenic or natural disturbance is important in maintaining plant species richness and structural heterogeneity in forests. The case studies reaffirm that a forest with a mosaic of closed canopy and open areas contributes to high forest biodiversity. This can inform forest managers who wish to integrate production and conservation.

Production and conservation are not mutually exclusive
Biodiversity conservation and agricultural production are often seen as antagonistic objectives. Large swathes of forested lands in accessible areas across the world have been cleared to make crop-fields and pastures especially since the eighteenth century.

Ecosystems were altered, habitats destroyed and fragmented, and several species were wiped out (Wilson 1992). In recent decades however, there is evidence that some forms of agriculture, for instance, agroforestry, contribute to the biodiversity of agricultural landscapes. Paper II explores this concept and evaluates whether agroforestry contributes to the biodiversity of the mid-hills of central Nepal.

The study found that farmlands were consistently richer in tree species than the nearby and comparable forest at both plot (alpha richness) and landscape level (gamma richness), as well as throughout the elevational bands. Tree richness in general declined with elevation, such that the farmland-forest difference in richness was narrow above 1500 masl than below 1500 masl. This analysis further revealed that in spite of many shared species between forest and farmland they are different in composition, due to differences in the relative abundance (here frequency) of shared species and the presence of unique species in each land-use types. Contrary to expectation, introduced species formed a very small fraction of farmland diversity; instead native tree species principally used for fodder were the main components. The study sheds light on the ecological and management-related drivers that enhance tree species richness in the populated farmlands.

Higher richness in the farmlands compared to the forest seems obvious when we analyse agriculture, livestock husbandry and forests as an inseparable and interdependent component of subsistence livelihood on the mountain slopes of central Nepal. Farmers grow various trees within the farmlands for animal fodder, timber and fuelwood, fruit, and hedges (Acharya, 2006; Fonzen and Oberholzer, 1984). The higher tree diversity in farmland of the mid-hills is also a result of recent site history. Deforestation was at its peak a few decades ago and farmers started responding to this by growing trees for fodder and firewood on their private land (Carter and Gilmour, 1989). Planting trees in farmland supplements forest products when there is a shortage in the forest. This planting and retention of trees may explain the higher richness in the farmland. Community forestry posed restrictions on the open harvesting of forest products, which in turn, has promoted the management of farmland trees, so that together the overall tree species richness in these landscapes has been enhanced. Land

abandonment associated with labour migration has also contributed to tree establishment in farmlands, as evidenced in other parts of the world, for example, in the Mediterranean (Poyatos et al., 2003) and Latin America (Aide and Grau, 2004).

Results of this study depart substantially from the conventional wisdom on the agriculture-biodiversity relationship. Human impacts in ecosystems are pervasive, especially with agricultural expansion and intensification (Foley et al., 2005; Ramankutty and Foley, 1999). The expansion and intensification of agriculture is a major driver of forest shrinkage and biodiversity loss, and the threat to biodiversity is projected to increase with increased population growth and food demand (Millennium Ecosystem Assessment, 2005; Baillelie, 2004). Food production with a minimal ecological footprint is therefore an important development goal. Agroforestry, as practiced in the mid-hills of central Nepal and comparable locations elsewhere in the Himalaya, is shown to help achieve the goal of combining biodiversity conservation and agricultural production in a populated landscape.

This study concludes that an agricultural landscape can complement, but not substitute, the biodiversity conservation goal of protected areas by providing alternative habitats, refugia and landscape connectivity for floral and faunal species. Biodiversity conservation strategies and landscape planning should acknowledge the role of agroforestry in maintaining trees and associated biodiversity, and provisioning ecosystem services.

Declining disturbance: consequences for ecosystems and biodiversity
Land-use change has been an overriding driver of changes in ecosystems across the globe. In some areas land is used more intensely while in many other areas land-use intensity has declined. In many marginal and rural areas human engagement in forests and pastures has declined or ceased as a consequence of migration and the availability of off-farm opportunities. Formerly-managed forests and pastures, when abandoned or subjected to declined disturbance, will experience ecological consequences. Such ecological consequences were assessed in two different ecosystems – a mixed oak-rhododendron forest (Paper III) and grassland patches of temperate and subalpine mountains (Paper IV).

Land abandonment and decline in grazing pressure including other human activities such as selective felling of trees, in mountain pastures and forests as a consequence of outmigration from the mountain areas was an overriding phenomenon in the mountainous areas of Nepal over the last four decades. A case study explicitly reported for the first time that grasslands used as summer pastures by migratory herders have been transformed into shrubland and woodland. Native shrubs, mainly *Berberis angulosa, B. aristata* and *B. concinna,* which were in low abundance in the past have abruptly increased in their density and cover during the last two decades. Grasslands which had already been encroached by shrubs were also sites for the establishment of tree species, particularly *Rhododenron arboreum* (Paper IV). This encroachment costs not only grassland area but also the grassland-dependent flora. In another analysis, it was found that decline in traditional disturbance, mainly the lopping of canopy trees, led to an increase in forest canopy cover and a net loss in vascular plant species richness. However, the impact was variable across life forms (Paper III). These ecological changes are discussed from the point of view of the interface of social and ecological processes.

Globally, grasslands are undergoing changes, especially woody encroachment against a backdrop of climate and land-use changes (Archer, 1995; Van Auken, 2000). These two drivers individually or in tandem have contributed to the transformation of specific grasslands. Decline in grazing pressure and fire suppression are overriding land-use changes in grasslands. Pastoral abandonment and shrub encroachment are consecutive events in the grasslands of Gorkha – a clear indication of the cause-and-effect relationship. The proximate cause of changes in pastures is decline in anthropogenic disturbance while the underlying drivers are non-ecological in nature. Globalization, specifically rural outmigration, is an underlying driver. Migration as a global process is a source of social and economic changes elsewhere. Ecological impacts of migration are also clearly documented at different specific localities (Aide and Grau, 2004; Walters, 2016). Formerly-used pastures have reverted to forests (Perz and Skole, 2003; Rudel et al., 2005). Outmigration has led to a decline in human pressure on forest and pastoral resources in rural and marginal areas. The population of

