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Forest diversity in fragmented landscapes of northern
Ethiopia and implications for conservation

ABSTRACT

Deforestation and habitat fragmentation that arise largely due to the conversion of forests to other agricultural land-use types and over-utilization of forest resources to satisfy the food and energy requirements of the increasing population are major environmental concerns in northern Ethiopia. Understanding plant species diversity and spatial distribution along environmental gradients is crucial in the management of the remnant forest ecosystems. However, the ecology of the forest remnants in northern Ethiopia is poorly studied. The purpose of this study is therefore to (i) investigate plant species diversity and natural regeneration in relation to selected environmental factors, (ii) quantify the elevation patterns of species diversity and community composition, (iii) examine the extent and spatial distribution pattern of standing dead stems and the effect of mass tree dieback on forest structure and diversity, and (iv) compare the regeneration response of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* in an open-access forest area to a closed forest management system. The study was conducted in the Desa'a and Hugumburda Afromontane forest remnants, which are the largest forest fragments in northern Ethiopia and are national forest priority areas.

A total of 153 species belonging to 63 families was found in the study area; shrub and herb species dominate (ca. 70 %). The vegetation is mainly a dry Afromontane forest type with *Juniperus* and *Olea* as the dominant species; a riverine plant community in Hugumburda forest represents a moist forest type. Elevation, slope, soil depth, distance to the nearest stream, soil moisture, and forest disturbance are the main environmental factors influencing species distribution and partitioned plant communities.

The diversity of species and the composition of plant communities in Desa'a forest significantly respond to elevation. Species richness and diversity show a unimodal, hump-shaped relationship with elevation that peaked at mid elevation (1900 – 2200 m). The beta diversity values indicate medium species turnover along an elevational gradient. The percentages of dead standing trees (snags) due to natural disturbance at Desa'a forest are high for both *J. procera* (57 ± 7 %) and *O. europaea* subsp. *cuspidata* (60 ± 5 %), but show a decreasing trend with increasing elevation suggesting that restoration is more urgent at the lower elevations. Higher tree dieback at the lower elevation has pushed the tree species to the higher elevation by about 500 m, and this can lead to a shift in the forest-shrubland ecotone to higher elevations. Total stand density and basal area are reduced by 30 and 44 % when excluding snags of the two species, respectively. Thus, mass tree dieback of the two key species strongly influences the forest structure. High amounts of dead standing biomass are a particular risk in a fire-prone semi-arid forest environment, and controlling snag densities is of critical concern in the management of the remaining dry Afromontane forests in northern Ethiopia.

The natural regeneration of native tree species in both forest remnants is low. Exclosure was found to be an effective management option to improve the regeneration of *O. europaea*, but it does not improve the regeneration of *J. procera*. Thus, a closed management system in the open-access and degraded forests may not guarantee a successful regeneration of native woody species. It rather favors grass and herbaceous species and can lead to a gradual conversion of the forest land to wooded grassland. Most of the seedlings in forest remnants are shrubs, while tree species are less diverse and abundant. The standing vegetation is only partly represented in the seedling bank and many of the rare tree species, e.g. *Afrocarpus falcatus*, show poor or no regeneration. A smaller number of saplings than mature individuals suggest that locally some forest species are experiencing extinction. Thus, it is important to give conservation priority to the last Afromontane forest remnants in northern Ethiopia to achieve local, national and international biodiversity conservation goals.

KURZFASSUNG

Biodiversität in den Wäldern der fragmentierten Landschaften von Nordäthiopien und die Folgerungen für ihren Schutz

Abholzung und die Fragmentierung der Lebensräume, hauptsächlich als Folge der Umwandlung der Wälder in andere landwirtschaftliche Nutzungen sowie die Ausbeutung der Waldressourcen, um den Nahrungsmittel- und Energiebedarf der wachsenden Bevölkerung zu befriedigen, verursachen erhebliche Umweltprobleme in Nordäthiopien. Kenntnisse der Pflanzenvielfalt und räumlichen Verteilung entlang Umweltgradienten ist entscheidend bei der Bewirtschaftung der verbleibenden Waldökosysteme. Jedoch ist die Ökologie der noch vorhandenen Waldfragmente in Nordäthiopien nur wenig untersucht. Das Ziel dieser Studie ist daher (i) die Vielfalt der Pflanzenarten und ihre natürliche Regeneration im Zusammenhang mit ausgewählten Umweltfaktoren zu untersuchen, (ii) die höhenabhängige Verteilung der Artenvielfalt und die Zusammensetzung der Pflanzengemeinschaften zu quantifizieren, (iii) das Ausmaß und die räumliche Verteilung stehender toter Baumstämme sowie die Auswirkungen eines Baumsterbens auf die Waldstruktur und -vielfalt zu untersuchen, und (iv) den Einfluss eines geschlossenen Waldbewirtschaftungssystems mit dem eines zugänglichen Waldes auf die Regeneration von *Juniperus procera* und *Olea europaea* subsp. *cuspidata* zu vergleichen. Die Studie wurde in den afromontanen Wäldern Desa'a und Hugumburda, die größten Waldfragmente in Nordäthiopien und mit nationaler Schutzpriorität, durchgeführt.

Insgesamt 153 Arten aus 63 Familien kommen im Untersuchungsgebiet vor; Strauch- und Kräuterarten dominieren (ca. 70 %). Die Vegetation ist hauptsächlich vom trockenen afromontanen Waldtyp mit den dominierenden Arten *Juniperus* und *Olea*; eine gewässernahe Pflanzengesellschaft im Hugumburda Wald ist vom Typ Feuchtwald. Höhenlage, Hangneigung, Bodentiefe, Nähe zum nächsten Kleingewässer, Bodenfeuchte und anthropogene Störungen sind die wichtigsten Umweltfaktoren, die die Artenverteilung und die Zusammensetzung der Pflanzengesellschaften beeinflussen.

Die Artenvielfalt und die Zusammensetzung der Pflanzengesellschaften in Desa'a Wald sind signifikant abhängig von der Höhenlage. Artenreichtum und Diversität bilden eine unimodale Beziehung mit der Höhenlage; der höchste Wert ist bei einer mittleren Höhenlage (1900 - 2200 m). Die Betadiversitätswerte deuten auf einen mittleren Artenwechsel entlang eines Höhengradienten hin. Die Anteile stehender toter Baumstämme als Folge natürlicher Störungen im Desa'a Wald sind hoch, sowohl für *J. procera* (57 ± 7 %) als auch für *O. europaea* subsp. *cuspidata* (60 ± 5 %), zeigen jedoch einen abnehmenden Trend mit zunehmender Höhenlage, was darauf hindeutet, dass Rekultivierungsmaßnahmen in den unteren Höhenlagen dringender sind als in höheren. Das stärkere Baumsterben in den unteren Höhenlagen hat dazu geführt, dass das Vorkommen der betroffenen Baumarten sich um ca. 500 m nach oben verschoben hat. Dies kann auch zu einer Verschiebung der Wald-Buschland-Vegetation in höhere Lagen führen. Bestandsdichte bzw. Basalfläche sind um 30 bzw. 44 % reduziert wenn die stehenden toten Individuen der beiden Arten nicht berücksichtigt werden; das Absterben der beiden Hauptbaumarten beeinflusst also stark die Waldstruktur. Große Mengen toter Baumbiomasse sind ein besonderes Waldbrandrisiko in einem semi-

ariden Wald und die Kontrolle der Dichte des Totholzes ist von entscheidender Bedeutung bei der Bewirtschaftung der noch verbleibenden trockenen afromontanen Wälder in Nordäthiopien.

Die natürliche Regeneration der einheimischen Baumarten in den beiden untersuchten Waldfragmenten ist niedrig. Es zeigt sich, dass eingezäunte Flächen eine wirksame Bewirtschaftungsoption sind, um die Regeneration von *O. europaea* zu begünstigen. Diese Maßnahme bleibt jedoch ohne Wirkung auf *J. procera*. Daher würde ein Bewirtschaftungssystem mit Zugangsbeschränkungen in den offenen, degradierten Wäldern eine erfolgreiche Regeneration der einheimischen Holzgewächse nicht garantieren. Es werden eher Gras- und Kräuterarten begünstigt, was zu einer langsamen Umwandlung des Waldes in Grasland mit Gehölzen führen kann. Die meisten Keimlinge in den Waldfragmenten sind von Straucharten, während Baumarten weniger vielfältig bzw. zahlreich sind. Die bestandsbildenden Arten sind nur zum Teil in der Samenbank vertreten, und viele der seltenen Arten, z. B. *Afrocarpus falcatus*, zeigen wenig bzw. gar keine Regeneration. Die geringe Bedeutung von Jungwuchs im Vergleich zu den voll ausgewachsenen Baumindividuen deutet daraufhin, dass lokal einige bestandsbildenden Baumarten aussterben könnten. Daher muss den letzten afromontanen Waldfragmenten in Nordäthiopien eine hohe Schutzpriorität eingeräumt werden, auch um die lokalen, nationalen und internationalen Ziele zum Schutze der Artenvielfalt zu erreichen.

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1 GENERAL INTRODUCTION

1.1 Background

Biological diversity is the diversity of life at genetic, organism and ecological levels, and there have been attempts to include cultural biodiversity as a fourth component (Jeffries 2005). The various definitions of biodiversity are partly reviewed by Sanderson and Redford (1997), and a more comprehensive definition is given in the Convention on Biological Diversity (CBD 1992) where diversity is "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". In this thesis, diversity is considered at species level.

The roles of biodiversity are documented by many authors (Naeem et al. 1974; Loreau et al. 2001; Cardinale et al. 2006). Biodiversity plays a key role in ecosystem functioning and has been widely used as an indicator of ecosystem health (FAO 2005). According to the millennium ecosystem assessment (MA 2005), biodiversity provides four main services: (1) supporting (nutrient cycling, soil formation, primary production, etc.), (2) provisioning (food, fresh water, wood and fiber, fuel, etc.), (3); regulating (climate regulation, flood regulation, disease regulation, water purification, etc.), and (4) cultural (aesthetic, spiritual, educational, recreational, etc.).

Although biodiversity is understood as a key factor for the sustainability of life, biodiversity loss is one of the greatest environmental crises. The growing human population and the demand for natural resources have put great pressure on the biodiversity wealth of the world through deforestation, habitat fragmentation, and over-exploitation of species (Terborgh and van Schaik 1997; Noss 1999). Habitat loss and change, over-harvesting, pollution, and climate change have been the direct causes of global biodiversity loss (Wood et al. 2000), while population growth, changes in economic activities, socio-political factors, cultural factors, and technological change are indirect drivers (MA 2005). Besides these global factors, lack of technical knowledge and awareness, and political instability have exacerbated the problem in many developing countries (Ayyad 2003). Forest degradation in Sub-Saharan Africa,

for instance, has widely taken place because people gain immediate economic benefits from the forest-related economic activities (Mogaka et al. 2001).

Similarly, accelerated deforestation and habitat fragmentation that arise largely due to the conversion of forests to other agricultural land-use types and the over-utilization of forest resources to satisfy the food and energy requirements of the increasing population are major environmental concerns in Ethiopia (Machado et al. 1998; Tekle and Hedlund 2000; Friis et al. 2001; Taddese 2001; Teketay 2001; Zeleke and Hurni 2001; Dessie and Kleman 2007). With annual forest clearance of about 150,000 to 200,000 ha (Mogaka et al. 2001), the forest cover of Ethiopia was reduced to 16 % during the 1950s, and to 2.7 % by 1989 (Campbell 1991; EFAP 1994). The average forest decline between 1990 and 2000 in Ethiopia was 1 % (FAO 2007). Between 2000 and 2005, this value declined by 1.1 %, which exceeds the average value of east Africa (0.97), total Africa (0.62), and the world (0.18 %) (FAO 2007). Currently, natural forests in Ethiopia mainly occur in the south-western part of the country, while the forests that originally existed in central and northern Ethiopia have almost disappeared (EFAP 1994; Feoli et al. 2002; Bekele 2003).

According to pollen and charcoal studies in northern Ethiopia, forest disturbance has a 3000-year history (Darbyshire et al. 2003), and soil erosion following vegetation clearance in Tigray occurred in the middle Holocene (Bard et al. 2000). Around 50 BC, the pre-disturbance *Podocarpus-Juniperus* forest was converted into a secondary vegetation of *Dodonaea* scrub and grasslands that dominated the northern Ethiopia for 1800 years while *Juniperus*, *Olea* and *Celtis* spread around AD 1400 to 1700 (Darbyshire et al. 2003). The travertine deposition in the plateau of Tigray indicates the dense forest cover that once covered northern Ethiopia during the middle Holocene (Bard et al. 2000).

In 2003, the natural forest cover in Tigray was only 0.2 % of the total land mass of the region (Ministry of Agriculture 2003), indicating the severe forest degradation in the region. Currently, the western escarpment of the Great Rift Valley is the only site with an intact Afromontane forest cover in northern Ethiopia. The present study was therefore carried out on this escarpment which includes Desa'a and Hugumburda forests; these are national forest priority areas in Ethiopia. Conversion of forests to agricultural land (Nyssen et al. 2004), high dependency on biomass energy

(Hagos et al. 1999; Gebreegziabher 2007) and free grazing (EFAP 1994; Worku 1998; Feoli et al. 2002) are the major causes of forest degradation in northern Ethiopia. According to the Ministry of Agriculture (2003), fuel wood and charcoal contribute 69.2 and 2.5 % of the household energy consumption in Tigray, respectively.

Forest degradation and deforestation in Ethiopia entails several socio-economic and environmental challenges that have strongly affected the capacity of forests to provide ecosystem services (Badege 2001; Teketay 2001). Shortage of fuel wood is a serious problem in the region, and the use of animal dung and agricultural residues as household fuels has increased, which otherwise could be used as organic fertilizer (Gebreegziabher 2007). Deforestation is also a major reason for the accelerated soil erosion in the highlands of Ethiopia (Hurni 1988), where the annual soil loss is estimated to be 1493 million tons (Zelege and Hurni 2001). This again causes an estimated annual grain yield loss of 1-1.5 million tons (Taddese 2001). Following early human settlements, the extent of soil degradation in northern and eastern Ethiopia is higher than in other parts of the country (Zelege and Hurni 2001). Tamene and Vlek (2007) report a mean annual soil loss of 19 tons ha⁻¹ year⁻¹ in Tigray, which exceeds the mean values of Africa and the world. Large-scale degradation of forests has affected the natural regeneration of key native tree species in northern Ethiopia (Aynekulu et al. 2009; Wassie et al. 2009a), while favoring shrub and herb colonizers (Feoli et al. 2002).

Following the long history of land degradation, many land rehabilitation and conservation programs have been carried out in northern Ethiopia. A historical vegetation cover change study by Nyssen et al. (2009) indicates that the vegetation cover in northern Ethiopia has improved during the last century through land rehabilitation programs. Community woodlots and household tree plantations have also contributed to the improvement of the vegetation cover in northern Ethiopia (Jagger and Pender 2003). However, in relation to the scale of land degradation in the region, conservation efforts could not significantly contribute to reversing the land degradation process (Teketay 2001). The major drawbacks in the conservation efforts are related to policy setting and implementation, which are often criticized for lacking an active participation of the local people (Campbell 1991; Hagos et al. 1999). State ownership of land and forests and lack of forest property rights are also identified as causes of forest degradation in Ethiopia (Bekele 2003).

Many degraded sites have been managed as exclosures, and attempts have been made to document the regeneration and ecology of the plants in these exclosures. Exclosure is an assisted natural regeneration strategy to restore degraded forests by protecting areas from livestock intervention (Parrotta et al. 1997; Shono et al. 2007). Studies have indicated that vegetation recovery in the exclosures is quick, particularly in the younger stages (Mengistu et al. 2005; Abebe et al. 2006). Many of the exclosures on the degraded hillsides are covered with pioneer shrubs like *Acacia etbaica*, *Euclea racemosa* subsp. *schimperi*, *Dodonaea viscosa*, and grass and herb species. However, no significant improvements in species diversity and biomass production were found after a decade of closing (Asefa et al. 2003; Yayneshet et al. 2009), suggesting the need to introduce additional management measures to restore native key species.

Studies elsewhere indicate that restoration of the original flora may not be achievable for centuries, particularly in dry climates where moisture is a limiting factor (Woodwell 1994). Although exclosures in the degraded sites have shown promising results, the natural forest remnants are experiencing a retrogressive succession. For instance, in Desa'a forest, the originally dominating *J. procera* and *O. europaea*, have been gradually been replaced by encroaching light-demanding shrubs such as *Cordia purpurea* and *Tarchonanthus camphoratus* with increasing deforestation and forest degradation (Gebreegziabher 1999). This indicates that the natural forest remnants, which are expected to serve as sources of propagules (Aerts et al. 2006c) for the restoration of the native species in the degraded sites, are not able to sustain the populations of the relevant forest species. Thus, conserving the existing natural forest remnants needs conservation priority, otherwise a local extinction of plant species and their associated fauna may occur.

1.2 Problem statement

The dry lands constitute almost 50 % of the landmass, but they are fragile ecosystems mainly due to erratic rainfall (CBD 1992). Recently, conservation of biodiversity in the dryland ecosystems has been receiving greater international attention. Accordingly, the Convention on Biological Diversity has set goals to promote the conservation of the biological diversity of ecosystems, habitats and biomes (goal 1) and promote the

conservation of species diversity (goal 2) of the drylands by 2010 (UNEP/CBD 2006). This convention is relevant to Ethiopia where drylands constitute about 65 % of the landmass and forest habitat deterioration is high (Teketay 2001; Yirdaw 2001). However, lack of adequate understanding of biological resources and their interaction with the environment is among the major challenges when defining and implementing effective policies for the sustainable utilization and conservation of biodiversity resources in Ethiopia (EFAP 1994; Teketay 2001).

The study site is part of the eastern Afromontane (Tigray highlands) and the arid Horn of Africa (Afar lowlands) global diversity hotspots (Conservation International 2007). Despite the high conservation values of the natural forest remnants in northern Ethiopia, they are poorly studied (Friis 1992; Aerts et al. 2006c). Recently, studies have given emphasis to the restoration ecology in the exclosures (Mengistu et al. 2005; Abebe et al. 2006; Descheemaeker et al. 2006; Mekuria et al. 2007; Aerts et al. 2008; Yayneshet et al. 2009). However, except for a few management plans (BoANR and IDC 1997; Worku 1998), reports (e.g., TFAP 1996; Gebreegziabher 1999), and unpublished MSc theses (Hadera 2000; Janssen 2009), no detailed scientific investigation has been carried out in the large forest remnants in Tigray. To my knowledge no work has been published to date on the ecology of these forests. As a result, historical comparisons of the vegetation composition in northern Ethiopia relies more on paleo-botanical studies (Bard et al. 2000). Thus, a detailed study on the ecology of the existing forest remnants is the basis for defining appropriate conservation strategies before these lose their potential to provide ecosystem services. Income from forest-related economic activities account for the second largest share of the average total household income in Tigray (Babulo et al. 2009). Thus, it is important to develop the forestry sector to improve the rural livelihoods in northern Ethiopia.

The study focuses on two national forest priority areas in northern Ethiopia. The first study site covers large parts of Desa'a forest, which mainly occurs largely found on the western escarpment of the Great Rift Valley in northern Ethiopia. The second site covers Hugumburda forest, which is an isolated forest not only because the surrounding area has been cleared, but also because it is located in a secluded valley next to the parallel rift of Lake Hashenge. In such isolated areas, limited cross-pollination, inbreeding, and genetic drift are likely to negatively impact plant

populations. This is expected to be observed in the population structure of the trees: low numbers of seedlings, and smaller numbers of saplings than mature species. If so, the forests are facing local extinction, i.e., some tree species are still present, but will become locally extinct because there is no further regeneration. Thus, it is important to know the natural regeneration potential in relation to the standing vegetation.

Understanding plant species distribution patterns and plant community composition along environmental gradients also gives key information for effective management of forest ecosystems (Naveh and Whittaker 1979; Noss 1999; Lovett et al. 2000). The concept of identifying areas with high biodiversity along environmental gradients, for instance, has been used as a criterion for biodiversity conservation priority setting (Rudel and Roper 1997; Myers et al. 2000; Mittelbach et al. 2001; Breshears et al. 2005). Thus, it is important to identify plant species diversity and community composition along environmental gradients.

Moreover, understanding the extent of tree dieback and spatial patterns of dead standing trees (snags) is crucial in managing forest ecosystems (Craig and Friedland 1991; Gitlin et al. 2006). However, the status and roles of snags in the tropics have been less studied (Grove 2001). Mass tree dieback occurred on the escarpments of Desa's forest, and the occurrence of large snags in the dry Afromontane forest is a clear sign of forest degradation. For effective management of the existing forest remnants, it is imperative to investigate the influence of such mass tree dieback on the forest structure and diversity.

Natural regeneration is a site-specific ecological process, and it is usually difficult to characterize the factors that control regeneration processes (Schupp 1988; Khurana and Singh 2001). Studying the contribution of previous conservation efforts in improving the restoration of native species is important to plan further conservation strategies. This study thus assesses the regeneration response of key tree species to exclosure.

1.3 Objectives

The main objective of this study is to investigate the plant species diversity and natural regeneration in relation to selected environmental factors in two dry Afromontane forest remnants in northern Ethiopia as a basis for biodiversity conservation.

The specific objectives of the study are:

- Assessment of plant species diversity and natural regeneration in relation to selected environmental factors in Hugumburda forest;
- Assessment of the distribution of plant species and communities along an elevational gradient on the western escarpment of the Great Rift Valley;
- Investigation of the extent and spatial patterns of dead standing trees (snags) and effects of mass tree dieback on forest structure and diversity; and
- Investigation of the regeneration response of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* to exclosure.

The findings of this research can serve as decision support for conservation workers, policy makers, and other stakeholders when they develop appropriate measures to protect the diminishing natural forest remnants in northern Ethiopia.

1.4 Thesis layout

The thesis consists of eight chapters. Following the introduction, Chapter 2 provides an overview of the determinants of species diversity, methods for studying species diversity and the vegetation types of Ethiopia. Chapter 3 provides a brief description of the socio-economic and bio-physical characteristics of the study area and the study approach. Chapter 4 investigates (i) species and plant community compositions in relation to the selected environmental factors, and (ii) composition of the seedling in bank relation to standing vegetation. Chapter 5 examines (i) plant species and community compositions, (ii) species turnover (Beta diversity), and (iii) identifies areas with high species diversity for conservation priority setting along an elevational gradient. Chapter 6 investigates (i) extent and spatial patterns of mass tree dieback of *J. procera* and *O. europaea* subsp. *cuspidata*, (ii) applicability of NDVI of ASTER imagery in estimating percentage of mass tree dieback, and (iii) influence of mass tree dieback of the two species on the overall stand structure and species diversity. Chapter 7 investigates the regeneration response of *J. procera* and *O. europaea* subsp. *cuspidata* in the dry forest remnants in northern Ethiopia. Chapter 8 synthesizes the major findings of the research, the implications for conservation and management, and suggests further areas of research.

2 DRIVERS AND MEASUREMENTS OF SPECIES DIVERSITY AND VEGETATION TYPES OF ETHIOPIA: AN OVERVIEW

2.1 Determinants of biodiversity

Biodiversity varies in space and time, and understanding patterns and drivers of variation in biodiversity distribution has been a central topic in ecology. According to ter Steege and Zagt (2002), the determinates of biodiversity can be seen from both regional and local perspectives (Figure 2.1). Accordingly, regional biodiversity is determined by the ecological and evolutionary processes of speciation, immigration, and extinction, while local diversity is influenced by random extinction, competition, and adaptation (Terborgh and van Schaik 1997; ter Steege and Zagt 2002). A more comprehensive discussion on the patterns of species distribution is given by MacArthur (1972).

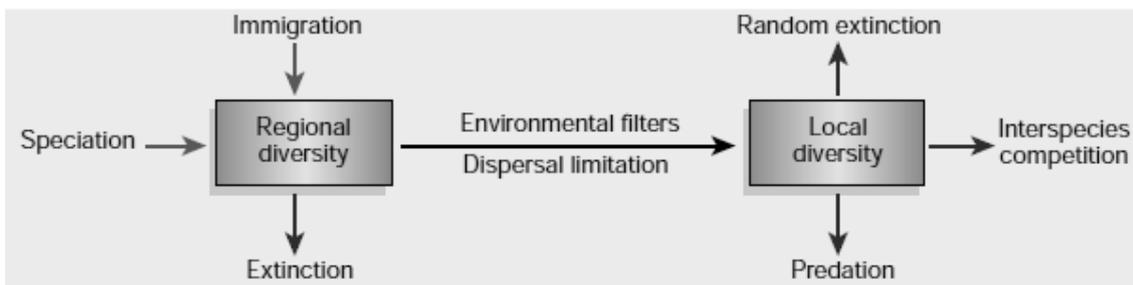


Figure 2.1 Drivers of regional and local species diversity. Green arrows indicate processes that increase diversity (species are added) and red arrows those that decrease it (species are lost) (source: ter Steege and Zagt 2002).