the high mountain areas in Nepal has declined during the last few decades (CBS, 2011), influencing resources in two ways. First, direct consumption of forest, pastoral and agricultural resources by humans and their livestock declines (Metz, 1994) and second, human intervention in terms of fire and grazing, which have a big role in shaping the landscape and ecosystem services, also change. This reduction in disturbance triggers secondary succession in the grasslands, which is considered a threat to biodiversity (Koch et al., 2015). In the specific case of pastures in Gorkha, the decline in human pressure and their livestock has caused a major change during the last four decades. The landscape was transformed as the dominant vegetation altered-- meadows used as summer pastures became covered by dense bushes, trees established, and grass and herbaceous vegetation cover declined. In general, shrub and tree cover increased at the expense of pastures. Fire, grazing and the harvesting of forest products had maintained the grass and forbs in the meadows. Fire is an important management tool in grasslands to control woody species expansion. With declined human pressure and abandonment, shrub and tree species were no longer controlled and thus the current bush and tree cover in the grasslands is an outcome of the declined disturbance.

The consequence of the withdrawal of anthropogenic disturbance in temperate forest is within the framework of disturbance-diversity theories (Connell, 1978; Denslow, 1987). Human or natural disturbances, especially the reduction of canopy trees, will directly influence the microenvironment in the field and sub-canopy layer, and a moderately disturbed forest has a mixture of shade and light which facilitates the coexistence of both shade-tolerant and intolerant species (see Vetaas, 1997). Reduction in disturbance implies increased canopy cover which homogenizes the light microenvironment of the forest understorey favouring shade-tolerant species and reducing light-adapted species. A sharp decline in herbaceous species richness between the two survey periods is related to the increased canopy closure. It was also evident that open areas have comparatively more species than relatively closed areas of the forest.

The intermediate disturbance hypothesis (Connell, 1978; Grime, 1973) not only depicts the spatial pattern of plant species richness but also predicts changes in richness as a consequence of change in disturbance over time. The unimodal relationship that was observed for some life forms when the disturbance gradient is long becomes linear when the disturbance gradient is truncated at it's upper end.

Protection of forest is an important strategy to assure conservation of biodiversity. Formerly-used forests have been protected in many places and such efforts have largely been successful in attaining their goal of increasing forest cover, biomass and timber volume. However, the outcome in terms of local biodiversity does not always concord with forest cover (e. g., Gautam et al., 2014). Similarly, abandonment of coppice forestry in temperate forests of central Europe caused decline in plant species richness (Mullerova et al., 2015). Plant richness following forest protection may depend on the previous level of disturbance, the type of forests, the species pool, and the extent and degree of protection. Forest succession theories, the intermediate disturbance hypothesis, and the environmental heterogeneity-diversity relationship provide important insights into the fate of plant diversity following the forest protection.

The two case studies of Papers III and IV clearly showed that disturbance is essential not only for maintaining species richness but also for keeping the existing landscape patterns and associated processes. Withdrawal of age-old disturbance can have undesirable consequences on biodiversity and ecosystem services. These findings can help forest and natural resource managers to integrate conservation with production forestry in a human-modified landscape.

Conclusions

This synthesis demonstrates the impacts that human disturbance in terms of use or management of resources can have on vegetation, mainly diversity and composition, in the different ecosystems of forests, grasslands and agroforests. The individual studies have shown that sustained anthropogenic disturbance or management, which has become an integral part of the ecosystem processes in these ecosystems, has contributed to plant species richness and composition. In the forests canopy disturbance, be it natural or anthropogenic, is an important process to maintain diversity and heterogeneity, similarly fire and grazing in the grasslands. Nevertheless, as ecological theories have established, there is a trade-off between disturbance and diversity. This provides important perspective in resource management in order to assure biodiversity conservation and regeneration of ecosystem services.

The diversity-disturbance relationship provides important insights to manage resources for ecosystem services and biodiversity in the context of fluctuating disturbance. Changes in the disturbance regime of ecosystems correlate with economic growth, climate change and demographic changes. Decreased disturbance does not necessarily result in better ecosystem and plant diversity; rather it may alter the ecosystem and landscape patterns. While higher disturbances, obviously, impedes the biodiversity and ecosystem services. Adjusting disturbance through management to optimizing production from forest and pastoral resources whilst having the least biodiversity footprints should, therefore, be a continuous process.

Conventional approaches to biodiversity conservation typically consider human disturbance to be inimical to biodiversity, and therefore conservation seek to preclude human activities. However, this approach has been confronted with growing evidences showing that many ecosystems and species have adapted to human disturbance and, disturbance can contribute to biodiversity and ecosystem health by increasing heterogeneity. The individual case studies I have presented also refute the conventional view that nature untouched is good and conservation should preclude human intervention. Rather, anthropogenic disturbance associated with low intensity

resource use is found to foster biodiversity and potentially ecosystem services. Since, livelihoods of a vast majority of rural population depend on use of primary resources; my findings suggest the potential of integration of biodiversity conservation with a sustainable livelihood. This is particularly relevant for forest management programmes like community forestry where conservation of biodiversity and supply of forest products to local people are shared goals.

Resource management and biodiversity conservation is a challenging task in the dynamic and complex social ecological system. In this regard, the findings of my study could be important in view of the landscape context on which individual resource units are positioned and livelihoods characterized by high resource dependence. Acknowledging the roles of disturbance in ecosystems as informed by theories coupled with findings pertaining to local ecosystem can contribute to understand the trade-off between management and ecosystem health. This study, therefore, recommends the intervention of anthropogenic disturbance as a strategy to conserve plant species diversity while continuing to meet the needs of dependent people. This thesis underscores that appropriately managed cultural landscapes including secondary forests can complement the goal of biodiversity conservation. Conservation in agricultural landscape and secondary forests, however, cannot be a substitute of strictly protected areas and larger reserves. It is because certain species need habitats of old undisturbed vegetation and large unfragmented forests to thrive.

Further perspectives

➢ The different ecosystems analysed in this synthesis are part of a multifunctional and complex landscape, and each ecosystem or resource unit has contribution in protecting biodiversity and providing ecosystem services for dependent population. There is a complex and multiscale interactions and trade off among human disturbance/management, ecosystem services and biodiversity. Analysing this trade-offs and interaction is desirable to understand the scenario on which diversity and ecosystem services could be optimal.