Latitude and elevation are important drivers of species distribution patterns (Gaston 2000; Lomolino 2001). However, the effect of these two factors varies with local, regional, and global scales, as well as with historical factors (ter Steege and Zagt 2002). The world's forests have passed through many evolutionary processes. Europe, which was as diverse as America in tree species, for instance, lost many of its tree species through the Pleistocene glaciations (MacArthur 1972). A palaeobotanic study by Bobe (2006), for instance, indicates that the differentiation of moist forests and drier Acacia woodlands in Africa occurred during the early Cenozoic period. Pollen studies in Kenya (Lamb et al. 2003) and northern Ethiopia (Darbyshire et al. 2003) indicate that

the flora of East Africa has experienced several changes due to climate change and anthropogenic disturbances.

At a global scale, diversity decreases with increasing distance from the equator (Gaston 2000; Mutke and Barthlott 2005; Kreft and Jetz 2007). However, the general species-richness pattern along latitudinal gradients is sometimes reduced due to other factors like longitude, elevation, topography, and aridity (Gaston 2000). There are several reasons for the higher species diversity in the tropics compared to other regions, one of which is the larger area of the tropics than of any other zone (Rosenzweig 1995). Larger ranges contribute to diversity by supporting large populations, which favor speciation through geographical barriers while reducing accidental extinction (Rosenzweig 1995; Gaston 2000). The influence of area *per se* as a determinant of diversity has however been doubted. Tokeshi (1999) argues that the area of the tropical region is not as large as that of all non-tropical areas combined. Temperate and boreal species seem to achieve large population sizes, and if evolutionary time scales are used, comparisons should be based on the area of palaeotropical zones rather than on the present day configuration of lands and climatic zones.

The other reason for large number of species in the tropics is the low temperature variability in space and time that increases the probability of similar habitats (Rosenzweig 1995). Constant and higher temperatures in the tropics also contribute to higher species diversity by increasing the rate of metabolism, which speeds up the passing of generations and increases the rate of mutation that again leads to new species (Tokeshi 1999). Although the influence of site productivity on diversity is debatable (MacArthur 1972; Gaston 2000), the higher productivity in the tropics than in the higher latitudes is often cited as a reason for the higher species richness in the tropics (Rosenzweig 1995; Kreft and Jetz 2007). MacArthur (1972) supports this assumption by stating that an area with zero production will not support any species and that more productive sites are more stable with time. In contrast, Tokeshi (1999) argues that site productivity does not have a direct effect on species richness, but should be considered as a surrogate for habitat heterogeneity.

Elevation plays a major role in plant species diversity and floristic formations, especially in mountainous areas (Gaston 2000; Kreft and Jetz 2007). Compared to species-latitude and species-area relationships, the species-elevation relationship is less

studied (Lomolino 2001). Elevation determines species distribution in montane systems by influencing area, climate, geographical isolation of montane communities, and feedback among zonal communities (Gaston 2000; Kreft and Jetz 2007). Species richness in mountainous landscapes, for instance, decreases with increasing elevation due to a decrease in land area per bioclimatic belt (Körner 2007). The effect of climate on species distribution is similar to its effect along latitudinal gradients, whereas area and geographical isolation can be explained by 'island biogeography' (Tokeshi 1999). According to the theory of island biogeography, the number of species in undisturbed islands is influenced by immigration, emigration and extinction (MacArthur and Wilson 1967). Immigration and emigration are influenced by distance from the main land, while extinction is inversely related to area (MacArthur and Wilson 1967).

The response of plant species distribution to elevation varies among ecosystems (Hegazy et al. 1998; Kessler 2000; Lovett et al. 2000; Sánchez-González and López-Mata 2005; Grytnes and Beaman 2006). Different life forms may also respond to elevation similarly (e.g., Sánchez-González and López-Mata 2005) or differently (e.g., Ren et al. 2006). Species richness along elevational gradients also depends on the scale of a study: A hump-shaped distribution pattern is commonly found when data are taken from a large elevation range, while a monotonic pattern is common with small elevation ranges (Nogues-Bravo et al. 2008). Generally, the hump-shaped pattern is more common than the monotonic pattern (Rahbek 1995).

Generally, habitat diversity is a widely accepted determinant of species diversity (Rosenzweig 1995; Pausas et al. 2003; Mutke and Barthlott 2005). The theory of spatial heterogeneity (Pianka 1966) states that more heterogeneous and complex physical environments support more diverse plant and animal communities. Kreft and Jetz (2007) indicate potential evapotranspiration, the number of wet days per year, and measurements of topographical and habitat heterogeneity are predictors of global species richness. Similarly, Linder (2001) found a strong correlation between maximum rainfall and species richness in Sub-Saharan tropical Africa. Similarly, species richness and endemism decrease with increasing latitude from the southern to the northern highlands of Ethiopia, which can be associated with a decline in precipitation (O'Brien 1993; Linder 2001).

Besides environmental drivers of species diversity, anthropogenic disturbance affects species diversity through habitat loss and habitat fragmentation (Rudel and Roper 1997; Lyaruu et al. 2000; Pimm and Raven 2000; Brooks et al. 2002). Habitat loss is the leading cause of species extinction (Pimm and Raven 2000). With the current rate of habitat loss, the rate of species extinction is in order of a thousand species per decade per million species (Pimm and Raven 2000). Biodiversity loss is more serious than other environmental threats because it is irreversible (Mittermeier et al. 1998). Habitat fragmentation affects biodiversity by reducing the area of a habitat, which reduces the persistence of a species, and through the negative edge effect that increases mortality while decreasing reproduction (Farhig 2003). Forest disturbance also affects species diversity by affecting certain species and size classes, and by changing the light environment of the understory (Slik 2004; Engelbrecht et al. 2007). According to the intermediate disturbance hypothesis (Connell 1978), intermediate disturbance promotes species diversity by facilitating regeneration of many species (Denslow 1980; Bongers et al. 2009). However, the influence of disturbance on species diversity is still a debate among ecologists. Recently, Bongers et al. (2009) showed that diversity in dry forests peaks more at a slight level of disturbance than at an intermediate level.

Identifying diversity hotspots can support conservation planning (Mittermeier et al. 1998; Myers et al. 2000). Conservation International (2007), for instance, used the world biodiversity hotspots to prioritize biodiversity conservation areas. The hotspot concept is based on species richness, endemism and threat (Reid 1998; Myers et al. 2000). Studies at global scale have documented less overlap among the three criteria (Stohlgren et al. 1997; Orme et al. 2005). Nearly half of the world's vascular plant species are endemic to 25 hotspots (Myers et al. 2000), of which 17 are in tropical forests each having at least 1500 endemic plant species (Brooks et al. 2002). These hotspots once covered 12 % of the land surface, but Brooks et al. (2002) reported that in 2002 such intact habitats were reduced to less than 1.4 % of the land largely due to habitat loss. Tropical moist forest constitutes most (85 %) of the deforested lands (Whitmore 1997). Despite the high expectation of extinction due to habitat deterioration, Whitmore (1977) observed that a large proportion of plant species were persistent in the remaining forests. However, many plant species have a too small population sizes to be viable, and this may increase the rate of extinction in the long

term (Whitemore 1997). The human population growth rate in the hotspots is higher than the average rates worldwide, suggesting that human-induced habitat loss is still a major threat (Cincotta et al. 2000). Mckee et al. (2004) found a strong relationship between population growth and number of threatened species. This makes conservation of biodiversity in the hotspots especially challenging.

The advancement in remote sensing and geo-information sciences has contributed greatly to the organization of the fragmented knowledge of species distribution and the determining factors. Recently, it has become possible to develop more accurate biodiversity maps on continental and global scales (Linder 2001; Kier et al. 2005; Mutke and Barthlott 2005). The global diversity map of Mutke (2005) indicates that the Chocó-Costa Rica region, the tropical eastern Andes, and northwestern Amazonia, eastern Brazil, northern Borneo, New Guinea, the South African Cape region, southern Mexico, the eastern Himalaya region, western Sumatra, Malaysia, and east Madagascar are major global centers of vascular plant diversity. Kier et al. (2005) also indicated that the tropical and sub-tropical moist broadleaf forest biomes are mega stores of global plant species diversity.

Recently, 9 new areas were included as part of the world biodiversity hotspots (Conservation International 2007). Among these are the Horn of Africa and eastern Afromontane hotspots that include large parts of the lowlands and the highlands of Ethiopia, respectively. However, Africa has fewer endemic species and is less rich in tropical species, which is probably due to the slow rate of geographical speciation (Rosenzweig 1995). Large-scale vegetation changes in Africa occurred due to the changes in the atmospheric moisture content driven by tropical sea surface temperature changes in the mid-Pleistocene (Schefus et al. 2003).

2.2 Plant communities

A plant community is defined as the collection of plant species growing together in a particular location that show a definite association or affinity with each other (Kent and Coker 1992). Plant community level study is a useful approach in conservation planning (Ferrier et al. 2009). The concept of plant community, for instance, provides useful information on the underlying environmental drivers of species distribution, as plants that live together have similar environmental requirements for their existence.

The principles of plant communities are based on either the continuum or on individualistic theories. Clements (1916) in his plant succession theory considered plant communities as one big organ (organismic concept) composed of various species, which repeats itself with regularity over a given region. In his holistic approach, forests, scrubs, and grassland are considered as major groups of vegetation, which can develop to climax communities with sufficient time and long-term stability. Gleason (1926) on the other hand considered plant species distribution as a continuum. Gleason takes environmental factors and tolerance ranges of species as determinants of the existence and abundance of a species in a given region. This viewpoint is known as the individualistic concept of the plant community.

Although differences still exist among ecologists on the concepts of plant communities, the Gleason's individualistic theory has been widely used (Callaway 1997). Plant ecologists who favor vegetation classification follow the approach of Clements and group species into communities. Those ecologists who do not believe in classification follow the continuum theory and arrange species along environmental gradients as continua, using ordination methods (Kent and Coker 1992).

2.2.1 Classification and ordination

Classification is to group together a set of individuals on the basis of their attributes, and is used to define plant communities. Hierarchical or non-hierarchical and the two-way species indicator analysis (TWINSpan) are the widely used quantitative classification techniques. TWINSpan operates on species presence-absence data, and its use is more limited because it performs poorly with more than one environmental gradient (McCune and Grace 2002). Cluster analyses group species using a distance matrix. The distance measures used in linking similar groups are categorized as Euclidean metrics (absolute and relative distance) or proportion coefficients (e.g., Sørensen and Jaccard) (McCune and Grace 2002).

Ordination simply means arranging items along a single or multiple axis, and is often used to seek and describe patterns (McCune and Grace 2002). Ordination involves the arrangement of vegetation samples in relation to each other in terms of their similarity of species composition (species ordination) and/or their associated environmental controls (sample units ordination). In gradient analysis, variations in

species composition are related to variation in associated environmental factors, which can usually be represented by environmental gradients. Correlation analyses between environmental factors and ordination axes scores can be used to identify and describe environmental factors that influence species distribution patterns (McCune and Grace 2002).

Ordination can be direct or indirect. With direct gradient analysis, sample units (e.g., plots) are ordinated based on measured environmental factors in those sample units (McCune and Grace 2002). Gradient analyses can be univariate where sample units are ordinated along a single environmental factor or multivariate. Species distribution along an elevational gradient, for instance, is a univariate gradient. Indirect ordination ordinated sample units considering the variation within the vegetation independently of the environmental data. Indirect gradient analyses are more widely used than direct gradient analyses (Kent and Coker 1992).

Indirect ordination is performed in ordination methods like principal component analysis, Bray-Curtis (polar) ordination, reciprocal averaging, correspondence analysis, and detrended correspondence analyses, while non-metric multi-dimensional scaling (NMS) and canonical correspondence analysis are rarely used (Kent and Coker 1992; McCune and Grace 2002). Each of the above ordination techniques has its pros and cons, and the choice of ordination method also depends on the type of the data, the sampling effort, and the objectives of a study (Southwood and Handerson 2000). Principal component analyses, for instance, require linear relationships between variables and normal distribution of variables (McCune and Grace 2002), which rarely occurs in vegetation data. McCune and Grace (2002) recommend the use of NMS in community ecology because it can be used with non-normal data and avoids the assumption of linear relationships between variables.

2.2.2 Measures of species diversity

Whittaker (1972) identifies alpha, beta, and gamma types of species diversity. Alpha diversity (species richness) is the number of species per standard size or community. Beta diversity is the difference in species diversity between areas or communities. It is sometimes called habitat diversity because it represents differences in species composition between different areas or environments (Whittaker 1972; Kent and Coker

1992). Since communities and habitats are often difficult to delineate, beta-diversity is measured among study plots (Mark 2001). The total or gamma diversity of a landscape, or geographic area, is a product of the alpha diversity of its communities and the degree of beta differentiation among them (Whittaker 1972). The difference between alpha and gamma diversity is a matter of scale, which is often subjectively defined (Peet 1974).

A large number of diversity indices have been used to measure species diversity. Magurran (2004) provided an in-depth review of concepts and measurements of diversity. Species richness, meaning a count of the number of plant species in a quadrat, area or community, is often equated with diversity. However, as Magurran states, most methods used in measuring diversity actually consist of two components. The first is species richness and the second is the relative abundance (evenness or unevenness) of species within a sample or community.

Whittaker (1972) considers species richness as a strong measure of species diversity. However, using species richness *per se* as a measure of diversity is criticized, because species richness is just one component of species diversity (Hurlbert 1971; Sanjit and Bhatt 2005). The Shannon index and Simpson's index of diversity, which combine species richness with relative abundance, are widely used in species diversity studies (Kent and Coker 1992). The Shannon index expresses the relative evenness or equitability of species, while Simpson's index (Simpson 1949) gives weight to dominant species (Whittaker 1972). The diversity indices are biased either on species richness or species evenness, which makes it difficult to obtain one robust index of diversity measurement (Magurran 2004). The Shannon index is insensitive to rare species (Sanjit and Bhatt 2005). Hill (1973) introduces ratios of the Shannon and Simpson's indices. Though the Hill ratios are not widely used in ecological studies, they describe community structures well (Peet 1974). They are relatively unaffected by species richness and tend to be independent of sample size (Peet 1974), which makes them desirable for comparison of diversity among groups. But they are sometimes difficult to interpret due to the convergence of the Hill's numbers to 1 with decreasing diversity values (Peet 1974).

2.3 Vegetation types of Ethiopia

Ethiopia has a complex relief and a variety of climates, and thus diverse habitats with rich flora and fauna. The vegetation of Ethiopia is diverse and ranges from afro-alpine vegetation to desert scrub. The total flora of Ethiopia consists of 6500 - 7000 species of which 12 % are considered endemic (Gebre Egziabher 1991; Teketay 2004). However, the flora of Ethiopia has not been exhaustively studied (Friis 1992). The recent discovery of *Acacia fumosa* (Thulin 2007), and *Asplenium balense* (Chaerle and Viane 2007) as new plant species from Ethiopia is evidence of this. A large proportion of the Eastern Afromontane and Horn of Africa biodiversity hotspots lie in Ethiopia, and the country is one of the biodiversity centers of the world (Conservation International 2007). The Ethiopian vegetation is highly influenced by climate, which is associated with elevation (Dugdale 1964). South-western Ethiopia receives more precipitation than other parts of the country due to the humid air coming from the Congo basin (Dugdale 1964). This westerly wind, however, cannot penetrate further than 30° E and rarely influences the Horn regions because the Ethiopian highlands act as barriers. The flora of southern Ethiopia is more similar to that of Kenya and Uganda than the flora of northern Ethiopia (Dugdale 1964). The vegetation on the Afromontane belt (900-3200 m) of Ethiopia has been under tremendous pressure from human activities and over grazing, which has led to the replacement of the evergreen forests by grasslands (Gebre Egziabher 1988).

The vegetation maps of Ethiopia were reviewed by Friis and Demissew (2001). The most frequently cited studies on the vegetation of Ethiopia include that of Pichi-Sermolli (1957), Breitenbach (1963), White (1983), and Friis (1992).

The extent and delineation of the vegetation maps of Pichi-Sermolli (1957) and Breitenbach (1963) are very similar, but differ in the descriptions and terminology of the mapping units (Friis and Demissew 2001). According to Pichi-Sermolli (1957), the vegetation of northern Ethiopia can be broadly classified as montane evergreen thicket and savanna. The common species in this vegetation type include *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, *Acokanthera schimperi*, *Carissa edulis*, and species of *Euclea*, *Rhamnus*, *Rhus* and *Maythenus* (Friis and Demissew 2001).

Breitenbach (1963) mapped the vegetation of Ethiopia and Eritrea into seven basic categories using a physiognomic approach. The seven categories are Lowland

steeps, Lowland savannahs, Lowland woodlands, Highland forests, Mountain woodlands, Mountain savannahs, and Mountain steeps. The sub-categories are based on local rainfall (arid, semi-arid, semi-humid, and humid) and stages of succession, which range from pioneer to climax types (Friis and Demissew 2001). According to Breitenbach's vegetation map, the three dominating vegetation types in Ethiopia in a decreasing order are Lowland steeps, Lowland woodlands, and Mountain savannahs (Friis and Demissew 2001). The vegetation of the study site is mainly Highland forests and Mountain savannahs. Highland forests are found between 1600 and 2600 m.a.s.l.

White (1983) classified the vegetation of Africa into 81 vegetation groups using physiognomy and floristic composition. Accordingly, the dominant vegetation types in Ethiopia are Forest transitions and mosaics, Woodland, Woodland mosaics and transitions, Bushland and thicket, Semi-desert vegetation, Grassland, Edaphic grassland mosaics, Altimontane vegetation, Azonal vegetation, and Desert. The vegetation on the lower escarpment is classified as bushland and thicket and the vegetation on the Tigrean plateau and the upper scarp as forest transition and mosaics.

Friis (1992) classifies the forests of the Horn of Africa into nine vegetation types. He followed the classification and terminologies of White (1983) and added the lowland semi-deciduous forest (dry peripheral semi-deciduous Guineo-Congolian forest) and the altitudinally transitional forest (transitional rain forest), which were identified after White's vegetation map had been published. According to the classification of the forests and forest trees of northeast tropical Africa (Friis 1992), Desa'a and Hugumburda forests are broadly categorized as dry single-dominant Afromontane forests, which are characterized by dry climate (annual precipitation less than 1000 mm) with *Juniperus procera* and *Olea europaea* subsp. *cuspidata* as dominant species. This dry single-dominant Afromontane forest of the escarpment and transition between single-dominant Afromontane forest and East African evergreen and semi-evergreen bushland that occurs between 1500 and 2400 characterizes the escarpments in northern Ethiopia.

The vegetation map of Ethiopia was later simplified into eight major vegetation types by Demissew (1996) as Afroalpine and sub-Afroalpine zone, dry evergreen mountain forest and grassland, moist evergreen mountain forest, evergreen scrub, *Combretum-Terminalia* and savanna, Acacia-Comiphora woodland, lowland

(semi-) evergreen forest, desert and semi-desert scrubland, and coastal vegetation (Demissew et al. 1996). According to Demissew (1996), dry evergreen mountain forest and grassland and evergreen scrub characterize the forest remnants in northern Ethiopia.

Based on the recent classifications of the ecosystems of Ethiopia (IBC 2005), Desa'a and the Hugumburda forests belong to the dry evergreen montane forest and grassland complex. According to FAO (2001), the eastern and western mountain system and tropical shrubland zones cover large parts of Ethiopia (Figure 2.2a). These ecological zones support large parts of the country's forests (Figure 2.2b).

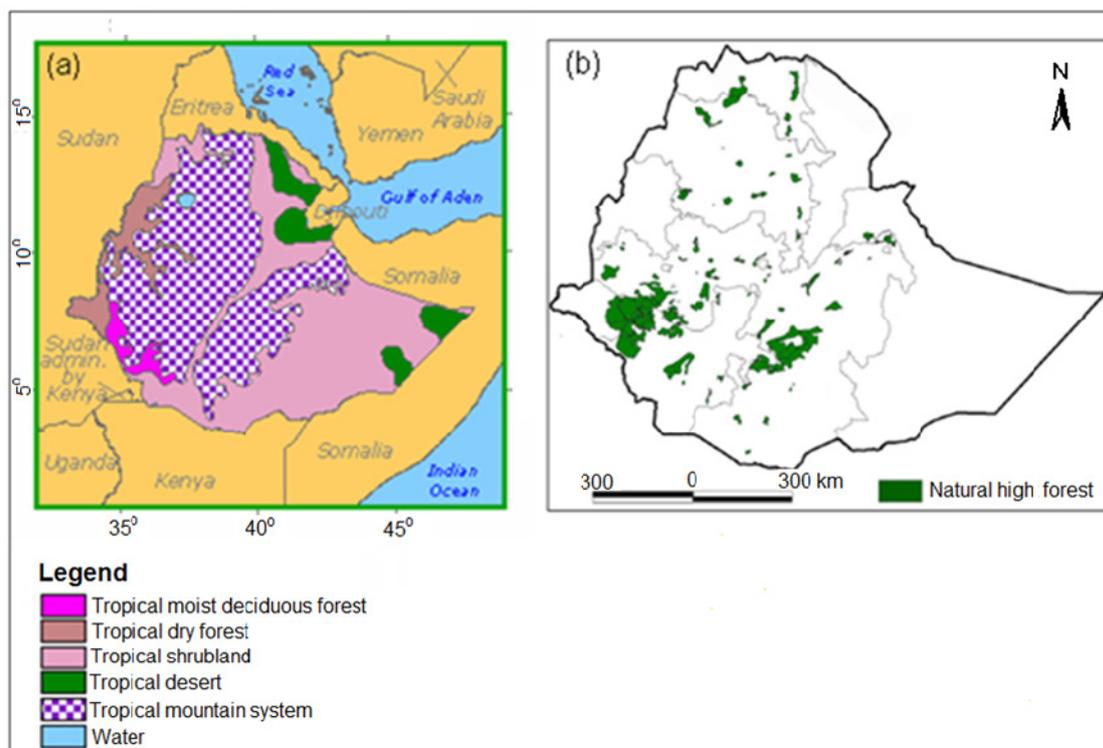


Figure 2.2 Ecological zones (a) (Map source: FAO 2001) and the fragmented natural high forests (b) (Map source: Ministry of Agriculture 2003) in Ethiopia.

The vegetation classification of White and Friis are criticized for lacking clarity particularly in distinguishing woodlands from forests (Erik 1994). A large part of the forest remnants in northern Ethiopia, particularly Desa'a forest, can be categorized as woodland characterized by an open canopy and single-story vegetation structure. Nevertheless, the vegetation classification by Friis (1992), which is widely used in Ethiopia, is also used in this study.

3 STUDY SITES AND GENERAL METHODS

3.1 Study area

3.1.1 Socio-economic context of Ethiopia

Ethiopia is an ancient agrarian country located between 3° and 15° N and 33° and 48° E covering an area of 1.13 million km². In 2007, the population of Ethiopia was 74.9 million and the annual growth rate 2.6 % (Federal Democratic Republic of Ethiopia Population Census Commission 2008). This makes Ethiopia the second most populous nation in Sub-Saharan Africa. The same report indicates that 84 % of the population lives in rural areas and is engaged in subsistence agriculture. The economy of Ethiopia is based on traditional subsistence agriculture, which suffers from frequent droughts. Food security and natural resource degradation are among the major challenges that Ethiopia has faced. A chronology of the droughts and famines in Ethiopia from 253 BC to 1992 indicates that Ethiopia has faced more than 17 droughts or famines in the 20th century, which were caused by either shortage or poor distribution of rainfall (Webb et al. 1992). Despite its poor performance, the agriculture sector still contributes 46.6 % of the GDP (NBE 2007) and 76.6 % of the exports, mostly coffee (EEA 2004).

3.1.2 Location

The study was conducted in Desa'a and Hugumburda Afromontane forest remnants, which are among the 58 national forest priority areas in Ethiopia. Desa'a forest is located about 80 km northeast of Mekelle, the capital of the Tigray regional state (Figure 3.1) covering an area of about 118,600 ha (BoANR and IDC 1997). Hugumburda forest is near Korem town about 140 km south of Mekelle. Two sites were located near the Esot (13°55'N, 39°49' E) and Agoro (13°39' N, 39°47' E) villages in Desa'a forest, and one site in Hugumburda forest (12°38' N, 39°32' E). A large part of Desa'a forest lies in the Tigray region and a small area in the Afar region, while Hugumburda forest is entirely in the Tigray region. The forests are mainly located along the western escarpment of the Great Rift Valley facing the Afar depression. The climate, soils and vegetation are diverse.