➢ This synthesis demonstrates that the continuation of traditional disturbance is essential to maintain the function and diversity of cultural landscapes. However, globalization, e.g. migration, has left forests and pastures abandoned which has several ecological consequences. Developed countries have invested to maintain traditional disturbances, for example, cultural heathland conservation in Europe. A lack of financial support in developing nations, however, makes conservation challenging in such nations. Supporting traditional resource management practices, for example transhumance herding, can have dual purposes: provision of a sustainable livelihood for local people and conservation of biodiversity.

➢ A case study on grassland conversion in the Himalaya as a consequence of withdrawal of anthropogenic disturbance opens up several obvious questions for analysis. It is imperative to know what area has been converted, how many grassland-dependent species have been affected, what the likely impacts will be on herders who are still continuing transhumance herding, what the consequences to ecosystem services will be and so on.

➢ Agroforestry practices in low-intensity agricultural landscapes make a notable contribution to conserving tree species richness. Tree diversity in turn, can play a role in conserving faunal diversity. Trees can provide alternative habitats, refuges and stepping stones, by providing landscape connectivity to avifauna. Moreover, agricultural landscape in hilly slopes is associated with higher

heterogeneity due to topography and scattered trees, which will support more species. It would be interesting to analyse how trees in agricultural landscapes support meta-populations of avifauna and to what extent they contribute to the connectivity and alternative habitats for other species.

➤ Canopy disturbance is an important process to maintain tree diversity in the Sal forests of Nepal. However, we lack information on gap-filling progression, transition probabilities, and growth rate of seedlings and saplings below canopy and in open areas in the Sal forests. Further studies should be dedicated to obtaining this information to allow future changes in the forest to be modelled and to optimally manage these resources for societal and ecological needs.

➤ Forests in the Himalaya and elsewhere are subjected to disturbances to the crown layer (canopy opening) as well at the ground layer (fire and grazing) and we do not know how these different disturbances interact to shape structure and composition of Sal forest. Therefore, better understanding of the interaction of the different disturbances in forest ecosystems would be desirable.

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I

Paper I

Do composition and richness of woody plants vary
between gaps and closed canopy patches in
subtropical forests?

Do composition and richness of woody plants vary between gaps and closed canopy patches in subtropical forests?

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Abstract

Questions: Do composition and richness of woody plants differ between gaps and closed canopy in subtropical forests, and does this difference vary across life stages of tree species? Is tree species richness in gaps a function of regeneration density?

Location: Subtropical *Shorea robusta* Gaertn (Sal) forest, central Nepal.

Methods: We collected vegetation data from two old-growth *S. robusta* forest stands. We sampled 128 plots of 100 m^2 equally spread between the two habitats: gap and closed canopy. In each plot, we recorded the total number of woody species, number of individuals of seedlings and saplings of tree species and measured the DBH of all saplings. We compared species richness and composition of total woody species, seedlings and saplings between the two habitats. We used ordination to analyse species composition, and an individual-based species accumulation curves to illustrate the effect of density on species richness.

Results: The species composition of total woody species and seedlings was similar in both habitats, but species composition of saplings differed between habitats. Total woody and seedling richness were similar between habitats at one site, but were richer under closed canopy at the other site. Sapling richness was higher in gaps at both sites and was a function of stem density at one site, but not at the other site.

Conclusions: Gaps are not always areas of higher woody species richness and therefore may be less important than expected for the overall species richness of woody plants. Instead, they are potentially important for enhancing local tree richness by increasing sapling richness. Gap disturbance is the primary driver of structural heterogeneity in forests where topographic and edaphic gradients are negligible.

Introduction

Forest canopy gaps differ from closed canopy or shaded understorey in terms of space, resources and, probably most importantly, light availability (Denslow 1987; Canham et al. 1990). Death and removal of dominant individuals also change the competitive hierarchy among the species in a forest, and different species will be favoured for growth in open areas compared to areas under a closed canopy. As a consequence, gaps and closed canopy areas are expected to support germination and growth of different suites of species, resulting in different composition and

richness between them (Denslow 1987; Swaine & Whitmore 1988; Vilhar et al. 2015).

Gaps can create higher richness compared to closed-canopy forests at different scales. At local scale a specific gap site is richer than its corresponding closed-canopy site (higher α-diversity), and at a broader scale forests with a mosaic of gaps have higher total richness than closed canopy forest (higher γ-diversity; Connell 1978; Denslow 1987; Muscolo et al. 2014). Gap partitioning *sensu* niche partitioning – a phenomenon by which species spatially partition space and resources in forest gaps from the gap centre to the edge (Grubb

1977; Denslow 1980, 1987) – is the main explanation for multispecies co-existence and consequent higher richness in the gaps. Besides niche partitioning, the disturbance creating the gaps is expected to reduce the effect of competitive exclusion by removing the canopy dominant from the forest, which may lead to higher species richness in the gaps (Connell 1978). Alternatively, it is also argued that higher richness in a gap is a positive function of the number of individuals (the density hypothesis; Brokaw & Busing 2000).

The gap partitioning hypothesis posits that gaps have a heterogeneous microenvironment due to within- and among-gap gradients in light and resources; such gradients are often associated with gap size (Rickleffs 1977; Denslow 1980, 1987; Brandani et al. 1988; Canham et al. 1990; Vilhar et al. 2015). Species with different resource requirements and competitive abilities can partition the available space according to the environmental differences along the gradients from the centre of the gap to a closed canopy, which in turn is likely to increase the species co-existence and richness in the gaps (Rickleffs 1977; Denslow 1980, 1987; Brandani et al. 1988; Lundholm 2009; Kern et al. 2013). However, prevalence of resource and microclimatic gradients within and among gaps do not necessarily lead to gap partitioning and higher richness (Hubbell et al. 1999; Brokaw & Busing 2000). Post-gap succession may also be contingent on competition between life forms (Schnitzer & Carson 2010), dispersal and recruitment limitations (Hubbell et al. 1999), and gap filling through advanced regeneration (Uhl et al. 1988). These processes may prevent gap partitioning and impede the potential richness (Hubbell et al. 1999; Brokaw & Busing 2000).