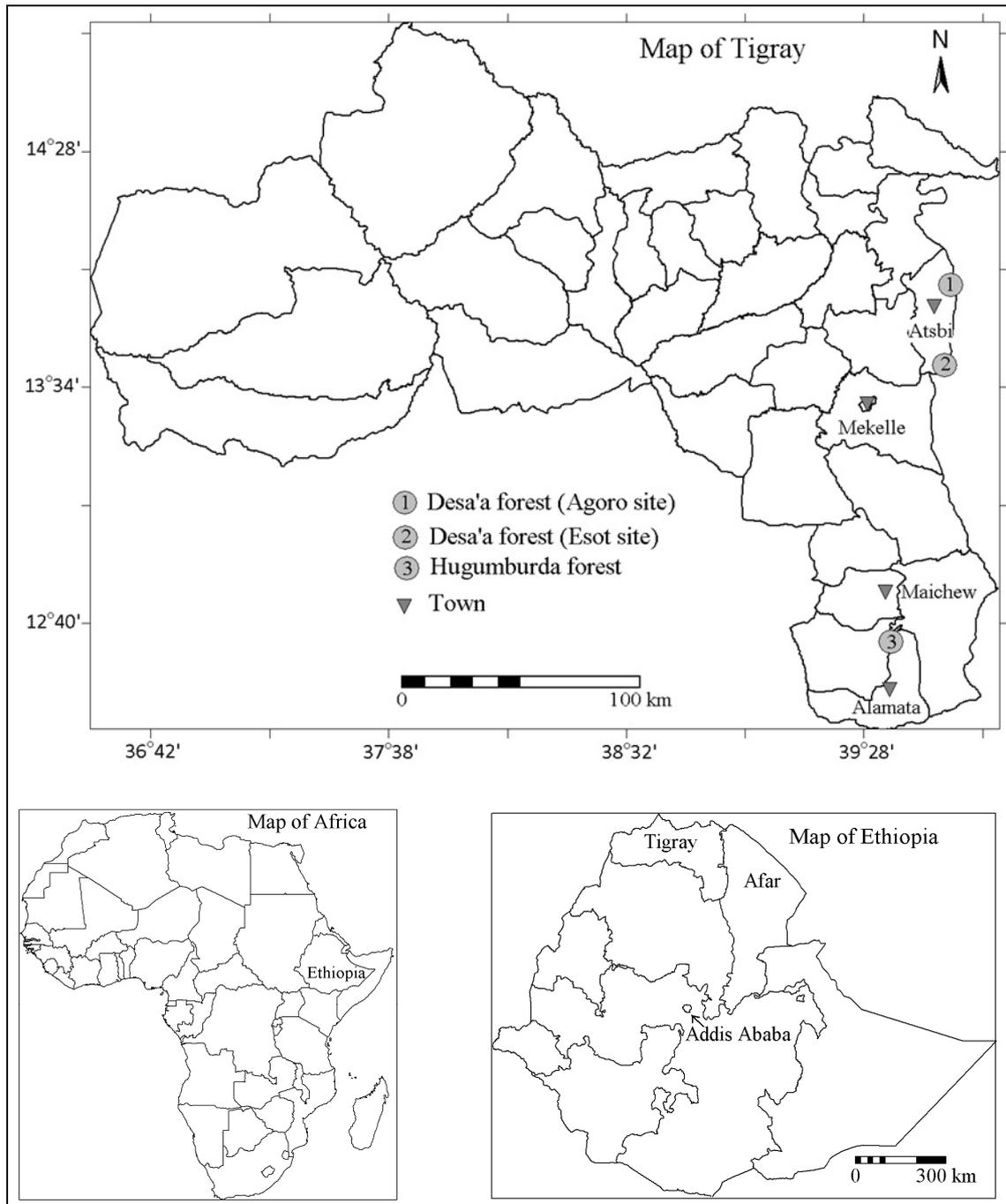


Figure 3.1 Location of the study sites.

3.1.3 Geology and soils

The study area has a diverse geological formation, which plays a major role in soil variability. A large part of Desa'a forest is formed on Enticho sandstone and Crystalline Basement (Asrat 2002). The dominant soil types are Leptosols, Cambisols, Vertisols, Regosols and Arenosols (BoANR and IDC 1997).

Hugumburda forest is formed on tertiary basalt, alkali-alluvial basalt and tuff (Worku 1998). The dominant soils are Leptosols and Regosols (Worku 1998). Large parts of the undulating terrains in northern Ethiopia are characterized by shallow soils and frequent rock outcrops, while relatively thick soils are found along valley bottoms.

3.1.4 Topography

Topographically, the study sites are characterized by plane to steep slopes frequently dissected by stream incisions. The study area lies in an elevational range between 1000 and 2760 m above sea level. About 45 % of the area has a slope class greater than 30 % (Figure 3.2).

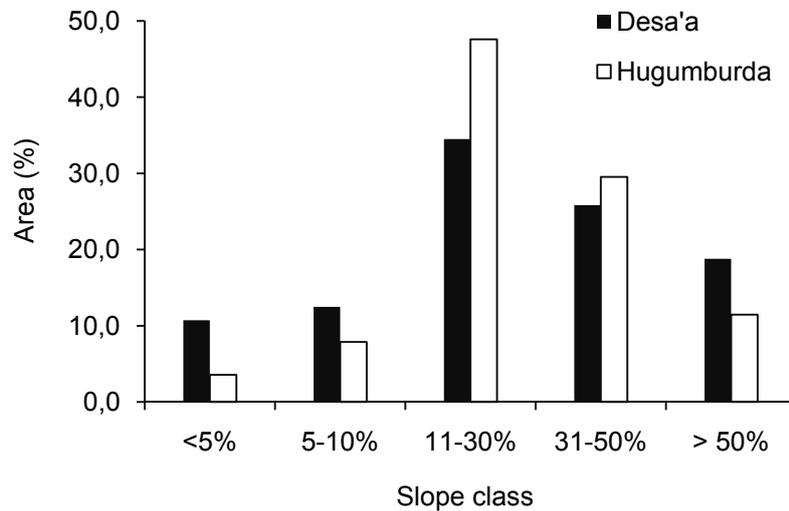


Figure 3.2 Slope classes distribution in Desa'a and Hugumburda forests, northern Ethiopia.

3.1.5 Climate

The study area is located in an semi arid agro-ecological zone where the climate is influenced by topography and exposure to rain-bearing winds (Nyssen et al. 2005). The wet rainfall season is between June and September, while the remaining months are more or less dry.

The rainfall and temperature data for Desa'a forest are based on a 9-year record (1999-2007) from Atsbi town. The plateau section of Desa'a forest receives a mean annual rainfall of 532 mm (Abegaz 2005). The climate of the study area is

influenced by elevation, where the decline in rainfall and increase in temperature from the upland plateau to the eastern escarp slopes are sharp (Degefu 1987).

The nearest meteorological station to Hugumburda forest is in Korem town. Based on 25-year climate data (1979-2005) recorded at Korem meteorological station, the study area receives a mean annual rainfall of 981 mm and the average annual temperature is 16 °C. The mean minimum (6 °C) and mean maximum (22 °C) temperatures were recorded in November and June, respectively (Figure 3.3a). The mean minimum and mean maximum rainfall were 492 and 1358 mm, in 1984 and 1998, respectively (Figure 3.3b).

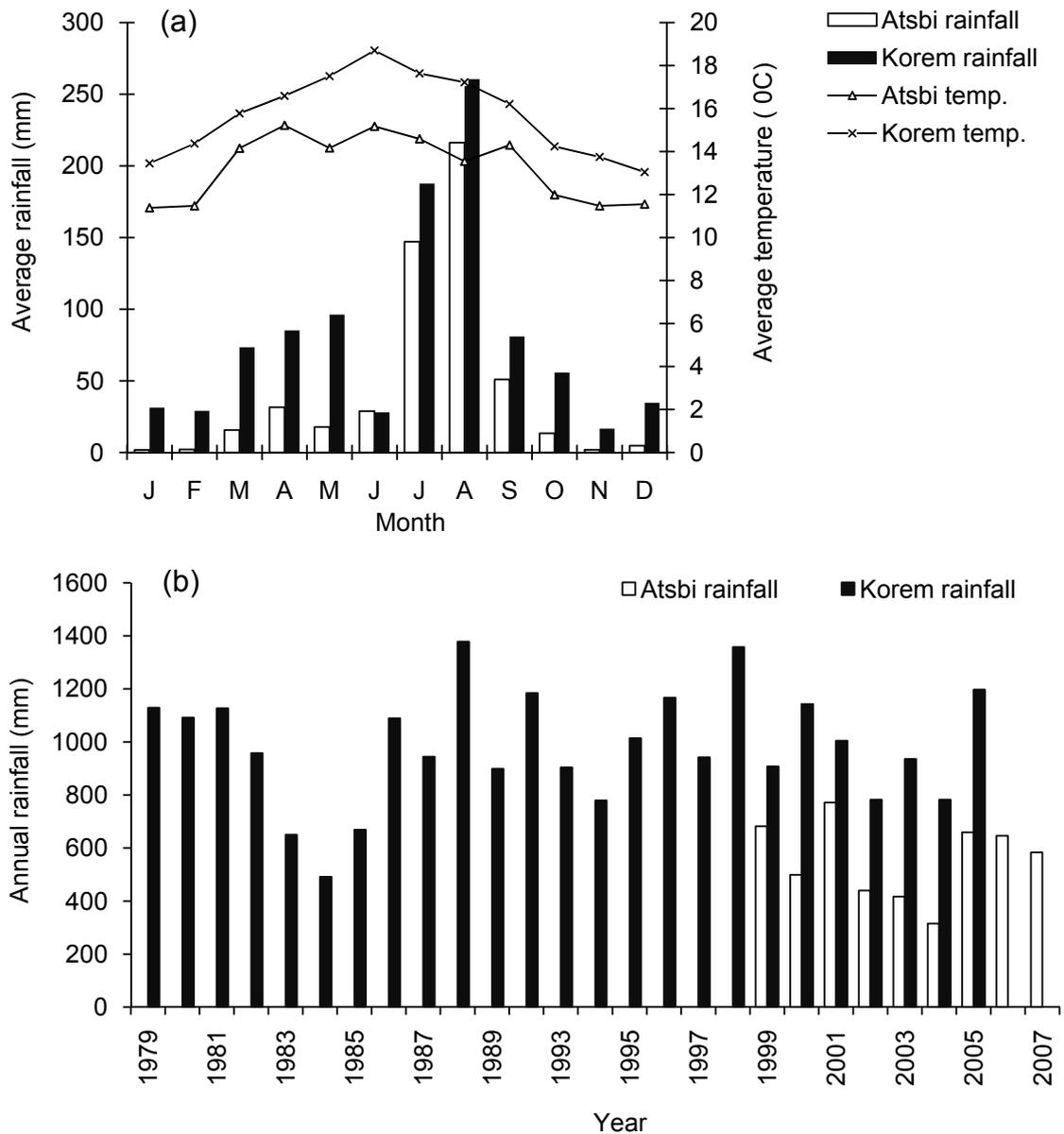


Figure 3.3 (a) Mean monthly rainfall and mean monthly temperature, and (b) annual rainfall recorded at Atsbi (Desa'a forest) and at Korem meteorological station (Hugumburda forest), northern Ethiopia.

3.1.6 Vegetation

Based on the classification of the forests and forest trees of northeast tropical Africa Friis (Friis 1992), Desa'a and Hugumburda forests are broadly categorized as dry single-dominant Afromontane forests, which are characterized by dry climate (annual precipitation less than 1000 mm) and with *Juniperus procera* in the canopy and *Olea europaea* subsp. *cuspidata* as dominant tree species. The study area provides diverse habitats for plants. The mesic Tigray highlands support species like *Erica arborea*. The

dry Afar lowlands with the Acacia woodlands are located at a short distance (ca. 5 km) from the highlands. The diversity of the two forests is largely dominated by herb and shrub species (ca. 70 %), while tree species contribute 30 % of the total vascular plant species (Figure 3.4).

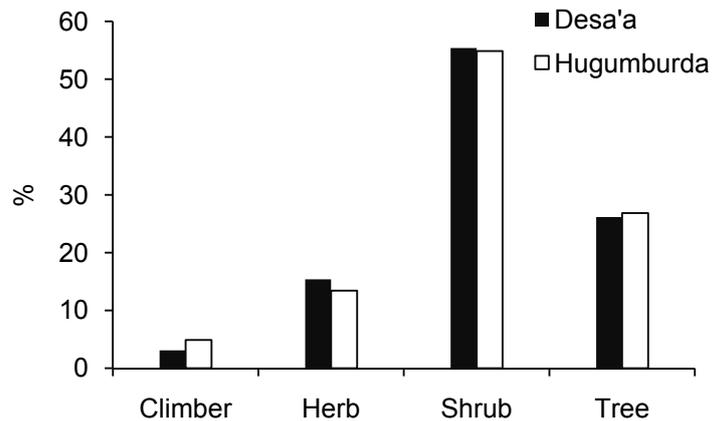


Figure 3.4 Life forms in Desa'a and Hugumburda forests, northern Ethiopia.

Hugumburda forest is the only more or less intact large forest with many locally rare tree species from the pre-disturbance period. *Afrocarpus falcatus* and other native tree species, which are rare in other parts of northern Ethiopia, are found in this forest. It is more protected, and more enrichment plantation activities have been carried out than in Desa'a forest.

A large part of Desa'a forest has been converted into agricultural land and grazing land. The scattered trees and stumps on the farm and grazing land are evidence of the shrinking of this forest (Figure 3.5a). According to Gebreegziabher (1999), fire is another major threat to the forest, where 1000 and 350 ha forest land was destroyed by fire in 1970 and 1998, respectively. Although more attention has been given to the anthropogenic cause of forest degradation, forest disturbance due to natural mass tree dieback is commonly observed in Desa'a forest (Figure 3.5d).