The density hypothesis asserts that gaps are sites of higher densities of individuals, and the observed higher richness is simply a function of higher density of smaller individuals (Denslow 1995; Busing & White 1997; Hubbell et al. 1999). Gap disturbance initiates gap-phase succession, which is characterized by an increase in density and growth of seedlings and saplings (Brokaw 1985; Chazdon 2014). Gap partitioning may be the most likely explanation for higher species richness in the gap, given that the richness is independent of the stem density (Brokaw & Busing 2000).

In gap-phase succession, all trees and woody species undergo rapid thinning with time after establishment of seedlings and saplings, and the thinning rate is species-specific (Runkle 2013). The species-specific thinning in the shade and the gap increase the likelihood of observing gap partitioning at the sapling stage (Dalling et al. 1998; Hart & Kupfer 2011; Runkle 2013; Cowden et al. 2014). Moreover, there are differences in the niche among life stages of trees (Grubb 1977; Poorter et al. 2005);

therefore, sapling composition may not parallel seedling composition between contrasting light regimes. It is therefore useful to analyse seedling and sapling composition separately between habitats in order to reveal whether differences in species composition are apparent only in a certain regeneration phase or life stage.

A comparison of richness between gap and closed-canopy plots is necessary to assess whether the gap plays a role in maintaining/enhancing species diversity in forests. However, there are very few studies that actually make such comparisons, as in Schnitzer & Carson (2001; but see McCarthy 2001). The few existing empirical studies making such comparisons are from either hyper-diverse tropical forest or low-diversity temperate forest (McCarthy 2001). Other studies assessing gap richness also suffer from methodological biases when they compare richness between sites that have different densities of individuals, as higher density may lead to higher richness (Kobe 1999a, b). To see if the richness differences are purely an effect of number of individuals, comparison of gaps and closed canopy should be standardized by the number of individuals (Chazdon et al. 1999). Understanding how species richness and composition across life stages vary in gaps and closed canopy is necessary for understanding how survival–growth trade-offs between regeneration stages in spatio-temporally varying environments contribute to the maintenance of woody species richness and co-existence in forests.

Subtropical *Shorea robusta* (Sal) forest is different from tropical and temperate forests in terms of diversity, light regime and canopy architecture, but has rarely been considered in gap disturbance and diversity-related studies. This paper compares plant species composition and richness between gaps and closed canopy areas in two Sal forest stands on the southern plains of Nepal. We aim to analyse: (1) differences in composition and richness of woody plants between gaps and closed-canopy plots; (2) whether the richness and composition patterns between habitats differ with the regeneration stage of trees; and (3) whether observed patterns are related to the effect of density of individuals. We propose that a compositional difference is expected due to different light regimes. We hypothesize that species richness (for the both regeneration stages of trees) will be higher in the gaps than under the closed canopy, consistent with conventional gap–disturbance theory. Richness will also be evaluated against the number of individuals using individual-based species accumulation curves to ascertain if richness in the gaps is a function of density. We do not test gap partitioning *per se*, rather we argue that if richness is higher in the gaps and is independent of stem density, it is most likely to be related to gap partitioning.

Methods

Study area

This study was conducted in the Chitwan district of Nepal. Chitwan is a dun valley between two Siwalik ranges. Dun valleys, like the Terai, are mainly flat land, made up of foreland basin deposits of Himalayan origin. Soil of the valley is largely homogenous, except for grain size variation in riverine habitats; mainly composed of quaternary alluvial deposits consisting of sandy loam, loam and clay developed over sand, gravel and boulders (Wesche 1996; Miehe et al. 2015). The climate is subtropical and monsoonal, with humid and hot summers and dry and cold winters. Average annual rainfall is 2200 mm (1971–2010), of which 80% falls during the monsoon (Jun to Aug), and average annual temperature is 24.6 °C (2000–2010; CBS 2011).

Shorea robusta (Sal) stands in the northern part of the Barandabhar Corridor Forest (BCF, site I) and the Kasara area of Chitwan National Park (CNP, site II) were sampled; these two sites are *ca.* 26 km apart. The areas of BCF and CNP are 105 and 932 km^2, respectively. The BCF is a north–south-oriented narrow strip of forest in the densely populated area of Chitwan and connects CNP with the Siwalik/Mahabharata range (Fig. 1). CNP – a UNESCO World Heritage site established in 1973 – is famous for the conservation of wildlife, including the one-horned rhino

and Bengal tiger. The forests at both sites are dominated by old-growth Sal stands with some riverine vegetation along streams and sand deposits. Sal is a member of Dipterocarpaceae, a tropical family mainly distributed in the Indo-Malayan region, and forms extensive mono-dominant forests in the southern part of the Himalayas, in the tropical to subtropical climate of the Indian subcontinent. Sal is a robust, gregarious and semi-deciduous tree species, and is an important high-value timber species extensively used in construction and furnishing. Sal-dominated forest, with *Dillenia pentagyna* as main subcanopy species, sandy loam soil, plain topography and similar climate are shared features of the two sites. Site I is slightly higher (220 m a.s.l.) than site II (180 m a.s.l.). *Clerodendrum viscosum* and *Leea crispa* at site I, and *Thameda arundanacea* and *Diplazium esculentum* at site II are the dominant sub-canopy species.