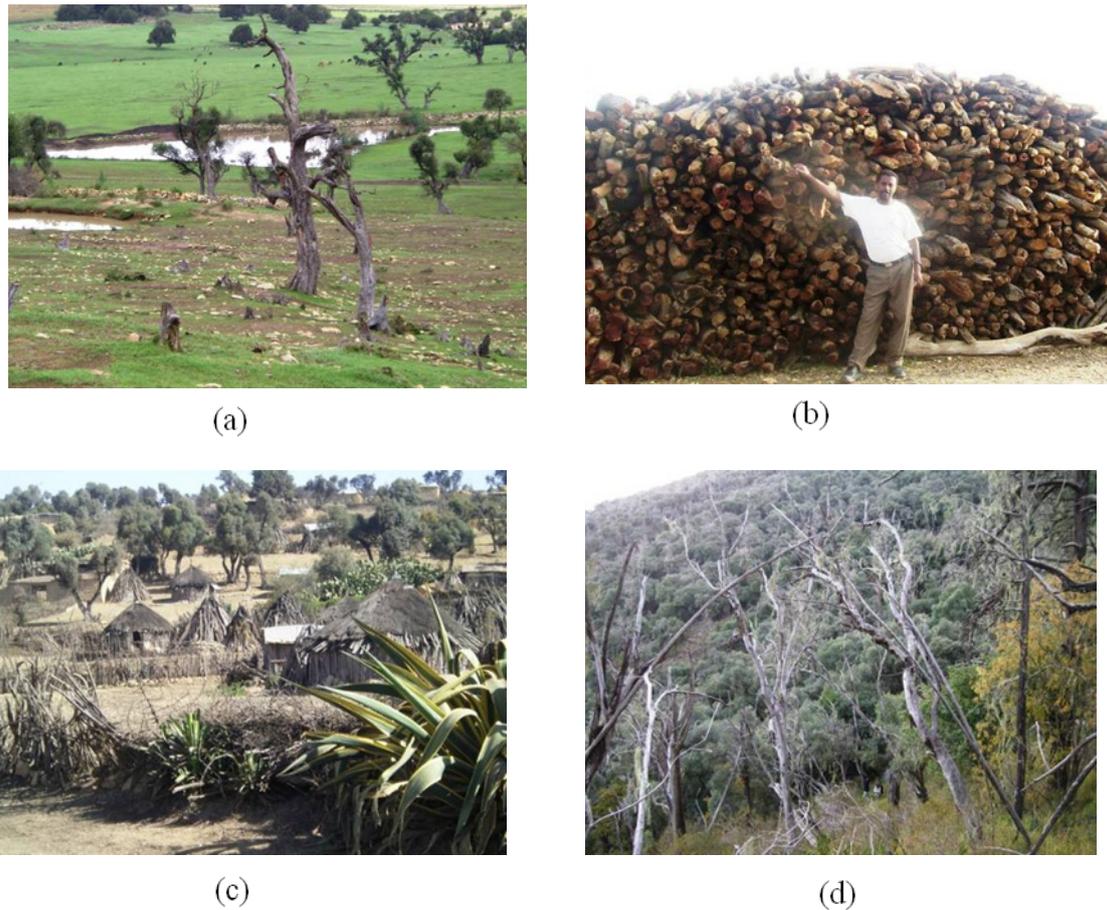


Figure 3.5 Anthropogenic and natural disturbances at Desa'a forest: (a) deforestation and forest conversion to agriculture around Agoro village, (b) confiscated fuelwood at the check point at Kalesh Emni village, (c) settlement at Agoro village, and (d), standing dead trees (snags) near Esot village, northern Ethiopia.

3.2 General methods

3.2.1 Site selection

This study focuses on the natural forest remnants in the Desa'a and Hugumburda forests, northern Ethiopia. Site selection was carried out using visual interpretation of the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) image and data from a reconnaissance survey conducted in 2006. In the larger Desa'a forest, two sites (Agoro and Esot) were selected. The results of this study are largely based on field data collected between June 2007 and May 2008.

3.2.2 Sampling design

Random selected plots are used to examine the role of exclosure on the seedling bank (Chapter 7), while systematic sampling was used for determining plant species diversity and natural regeneration, plant species diversity patterns along an elevational gradient on the western escarpment of the Great Rift Valley, and the effects of mass tree dieback on stand structure and diversity (Chapter 4, 5, and 6). Since the study sites are mainly on hilly terrain, transects were established along elevation and plots were established at 100 m elevational intervals along a W-E direction. To adequately cover the two forests, transects were established at 1-km intervals. A base map showing transects and plots were produced using 1:50,000 scale topographic maps in a GIS environment, and a GPS device was used to establish the plots in the field.

The vegetation data were collected using 10 m × 10 m, 10 m × 20 m, 20 m × 20 m, 20 m × 40 m, 40 m × 40 m, and 50 m × 50 m nested plots (Figure 3.6), which were used to determine species-area relationships (Kent and Coker 1992). Plot areas were corrected when these were on slopes steeper than 10 %. All stems with a diameter at breast height (DBH) > 5 cm and all diameter classes of the target species (i.e., *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, and *Afrocarpus falcatus*) were measured in all nested plots, while stems with DBH < 5 cm were measured in 20 m × 20 m nested plots. In all cases, data on the seedling were collected using 10 m × 10 m nested plots. A total of 286 plots (106 from Agoro; 115 from Esot, and 65 from Hugumburda) were studied.

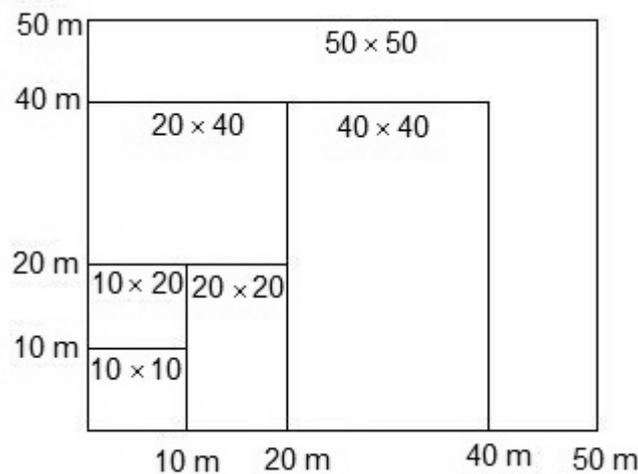


Figure 3.6 Layout of a nested plot used in vegetation data collection.

3.2.3 Vegetation data

Abundance, frequency, stand density, and basal area per hectare were determined for all trees with a height > 1.5 m and diameter > 2 cm at breast height (DBH), while those smaller than these minimum values were counted and included in the abundance and frequency data. Species were identified in the field and at the National Herbarium, Addis Ababa University; nomenclature follows the Flora of Ethiopia and Eritrea (Hedberg and Edwards 1989; Edwards et al. 1995; Hedberg and Edwards 1995; Edwards et al. 1997; Edwards et al. 2000; Hedberg et al. 2003).

3.2.4 Environmental data

The environmental variables used in this study were elevation (taken from a topographic map), slope (measured with clinometer), aspect (measured using compass), soil depth (measured using pits), distance to the nearest stream, and extent of disturbance (subjectively rated as 0 = no disturbance, 1 = slightly disturbed, 2 = moderately disturbed, and 3 = highly disturbed) based on grazing intensity, cut stems, and human trails). Distance to the nearest stream was measured by overlaying the plots on the drainage map in ILWIS 3.3 GIS software.

4 PLANT SPECIES DIVERSITY AND NATURAL REGENERATION IN AN ISOLATED AFROMONTANE FOREST, NORTHERN ETHIOPIA

4.1 Introduction

Understanding species distribution patterns along environmental variables is a central component of plant ecology (Rosenzweig 1995). Topographical, climatic, and edaphic factors are widely considered as determinants of species distribution and community structure (Whittaker et al. 2003; Currie et al. 2004). The effect of environmental variables on species diversity depends on the spatial scale (Whittaker et al. 2003; Laurance 2004; Nogues-Bravo et al. 2008). Habitat disturbance, for instance, affects species diversity at the local scale (species diversity within a plant community), while soil, topography, elevation, and drainage are considered as landscape-level determinants of species diversity (Whittaker et al. 2003). Forest disturbance also influences species diversity through alteration and fragmentation of forests, which is a serious concern in the management of tropical forests (Laurance and Bierregaard 1997). Fragmentation affects species diversity by reducing areas, which leads to a small number of individuals and species (Rosenzweig 1995; Whittaker et al. 2003).

The Ethiopian highlands constitute large parts of the Afromontane regions of Africa, which stretch from Cameroon to eastern Africa (White 1983), where biodiversity hotspots exist (Conservation International 2007). However, as in many tropical forests, forest disturbance (natural and anthropogenic) has changed the structure and floristic composition of forests in northern Ethiopia for centuries (Darbyshire et al. 2003). Currently, only a few natural forest remnants are left as islands in the landscapes dominated by agriculture (Aerts et al. 2006c).

Hugumburda forest is unique in the sense that it is (1) the only well-protected large Afromontane forest remnant in northern Ethiopia, and (2) an isolated forest not only because the surrounding area has been cleared, but mainly because it is located in a secluded valley next to the parallel rift of Lake Hashenge. Thus, it is an isolated island of forest in a landscape dominated by crop and grazing land. In such isolated areas, limited cross-pollination, inbreeding, and genetic drift (Ellstrand and Elam 1993) are likely to negatively impact plant populations (Reed and Frankham 2003; Hirayama et al. 2007). This can be observed in the population structure of the trees, i.e., a low

number of seedlings as well as a smaller number of saplings than of mature individuals. In this case, the forest will face extinction, i.e., some tree species are still present, but will become locally extinct because of poor or no regeneration.

The present study investigates (i) plant species diversity and community structure in relation to environmental variables, and (ii) composition of the seedling bank in relation to the standing vegetation in Hugumburda forest, northern Ethiopia.

4.2 Material and methods

4.2.1 Study site

The study was conducted in Hugumburda forest, which is an isolated natural forest remnant in Tigray and is listed as a national forest priority area in Ethiopia. The study site is located between 12°36' and 12°40' N and 39°31' and 39°34' E (Figure 4.1) and elevation ranges between 1860 and 2700 m a.s.l. Topographically, the study area is largely characterized by undulating to steep terrain, which is frequently dissected by stream incisions. The area is formed on tertiary basalt, alkali-alluvial basalt, and tuff (Worku 1998). The dominant soils are Leptosols and Regosols (Worku 1998). The soils are shallow on the slopes, while the valley bottoms have thick alluvial deposits. The mean annual rainfall is 981 mm and the mean annual temperature is 16 °C.

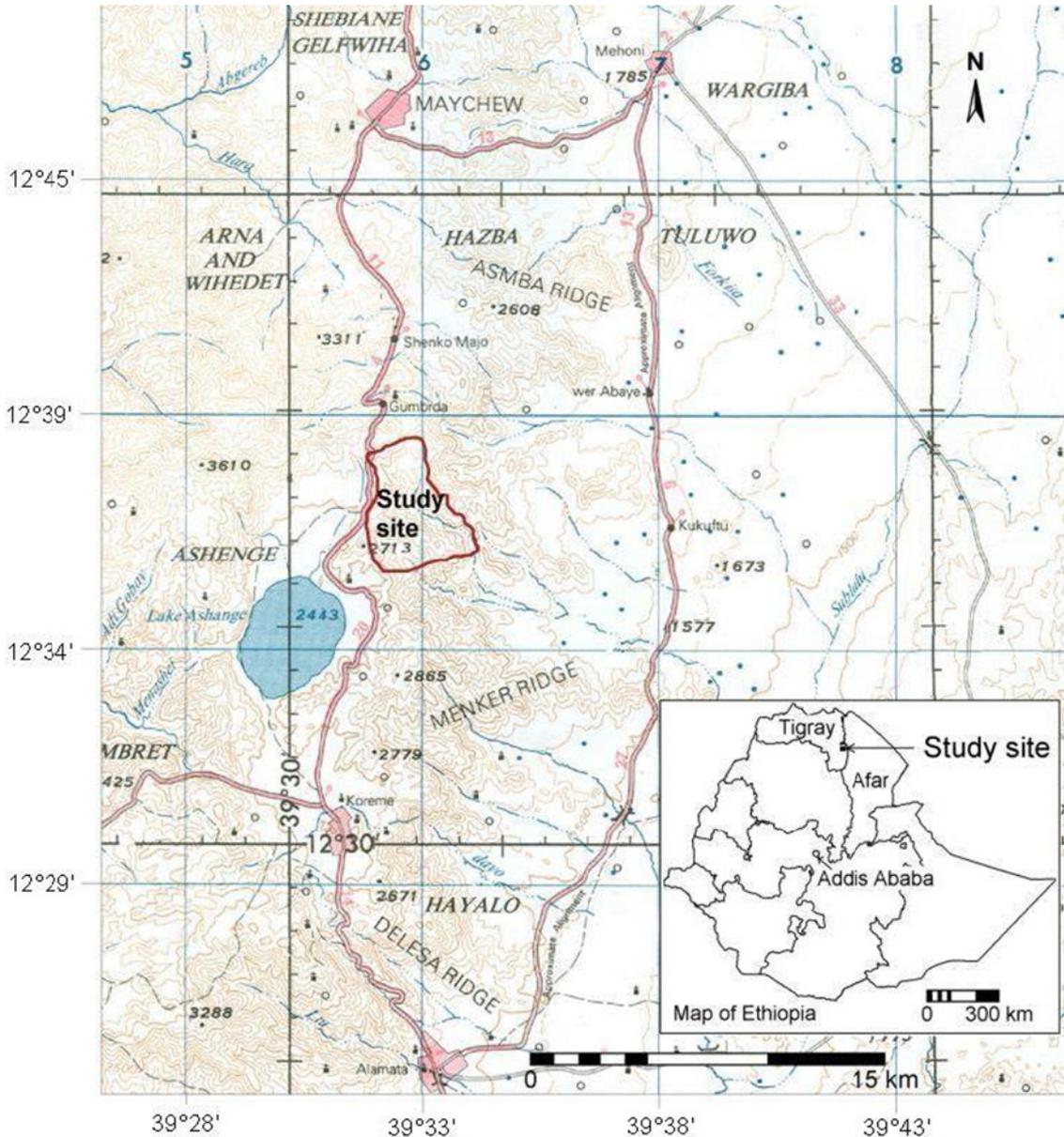


Figure 4.1 Location of the study site.