Forest management and disturbance

The two forests differ in management regime, and hence use and disturbance intensity. Forest at site I is used by local people for forest products, firewood, fodder and timber, and for grazing livestock (Wesche 1996). Site II is in the core area of the park, and is not used for forest biomass extraction or livestock grazing. However, people are occasionally allowed to harvest dry firewood and thatching grass, under monitoring. Rhino, deer and elephant are the
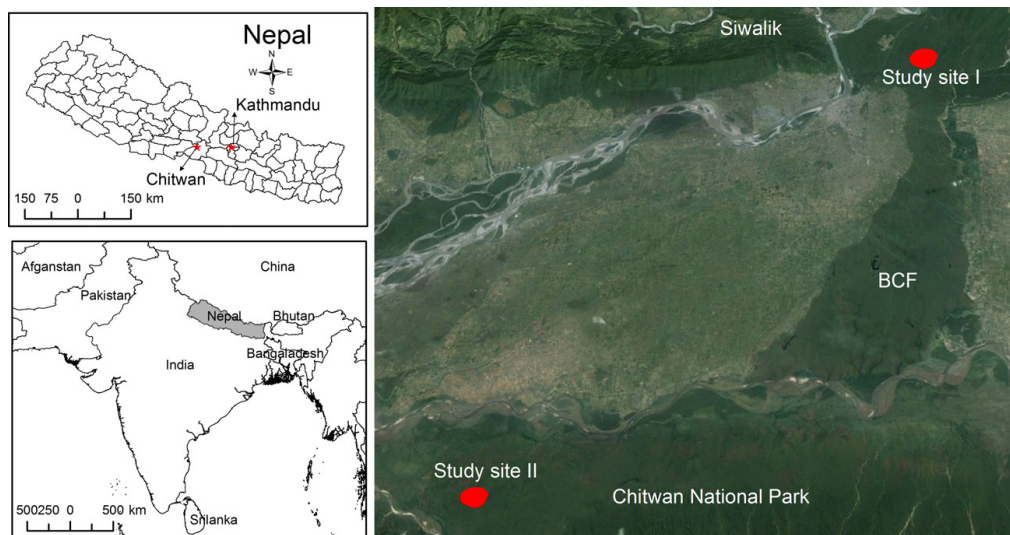

Fig. 1. Location map of the study area showing Chitwan district and the Barandabhar Corridor Forest (BCF – study site I) between Chitwan National Park (CNP – study site II) and the Siwalik mountain range in lower central Nepal. The sites are ca. 26 km apart.

main browsers. Fire in the ground stratum during dry season (Apr–May) is common at both sites, but the frequency is higher at site I.

Both sites have a mosaic of gaps and closed canopy patches formed by natural and anthropogenic disturbances. A gap may be formed by the death or removal of a single or multiple trees (Sapkota & Oden 2009). Sal is the exclusive gap maker at both sites. Gap formation was caused by natural death and windthrow at site II, and natural as well as anthropogenic felling at site I.

Sampling design

Sampling was designed to compare species composition and richness between the two habitats (gap and closed canopy) within a forest. We define a gap as an area where the canopy was opened by a gap > 100 m^2, and we did not set an upper limit of gap size, as did McCarthy (2001). Setting the lower limit at 100 m^2 is admittedly somewhat arbitrary, but it avoids gaps caused mainly by branch breakage and smaller than the plot size. We define canopy or closed canopy as an area where crown cover is >40% and trees forming the crown cover are >25 m tall. We placed plots under the canopy where it was continuous and the canopy cover immediately above and around the plot was more or less homogenous, but avoided canopy formed by only one or two isolated trees to ensure that plots were under a 'true canopy'. We also avoided canopy formed by trees that were approaching gap-filling height of 15–20 m; this consequently excluded older gaps.

Vegetation data were collected in plots of 10 m × 10 m (0.01 ha) laid out along two transect lines in each site, which were at least 400 m apart. In each site, we aimed to place plots (representing both habitats) along a azimuthal line at regular intervals of 100 m, but due to our definitions of canopy and gap we allowed for distances of up to 80 m left and right from the line; plots in a transect may or may not be paired. Areas with streams, marshlands, trails or unusual disturbances on the ground were avoided. An equal number of plots (32) in the gaps and in closed canopy (32) were sampled at each of the two sites, yielding a total of 128 plots.

We included only woody vegetation that encompassed all species with woody stems. In a one-time sampling design, a considerable fraction of the herbaceous species would have been missed, hence we did not include herbaceous species. We recorded all the species of trees, shrubs and woody climbers present in a plot and pooled them to obtain total richness of woody species, hereafter called 'total woody species'. Individuals of tree species were categorized into two regeneration stages: seedling (10–150 cm tall) and sapling (height > 150 cm and DBH < 10 cm). We thus have three groups: total woody, seedlings and

saplings; the latter two are life or regeneration stages of trees, to compare between habitats for their composition and richness. We counted the number of individuals of seedlings and saplings for each species, and measured DBH (137 cm above ground) of saplings. We also counted the number of individuals of mature trees (DBH > 10 cm) at site II; they were not considered for site I as their density/richness was influenced by illegal and preferential harvesting of mature trees. We measured the extended gap area and considered gaps to be ellipsoidal following the protocol of Runkle (1992). We also identified the gap-forming trees and the causes of gap formation by observing snags, stumps and logs. Canopy cover was measured using a spherical densiometer. Plant species were identified using Grierson & Long (1983-2001). We also estimated the ground vegetation cover as percentage (up to 1-m tall) in each plot.

Data analyses

Preliminary analyses were done to decide whether to pool the data from the two sites and to check for differences in species composition and richness between sites. The two sites were found to have different species composition in ordination space. Variance of species richness between the two sites was also different for all three metrics. Based on these exploratory analyses we decided to treat the two sites separately.

Detrended correspondence analysis (DCA; Hill & Gauch 1980), an indirect gradient analysis, with supplemental categorical environmental variables, was used to assess the difference in species composition between the two habitats. We also performed constrained ordination to evaluate more directly if the composition of the three groups differs between the two habitats. The purpose of the species composition analysis was to analyse whether gaps and closed-canopy plots had similar sets of species or not. The choice of using abundance or binary data for the analysis was an *ex-post* decision based on the preliminary analysis. Sal shares more than 40% and 50% seedling abundance in sites I and II, respectively. Sal seedling density, in turn, was three times higher in gaps than in the closed canopy at site I; while it was four times more in gaps at site II. Sal alone, therefore, can influence the species composition analysis if abundance data as such are considered in the ordination analysis. To avoid problems associated with these differences in abundance we used presence–absence data in the ordinations. We also used log-transformed abundance data after removing Sal in the ordination, and found that the result was not different from using binary data. We used redundancy analysis (RDA) for all woody species and seedlings, and CCA for saplings; this choice was based on the gradient length of the first DCA axis (RDA when <2.0 and

CCA when >2.0). The direct ordinations were performed with a single binary environmental variable, corresponding to gap or closed canopy. We tested the significance of this variable with a Monte Carlo permutation test with 499 iterations using CANOCO 5 (Šmilauer & Lepš 2014).

We compared species richness (number of species per plot) between habitat types using t-tests; we did not consider gap and closed canopy plots to be paired. We also used a rank-abundance curve (RAC) to compare and visualize richness and dominance of seedlings and saplings between the habitats (Magurran 2004). We used log 10 (number of individuals + 1) data to plot the RAC. The pattern of species richness along the gap size was analysed for total woody species, seedlings and saplings separately for the two sites using a GLM (McCullagh & Nelder 1989) with a log-link function. A GLM was used because the response variable (species richness) is count data and the error is assumed to have a Poisson distribution.

To account for differences in the number of individual 'density effects' when comparing species richness between the two habitats, species accumulation curves (SACs) with rarefaction were used (Denslow 1995; Kobe 1999b; Gotelli & Colwell 2001). We also compared sapling richness in gaps with tree richness in gaps and canopy using SAC to ascertain if gaps are really richer than closed canopy. We used individual-based SACs in the vegan package in R (R Foundation for Statistical Computing, Vienna, AT).

Results

General gap attributes

Gap and closed canopy plots were different in terms of tree size and ground cover. Larger-sized trees were present in all the closed canopy plots, while gaps, by definition, had only trees of smaller size. Saplings were more abundant in gap plots than under closed canopy. Total ground cover of vegetation was 35% in gaps and 52% below canopy at site I, while it was 23% and 18% in gaps and closed canopy, respectively, at site II. Mean gap size was 373 and 799 m^2 at sites I and II, respectively. Sal formed the canopy in 90% of the plots and *Dillenia pentagyna* was the most common sub-canopy tree. Average canopy cover in the closed canopy was 70% at both sites.

Species composition

The DCA showed no difference in species composition of total woody species and seedlings between the two habitats, whereas the composition of saplings was conspicuously different (Fig. 2a,b). Constrained ordination (RDA and CCA) verified this but explained only a small proportion of the variation for all three groups (Table 1), and only
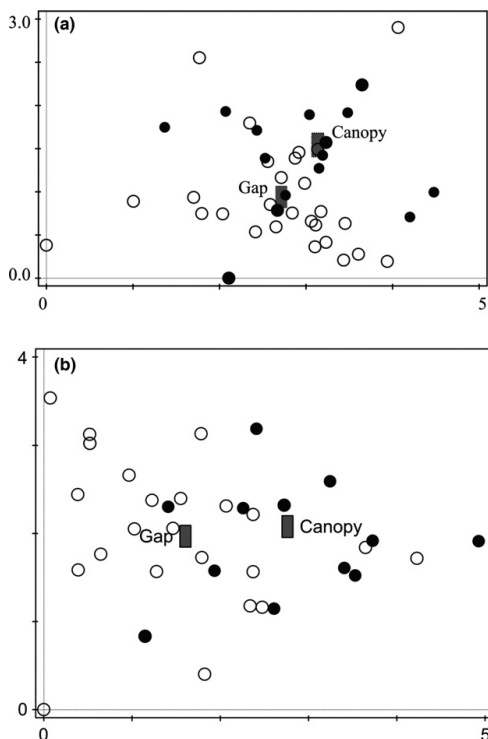

Fig. 2. DCA diagram along first and second ordination axes for saplings for (**a**) site I and (**b**) site II. Empty circles are gap plots and filled circles are closed canopy plots, boxes represent habitat types: gap and closed canopy.

Table 1. Summary statistics of the constrained ordination analyses (RDA and CCA). First ordination axis was constrained to environmental variables with gap and closed canopy as categorical variables.

	Site I			Site II		
	TW*	SI*	SP†	TW*	SI*	SP†
Var expl (%)	1.4	1.9	5.3	2.2	2.4	5.1
Pseudo F	0.9	0.9	3	1.4	1.5	2.4
P-value	0.684	0.596	0.002	0.075	0.052	0.002

Var expl, Variance explained; TW, Total woody species; SI, Seedlings; SP, Saplings.
*RDA.
†CCA.

the difference in sapling composition was significant ($P < 0.05$).

The frequency occurrence of seedlings and saplings between habitats also matched the compositional pattern visualized in the ordinations, i.e. similarities in seedlings

and differences in saplings between habitats. Most of the species in the seedling stage had more or less equal frequency of occurrence between the two habitats, and the most common species maintained the trend at both sites (Appendix S1). Contrary to the seedling pattern, almost all of the saplings had a higher frequency in the gaps, and some were restricted to gap plots only: eight out of 23 species at site I and five out of 15 at site II. Sal, the dominant canopy species as well as gap-forming tree at both sites, appeared to be subdominant as a sapling in the gaps of both sites.

Species abundance pattern, as depicted by the steepness of the RAC, also complemented the results visualized by ordination and frequency occurrence diagrams (Fig. 3a,b).
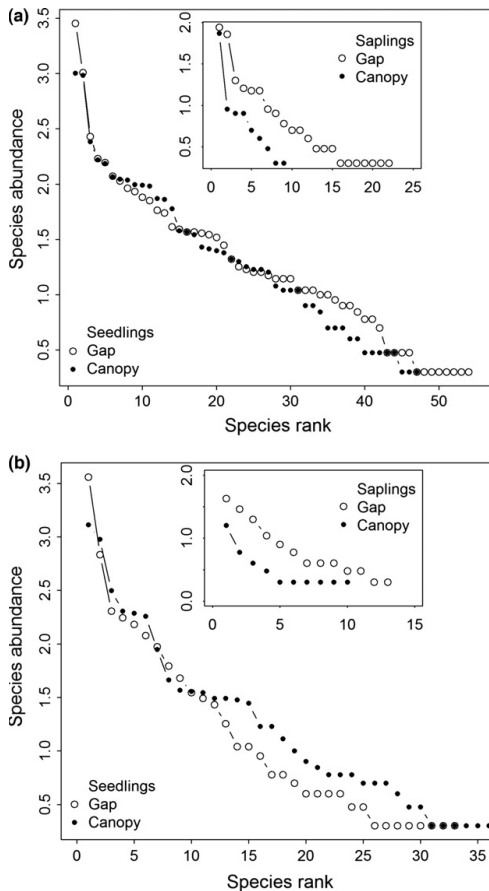

Fig. 3. Rank abundance curves for seedlings and saplings (inset) for (**a**) site I, and (**b**) site II. Species abundance is presented as log10 (density + 1)

RAC for saplings in closed canopy plots was steeper and shorter than for the gap plots. The curve suggests that saplings in closed canopy were dominated by a single species, *Dillenia pentagyna* at both sites, and other species were relatively less abundant, while it was dominated by the two species although other species were also common in the gaps.