4.2.2 Data collection

Data on the standing vegetation were collected in 65 (50 m × 50 m) nested plots (Figure 3.6) established at 100-m elevation intervals along W-E parallel transects, which were spaced 1 km apart. The seedling bank composition and density were determined in 10 m × 10 m plots. All woody plants were identified and counted, and diameter at breast height (DBH) was measured for plants with height > 1.5 m and DBH > 2 cm. Species were identified in the field and at the National Herbarium, Addis Ababa University.

The environmental variables used in this study are elevation (taken from a topographic map), slope (measured with a clinometer), soil depth (measured in pits), distance to the nearest stream (measured by overlaying the plots on the drainage map in a GIS), and extent of disturbance was subjectively ranked based on grazing intensity, cut stems, and human trails (0 = no disturbance, 1 = slightly disturbed, 2 = moderately disturbed, and 3 = highly disturbed).

4.2.3 Data analysis

Forest structure and diversity

The importance of a species is determined by calculating the importance value index (IVI), which is obtained by summing up relative density, relative dominance and relative frequency of a species (Mueller-Dombois and Ellenberg 1974). Density of a species is the number of individuals per hectare, frequency is the percentage of plots in which a species occurs, and dominance of a species is the sum of the basal area of individual stems.

Hill's (1973) diversity numbers were derived from the Shannon diversity and Simpson's index of diversity indices which are unaffected by species richness and tend to be independent of sample size. N_0 ($= \gamma$) to determine species richness in plant communities, N_1 ($= \exp(H')$), and N_2 ($= D^{-1}$) are used to calculate species richness and diversity, and E_1 ($= N_1/N_0$) to calculate species evenness for every plot: γ is total species richness; H' is Shannon diversity index; D is Simpson's index of diversity. Similarity between seedling and standing vegetation species composition was determined using the Sørensen coefficient of similarity (Krebs 1989).

Topographic information was derived from a digital elevation model, which was generated from a topographic map. Topographic wetness index (TWI) (Eq. 4.1), which indicates the spatial distribution of soil moisture and ground water flow, is generated from the digital elevation model of the study area by computing the upslope contributing area of a grid in relation to the slope gradient (Beven and Kirkby 1979) in a GIS environment. The digital elevation model is developed using the topographic map (1:50,000 scale).

$$TWI = \ln \left(\frac{a}{\tan(\beta)} \right) \quad (4.1)$$

where TWI is topographic wetness index, a is upslope contributing area of a grid (flow accumulation), and β is slope gradient.

The species-area curve was determined using the number of species recorded in the nested plots. The vegetation of moist and dry forests was delineated by overlaying the plots that belong to either of the plant communities on the map of the study area in GIS. The location map, distance to the nearest stream, topographical wetness index, and a map showing the plant communities were developed using ILWIS 3.3 GIS software (ITC 2001).

Cluster analysis

A multivariate hierarchical clustering using the Euclidean distance and Ward's group linkage method, and indicator species analysis were performed to identify plant communities (McCune and Grace 2002). The dendrogram was scaled using Wishart's objective function that measures the percent information remaining at each level of clustering and pruned at the minimum average P-value of the indicator species (McCune and Grace 2002). The indicator value of a species was calculated using Dufrene and Legendre's (1997) method, which considers the abundance of a species in a group and its distribution among plots within a group. The statistical significance of the indicator values of a species was tested with the Monte Carlo permutation test. The difference in the floristic compositions among the plant communities was tested with the nonparametric Multi-Response Permutation Procedure (MRPP; Biondini et al. 1985). The P-value in MRPP, which is associated with the test statistics (T), evaluates if the observed differences among groups are due to chance and the chance-corrected within-group agreement (A) measures within group homogeneity. When all items within groups are identical, $A = 1$. when $A = 0$, the heterogeneity within groups equals the expectation by chance, while $A < 0$ when there is less agreement within groups than expected by chance (McCune and Grace 2002).

Ordination

Nonmetric multidimensional scaling (NMS) ordination was used to investigate the environmental factors that influence the structure of the plant communities. NMS is the most effective ordination method for ecological community data (McCune and Grace 2002) and avoids the assumption of linear relationships among variables (Clarke 1993). NMS was run using the Sørensen distance measure, 6 starting dimensions, 50 iterations and an instability criterion of 0.00001 (McCune and Mefford 1999). Spearman rank correlation was used to determine the bivariate relationships between explanatory variables and ordination axes scores.

Clustering, indicator species analysis, Monte Carlo test, MRPP, and NMS analyses were conducted in PC-ORD 5.0 software (McCune and Grace 2002).

Statistical analyses

Differences in stand structure and environmental variables among plant communities were tested using MANOVA, and the post hoc Tukey's test was used for pair-wise multiple comparisons. Nonparametric Kruskal–Wallis ANOVA and pair-wise comparison (Siegel and Castellan 1988) were used to test differences between communities in diversity measures. All tests of statistical significance were decided at $\alpha = 0.05$ level. The statistical analyses was conducted in SPSS 13.0 for Windows (SPSS Inc. 2004).

4.3 Results

4.3.1 Floristic composition and diversity

A total of 79 species belonging to 51 families was recorded in the 65 plots (Table 4.1). The forest has an overall stem density of 1218 ± 74 stems ha^{-1} (mean \pm SE), a basal area of 9.23 ± 1.08 m^2 ha^{-1} , species richness of 22 ± 1 species per plot (0.25 ha), evenness of 0.75 ± 0.01 , Shannon diversity of 2.31 ± 0.05 , and Simpson index of 0.83 ± 0.01 . The three most abundant families were Fabaceae (5 species), Asteraceae (4), and Anacardiaceae (4). Regarding plant life forms, the forest is composed of 56 % shrub, 28 % tree, 12 % herb, and 4 % liana species. *Cupressus lusitanica*, *Eucalyptus camaldulensis* and *Acacia saligna* are exotic species, while the remaining species are native. *Juniperus procera*, *Olea europaea* subsp. *cuspidata* and *Cordia purpurea* are the

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northern Ethiopia

three dominant species that contributed 40 % of the total species abundance (Table 4.1). The three most frequent species were *Carissa edulis*, *Olea europaea* subsp. *cuspidata*, and *Juniperus procera*, which occurred in 95, 93 and 89 % of the plots, respectively. Of all species 21 % were rare species, and were recorded only in three plots.

Table 4.1 Species identified in 65 plots (16.25 ha) in Hugumburda forest, northern Ethiopia

No.	Family	Species	Life form ^a	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Frequency (%)	IVI
1	Cupressaceae	<i>Juniperus procera</i> Hochst. ex Endl.	t	190.3	4.47	89.39	67.9
2	Oleaceae	<i>Olea europaea</i> L. subsp. <i>cuspidata</i> (Wall ex G. Don.) Cif.	t	156.4	1.5	93.94	33.3
3	Fabaceae	<i>Cadia purpurea</i> Ait.	s	147.1	0.44	69.7	19.8
4	Apocynaceae	<i>Carissa edulis</i> Vahl	s	103.0	0.34	95.45	16.4
5	Celastraceae	<i>Maytenus senegalensis</i> (Lam.) Exell	st	95.3	0.19	90.91	13.9
6	Anacardiaceae	<i>Rhus natalensis</i> Bernh. ex Krauss	t	93.3	0.11	86.36	12.8
7	Fabaceae	<i>Acacia abyssinica</i> Hochst. ex Benth.	t	24.3	0.24	74.24	7.97
8	Pittosporaceae	<i>Pittosporum viridiflorum</i> Sims	t	18.3	0.28	66.67	7.55
9	Flacourtiaceae	<i>Dovyalis verucosa</i> (Hochst.) Warb	st	36.2	0.02	81.82	6.9
10	Myrsinaceae	<i>Myrsine africana</i> L.	s	36.3	0.01	66.67	6.11
11	Anacardiaceae	<i>Rhus glutinosa</i> A. Rich.	t	16.9	0.08	77.27	5.73
12	Sapindaceae	<i>Dodonaea viscosa</i> Jacq.	t	27.0	0.04	68.18	5.71
13	Lamiaceae	<i>Premna resinosa</i> Schauer	s	13.2	0.23	40.91	5.39
14	Rhizophoraceae	<i>Cassipourea malosana</i> Alston	t	16.1	0.15	48.48	5.15
15	Cupressaceae	<i>Cupressus lusitanica</i> Mill.	t	9.9	0.28	13.64	4.47
16	Fabaceae	<i>Pterolobium stellatum</i> (Forssk.) Brenan	c	17.5	0.01	59.09	4.27
17	Santalaceae	<i>Osyris quadripartita</i> Salzm ex Decne.	s	14.1	0.02	62.12	4.24
18	Rubiaceae	<i>Psydrax schimperiana</i> (A. Rich.) Brid.	st	10.3	0.06	57.58	4.16
19	Sterculiaceae	<i>Dombeya torrida</i> (J.F. Gmel.) Bamps	t	8.9	0.01	60.61	3.57
20	Ulmaceae	<i>Celtis africana</i> Burm. f	t	8.7	0.12	31.82	3.52
21	Rutaceae	<i>Teclea simplicifolia</i> I. Verd.	t	12.9	0.01	51.52	3.49
22	Podocarpaceae	<i>Afrocarpus falcatus</i> (Thunb.) C.N. Page	t	13.6	0.14	18.18	3.43
23	Fabaceae	<i>Calpurnia aurea</i> Benth.	st	11.5	0.02	46.97	3.3

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Table 4.1 continued

No.	Family	Species	Life form ^a	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Frequency (%)	IVI
24	Asparagaceae	<i>Asparagus racemosus</i> Willd.	hs	9.5	0.01	51.52	3.2
25	Verbenaceae	<i>Clerodendrum myricoides</i> R.Br.	s	10.9	0	46.97	3.09
26	Lamiaceae	<i>Becium grandiflorum</i> (Lam.) Pic.Serm.	s	16.5	0	34.85	2.96
27	Ebenaceae	<i>Euclea racemosa</i> Murray subsp. <i>schimperii</i> (A. DC.) F. White	s	8.1	0.01	46.97	2.94
28	Solanaceae	<i>Solanum schimperianum</i> Hochst.	h	15.3	0	36.36	2.91
29	Rubiaceae	<i>Canthium setiflorum</i> Hiern	s	9.2	0	43.94	2.78
30	Melanthaceae	<i>Bersama abyssinica</i> Fresen.	t	8.6	0.07	21.21	2.45
31	Apocynaceae	<i>Acokanthera schimperii</i> (A. DC.) Benth. & Hook.f. ex Schweinf.	st	5.3	0.05	25.76	2.2
32	Rhamnaceae	<i>Sageretia thea</i> (Osbeck) M.C. Johnst.	s	6.3	0.01	31.82	2.09
33	Euphorbiaceae	<i>Clutia abyssinica</i> Jaub. & Spach.	s	5.6	0	31.82	1.92
34	Moraceae	<i>Ficus palmata</i> Forssk.	st	6.0	0	28.79	1.81
35	Cactaceae	<i>Opuntia ficus-indica</i> (L.) Mill.	st	6.9	0.01	21.21	1.65
36	Sapindaceae	<i>Allophylus abyssinicus</i> Radlk.	t	1.4	0.07	16.67	1.64
37	Oliniaceae	<i>Olinia rochetiana</i> A. Juss.	st	3.7	0.01	25.76	1.61
38	Crassulaceae	<i>Kalanchoe</i> sp.	s	9.3	0.02	13.64	1.58
39	Tiliaceae	<i>Grewia ferruginea</i> Hochst.	st	5.8	0.03	18.18	1.58
40	Anacardiaceae	<i>Rhus</i> sp.	t	1.9	0.03	16.67	1.23
41	Polygonaceae	<i>Rumex nervosus</i> Vahl	h	2.2	0	19.7	1.08
42	Euphorbiaceae	<i>Clutia lanceolata</i> Jaub. & Spach	s	3.1	0	16.67	1.01
43	Ranunculaceae	<i>Clematis sinensis</i> Lour.	sc	1.8	0	18.18	1
44	Myrtaceae	<i>Eucalyptus camaldulensis</i> Dehnh.	t	0.3	0.07	1.52	0.85
45	Moraceae	<i>Ficus thonningii</i> Blume	st	0.3	0.04	7.58	0.81
46	Aloaceae	<i>Aloe camperi</i> Schweinf.	h	1.7	0	13.64	0.76
47	Flacourtiaceae	<i>Dovyalis abyssinica</i> (A. Rich.) Warb.	st	1.4	0	12.12	0.68
48	Verbenaceae	<i>Lantana viburnoides</i> (Forssk.) Vahl	s	1.2	0	12.12	0.66