Species richness and abundance

At site I, we recorded 58 tree, 22 shrub and six climber species, while at site II there were 40 tree, 12 shrub and six climber species (Appendix S2). Sapling richness was a subset of seedling richness at both sites. Gaps and closed canopy plots at site I were similar in terms of total woody and seedling richness, while closed canopy plots were richer than gaps at site II (Table 2). Gaps at both sites had higher sapling richness than in the closed canopy. Total woody and seedling richness did not change along the gap size at either site. Similarly, sapling richness at site II was not a function of the gap size gradient, but at site I it declined with gap size, although the relationship was rather weak (Appendix S3). Mean seedling density (number of individuals per plot) was significantly higher in the gaps than under the closed canopy at both sites (Table 2). Similarly, the mean sapling density in the gaps was more than twice that of the closed canopy at both sites.

The rarefaction SACs between habitats for seedling richness at both sites, and sapling richness at site I, support the test results of richness (Table 2, Fig. 4a,b), i.e. the observed difference in richness between habitat types was reaffirmed after accounting for stem density. At site II, SAC for sapling richness in both habitats (Fig. 4b) ascended together, implying that for an equal number of individuals, richness is the same. Therefore, the observed difference in sapling richness at site II appeared to be a function of the density of plants. Here, saplings in the gaps were as rich as mature trees, but they outnumbered mature trees of closed canopy. Mature trees in the gaps were richer than their counterparts in closed canopy (Fig. 5).

Discussion

Species composition and dispersal limitations

We did not find any compositional differences in total woody species and seedlings in gaps and closed canopy, such compositional similarities in gap understorey mosaics are not uncommon (Nagel et al. 2010; Yao et al. 2015). Dispersal and recruitment limitations, in addition to the variation in light, are likely to affect species composition in the gaps and closed canopy (Dalling et al. 1998; Hubbell et al. 1999). However, the observed compositional similarity suggests that the majority of species in these forests are

Table 2. Mean and SE of mean for species richness and abundance in gap and closed canopy plots at each site (number of plots in each habitat for each site is 32). The difference in means was tested using Welch t-test.

	Site I - BCF		Site II - CNP	
	Canopy	Gap	Canopy	Gap
Total woody Richness	24.09 ± 0.74	25.66 ± 0.79	15.43 ± 0.60	13.41 ± 0.43**
Seedlings	16.44 ± 0.56	17.47 ± 0.68	11.75 ± 0.32	10.16 ± 0.29**
Saplings	1.69 ± 0.18	4.00 ± 0.37***	0.81 ± 0.16	2.28 ± 0.25**
Abundance				
Seedlings	117 ± 6.19	175 ± 13.94***	114 ± 8.39	196 ± 16.07***
Saplings	3.31 ± 0.56	8.22 ± 0.77***	1.0 ± 0.19	3.9 ± 0.49***

**$P < 0.001$, *$P < 0.01$.
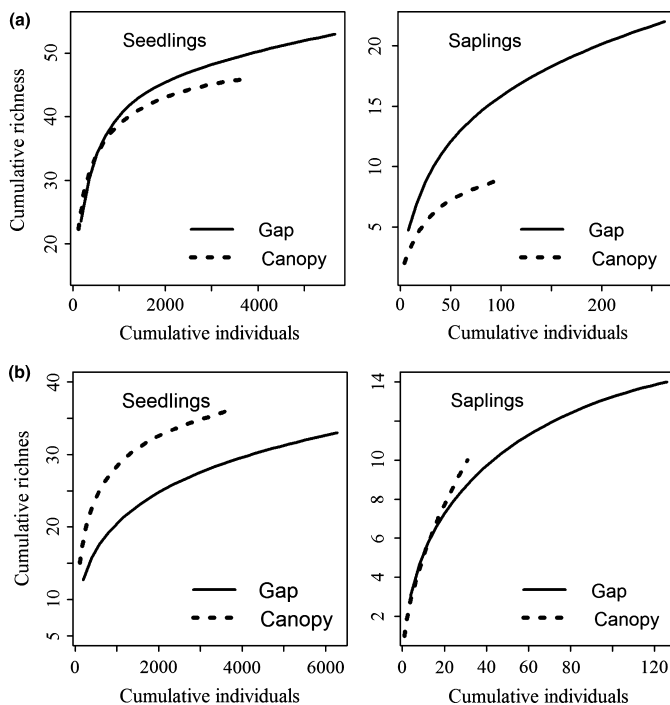
Fig. 4. Species accumulation curves for seedlings and saplings for (**a**) site I and (**b**) site II.

not dispersal-limited. Both of the forests are grazed by herbivores, which can potentially homogenize composition in gaps and under closed canopy (Rooney 2009; Holmes & Webster 2011). Additionally, the majority of forest species can grow under varying light environments, and the fact that their juveniles can survive in shade as low-growing individuals (survival in low light) is also a likely explanation for homogeneity in composition in gaps and closed canopy. The ability of species to grow under varying light

environments suggests that the majority of the forest species are generalists rather than niche-differentiated specialists (Lieberman et al. 1995).

The compositional difference between gaps and closed canopy, however, was evident in the saplings for gaps, which had some unique sapling species and higher abundances of those species shared by both habitats. The partitioning of saplings between gaps and closed canopy in the forest may best be explained by the occurrence of spatial
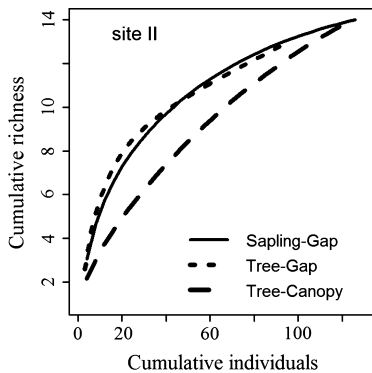
Fig. 5. Comparisons of species accumulation curves of saplings in gaps with trees in both habitats; gaps/closed canopy, at site II.

variation in light between the two habitats, the requirement of light for growth release of such plants (Kobe 1999a; Ruger et al. 2009; Philipson et al. 2012) and selective mortality of seedlings along the successional chronosequence. Light is the most limiting resource for plant growth under a closed canopy and growth spurts are apparent upon exposure to higher light (Montgomery & Chazdon 2002; Ruger et al. 2009; Philipson et al. 2012). Higher abundance of some light-demanding species, e.g. *Shorea robusta*, *Terminalia alata*, *Litsea monopetalla* and *Mallotus phillipensis,* in the gaps confirms their gap-dependent growth. The higher abundance of subdominant species in the gaps may increase their likelihood of establishment, thus gaps provide an opportunity for infrequent and subdominant species to establish. The most abundant species in the sapling stage at both sites – *Shorea robusta* and *Dillenia pentagyna* – are known for fire tolerance (Wesche 1996). Fire, along with light, may act as a filter in the seedling to sapling transition.

The similarity in seedling, but differences in sapling composition, in gaps and closed canopy clearly indicate that there is a life-stage trade-off between survival in low light and growth in high light (survival–growth trade-off). This segregation of life stages of trees in spatio-temporally varying environments is a plausible explanation for the observed seedling–sapling patterns in the Sal forest, and a potential mechanism for species co-existence in forest ecosystems (Wright 2002).

Total woody species and seedling richness: Gaps are not always richer

We did not find higher richness of total woody species and seedlings in gaps compared to closed canopy; instead the opposite was true for site II. However, for saplings our

hypothesis stands, as total and mean sapling richness was markedly higher in the gap plots at both sites (saplings are discussed in the following section). These findings contradict the conventional forest gap disturbance theories, which expect higher richness in the gap environment (Connell 1978; Denslow 1980, 1987); gaps are reported to be richer than closed canopy in tropical forests (Busing & White 1997; Hubbell et al. 1999; Schnitzer & Carson 2001). Our results show that species richness (total woody species and seedlings) is not related to the gap size gradient. A negative, but weak, relationship of sapling richness at one site but not the other indicates that richness and gap size relationship are not a generalizable phenomenon. Individual studies also do not confirm the relationship as a consistent pattern, as some report no relationship (Obiri & Lawes 2004; Nagel et al. 2010), while others find a positive relationship between them (Denslow 1980; Kern et al. 2013), at least for shade-intolerant species.

Competition between different plant life forms in the post-gap succession may prevent the gap from attaining its potential richness. Liana, dense shrub and high grass cover, individually or in combination, can preclude or suppress tree regeneration, and in some cases even alter the successional trajectory in canopy gaps, thus preventing canopy gaps from achieving higher richness (Royo & Carson 2006; Schnitzer & Carson 2010). At site II, the grass *Themeda arundanacea* had substantially higher cover in gap plots relative to closed canopy plots, and may have inhibited woody and tree species richness. Higher grass cover in gaps may reduce tree recruitment or seedling survivorship by acting as a biological filter (Royo & Carson 2006). However, our coarse estimation of grass cover did not allow us to draw inferences on grass cover and species richness relationships.

Compositional similarity between habitats indicates that seedlings can survive in both habitats, which is the likely explanation for similar richness of total woody species and seedlings in this study. Even in the shaded understorey, light penetrates through discrete openings between the leaves and nearby gaps, which makes some light available below the canopy (Canham et al. 1990; Yao et al. 2015), and this may be enough for species to survive at a low growth rate under the canopy (Montgomery & Chazdon 2002). Sal forest foliage density and vertical stratification allow some light through to the ground layer so the effect of shade is less strict than in more densely foliated and multi-layered tropical forests.

Gaps are richer in saplings

We found higher richness and density of saplings in the gaps. Our result contradicts the findings of Sapkota et al. (2009) from a similar forest in the region, and a few other

studies from elsewhere (Uhl et al. 1988; Busing & White 1997; Nagel et al. 2010), which report that gaps do not enhance sapling density and richness. These studies argue that gaps may be occupied by advance regeneration of shade-tolerant species. However, more species-rich gaps in the sapling stage are not uncommon (Hart & Kupfer 2011; Cowden et al. 2014).

Higher sapling richness in the gap is related to the requirement for light for growth of seedlings. Light availability in the gap increases the likelihood of seedlings establishing into saplings (growth in higher light). Gaps at both sites were not only richer but also had a higher density of saplings; this increased richness is likely to be associated with stem density. The observed high richness in gaps in tropical forests has been attributed to a higher number of individuals and is considered as 'spurious' richness (Hubbell et al. 1999). SACs suggested higher richness in the gaps at site I, but for site II richness was similar between the two habitats. Our SACs suggested there was no 'density effect' for saplings at one site, while an effect was apparent at the other site. Regardless of whether higher sapling richness is independent of stem density or not, a considerable fraction of the saplings were exclusively present in gaps at both sites, supporting the idea that gaps are important sites for tree regeneration and diversity. The comparison of mature trees between habitats, as visualized with SACs, rejects that gap richness is a function of stem density, supports that gaps are richer than closed canopy and reaffirms the importance of gap disturbance in maintaining tree richness in subtropical forests.

Conclusions

Survival–growth trade-offs between life stages of trees in gap–understorey mosaics is the most plausible explanation for similar seedling but different sapling composition and richness in the contrasting light environments. Gap partitioning as a mechanism for species co-existence in the gaps is a rather weak explanation, considering total woody species and seedling richness in our study. The higher richness of saplings in the gaps may or may not be a function of stem density; nevertheless, this higher richness and the occurrence of some gap-specific saplings supports the idea that gaps provide important regeneration niches for some tree species. Higher sapling richness in gaps and spatial segregation of tree life stages between gap and closed canopy environments indicate that gap creation could be used as a management strategy to enhance tree species richness and structural heterogeneity. We conclude that the role of gaps in enhancing overall woody species richness in subtropical forest may not be as critical as previously thought, but that gaps are important in maintaining tree richness.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species composition as depicted by the frequency of seedlings and saplings.

Appendix S2. List of all woody species (trees, shrubs and climbers) recorded in both study sites.

Appendix S3. Generalized linear model (GLM) summary statistics.