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Table 4.1 continued

No.	Family	Species	Life form ^a	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Frequency (%)	IVI
49	Vitaceae	<i>Cissus quadrangularis</i> L.	h	1.2	0.01	7.58	0.55
50	Rosaceae	<i>Rosa abyssinica</i> R.Br	s	0.7	0	10.61	0.55
51	Solanaceae	<i>Solanum incanum</i> L.	h	0.9	0	9.09	0.49
52	Berberidaceae	<i>Berberis holstii</i> Engl.	st	0.6	0	9.09	0.46
53	Lamiaceae	<i>Leucas abyssinica</i> Briq.	h	2.5	0	3.03	0.34
54	Malvaceae	<i>Pavonia urens</i> Cav.	hs	0.7	0	6.06	0.34
55	Sapotaceae	<i>Spiniluma oxyacantha</i> (Baill.) Aubrev.	t	0.6	0	6.06	0.33
56	Oleaceae	<i>Olea capensis</i> L. subsp. <i>macrocarpa</i> (C.H. Wright) I. Verd.	t	0.4	0	4.55	0.28
57	Ericaceae	<i>Erica arborea</i> L.	st	0.5	0	4.55	0.26
58	Oleaceae	<i>Jasminum abyssinicum</i> R.Br.	sc	0.4	0	4.55	0.24
59	Phytolaccaceae	<i>Phytolacca dodecandra</i> L'Hér.	S	0.4	0	4.55	0.24
64	Asteraceae	<i>Echinops giganteus</i> Hort. Ex Dc.	sh	0.2	0	4.55	0.22
61	Celastraceae	<i>Gymnosporia</i> <i>senegalensis</i> (Lam.) Loes.	s	0.7	0	3.03	0.2
62	Tiliaceae	<i>Grweia</i> sp.	st	0.6	0	3.03	0.18
63	Malvaceae	<i>Abutilon longicuspe</i> Hochst. ex A.Rich.	s	0.3	0	3.03	0.16
64	Fabaceae	<i>Acacia etbaica</i> Schweinf.	t	0.6	0	1.52	0.15
65	Clusiaceae	<i>Hypericum quartinianum</i> A. Rich.	h	0.1	0	3.03	0.15
66	Anacardiaceae	<i>Rhus vulgaris</i> Meikle	st	0.1	0	3.03	0.15
67	Fabaceae	Hochst. & Steud.	s	0.1	0	3.03	0.15
68	Rosaceae	<i>Hagenia abyssinica</i> J.F.Gmel.	t	0.1	0	1.52	0.13
69	Sapindaceae	<i>Pappea capensis</i> Eckl. & Zeyh.	t	0.1	0	1.52	0.11
70	Amaranthaceae	<i>Alternanthera nodiflora</i> R.Br.	h	0.1	0	1.52	0.1
71	Asteraceae	<i>Psiadia punctulata</i> Vatke	s	0.2	0	1.52	0.08
72	Leguminosae	<i>Acacia saligna</i> (Labill.) H. L. Wendl.	t	0.1	0	1.52	0.08
73	Asteraceae	<i>Laggera tomentosa</i> (Sch. Bip. ex A. Rich.) Oliv. & Hiern	s	0.1	0	1.52	0.08
74	Leguminosae	<i>Colutea abyssinica</i> Kunth & C.D.Bouche	s	0.1	0	1.52	0.07
75	Euphorbiaceae	<i>Euphorbia tirucalli</i> Forssk.	st	0.1	0	1.52	0.07

Plant species diversity and natural regeneration in an isolated Afromontane forest,
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Table 4.1 continued

No.	Family	Species	Life form ^a	Density (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Frequency (%)	IVI
76	Euphorbiaceae	<i>Ricinus communis</i> L.	st	0.1	0	1.52	0.07
77	Asteraceae	<i>Vernonia amygdalina</i> Delile	st	0.1	0	1.52	0.07
78	Asteraceae	<i>Vernonia auriculifera</i> Hiern.	st	0.1	0	1.52	0.07
79	Rhamnaceae	<i>Ziziphus spina-christi</i> Willd.	st	0.1	0	1.52	0.07
Total				1235.9	9.23	2177.27	300

^a indicate plant life forms: climber (c), herb (h), shrub (s), tree (t), herb or shrub (hs), shrub or climber (sc), and shrub or tree (st)

4.3.2 Species-area relationship

A significant relationship was found between species richness and area, which is explained by a power function of the form: $S = cA^z$, where S is number of species, A is area and c and z are constants (Figure 4.2). The number of species recorded in the minimum (100 m²) and maximum (2500 m²) plot area were 8 and 22, respectively. The number of species increased steadily with increasing area and did not approach an asymptote level within the plot size ranges.

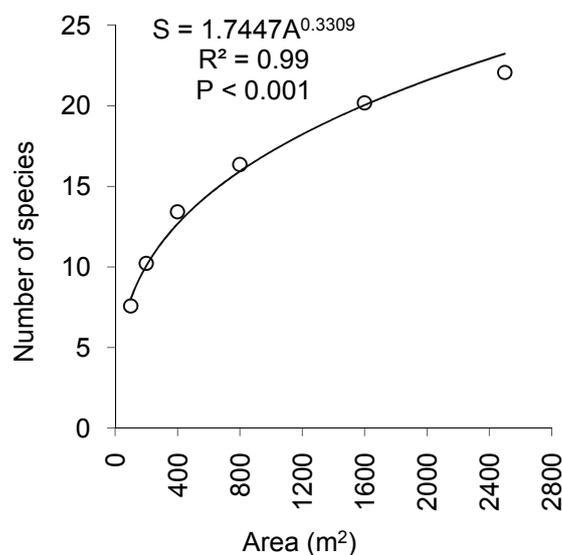


Figure 4.2 Species-area relationship at Hugumburda forest, northern Ethiopia.

4.3.3 Plant communities

The hierarchical cluster and indicator species analyses identified three plant communities: *Juniperus procera*—*Maytenus senegalensis*, *Pterolobium stellatum*—*Celtis africana*, and *Cadia purpurea*—*Opuntia ficus-indica*, which were represented by 70, 64, and 48 species, respectively (Table 4.2). The MRPP test indicates that the three plant communities significantly differ in their species composition ($T = -2.87$, $P < 0.001$), and the similarity among plots in their species composition within a community (homogeneity within groups, A) is 0.12.

Table 4.2 Summary statistics for the indicator species of the three plant communities in Hugumburda forest, northern Ethiopia

Species	Indicator Value ^a (%)			P
	C1	C2	C3	
Cluster 1 (39 plots)	<i>Juniperus procera</i>—<i>Maytenus senegalensis</i> community (C1)			
<i>Juniperus procera</i> ^[t]	71	17	5	< 0.001
<i>Maytenus senegalensis</i> ^[st]	65	22	6	< 0.001
<i>Dodonaea viscosa</i> ^[s]	61	7	6	< 0.001
<i>Acacia abyssinica</i> ^[t]	57	5	17	0.002
<i>Pittosporum viridiflorum</i> ^[t]	54	18	2	0.012
<i>Osyris quadripartita</i> ^[st]	52	10	4	0.003
<i>Dovyalis verucosa</i> ^[st]	50	27	6	0.004
<i>Olea europaea</i> subsp. <i>cuspidata</i> ^[t]	50	15	28	0.041
<i>Myrsine africana</i> ^[st]	46	33	0	0.042
<i>Clusia abyssinica</i> ^[s]	33	5	0	0.044
Cluster 2 (13 plots)	<i>Pterolobium stellatum</i>—<i>Celtis africana</i> community (C2)			
<i>Pterolobium stellatum</i> ^[sc]	15	61	3	< 0.001
<i>Celtis africana</i> ^[t]	3	60	1	< 0.001
<i>Rhus natalensis</i> ^[st]	19	59	14	0.002
<i>Bersama abyssinica</i> ^[t]	2	52	0	< 0.001
<i>Ficus palmate</i> ^[s]	0	49	1	< 0.001
<i>Allophylus abyssinicus</i> ^[t]	2	39	0	< 0.001
<i>Ficus thonningii</i> ^[t]	0	38	0	< 0.001
<i>Afrocarpus falcatus</i> ^[t]	1	36	0	0.007
<i>Rosa abyssinica</i> ^[s]	1	28	0	0.012
Cluster 3 (13 plots)	<i>Cadia purpurea</i>—<i>Opuntia ficus-indica</i> community (C3)			
<i>Cadia purpurea</i> ^[s]	5	6	84	< 0.001
<i>Opuntia ficus-indica</i> ^[s]	0	7	61	< 0.001
<i>Solanum schimperianum</i> ^[s]	2	3	56	0.002
<i>Clerodendrum myricoides</i> ^[s]	11	5	46	0.009
<i>Canthium setiflorum</i> ^[s]	11	3	40	0.023
<i>Euclea racemosa</i> subsp. <i>schimperi</i> ^[s]	8	11	40	0.027

^a Only indicator species with significant values ($P < 0.05$) are shown in a decreasing order of their indicator values. Indicator values range from 0 (no indication) to 100 % (perfect indication). Superscripts indicate species life forms: shrub (s), tree (t), shrub or climber (sc), and shrub or tree (st)

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The three plant communities significantly differed in their tree species density and basal area, but not in their shrub, herb, overall stem densities, and basal area (Table 4.3). The *Pterolobium stellatum*—*Celtis africana* community is more species diverse than the other communities, while the *Cadia purpurea*—*Opuntia ficus-indica* community has the least species diversity.

Table 4.3 Comparison of vegetation structure and diversity (mean \pm SE) among plant communities in Hugumburda forest, northern Ethiopia

Attribute	<i>J. procera</i> — <i>M. senegalensis</i> community (n = 39)	<i>P.stellatum</i> — <i>C. africana</i> community (n = 13)	<i>C. purpurea</i> — <i>O. ficus-indica</i> community (n = 13)		
MANOVA*				F	P
Tree density (stem ha ⁻¹)	731 (64) ^a	519 (102) ^{ab}	287 (66) ^b	7.56	0.001
Shrub density (stem ha ⁻¹)	574 (67) ^a	430 (41) ^a	760 (87) ^a	2.74	0.073
Herb density (stem ha ⁻¹)	28 (4) ^a	23 (11) ^a	72 (35) ^a	2.92	0.061
Overall stem density (stem ha ⁻¹)	1333 (102) ^a	972 (132) ^a	1119 (137) ^a	2.09	0.132
Seedling density (seedling ha ⁻¹)	11489 (2143) ^a	17192 (3089) ^a	2169 (3089) ^b	6.09	0.004
Basal area (m ² ha ⁻¹)	11.1 (1.5) ^a	7.7 (2.0) ^a	5.0 (1.6) ^a	3.1	0.050
Kruskal–Wallis ANOVA**				χ^2	P
Hill's N_0 (total species richness)	70	64	45	—	—
Species richness (average per plot)	22 ^a	25 ^a	17 ^b	17.45	< 0.001
Hill's N_1	11.12 (0.60) ^a	14.54(0.93) ^b	6.81(0.80) ^c	17.39	< 0.001
Hill's N_2	8.14 (0.60) ^a	11.26 (0.98) ^b	4.53 (0.61) ^c	26.26	< 0.001
Hill's E_1	1.43 (0.03) ^{ab}	1.34 (0.54) ^a	1.54 (0.05) ^b	25.21	< 0.001

* indicates significant differences between groups according to Tukey's HSD test

** indicates significant differences between groups according to nonparametric Kruskal–Wallis multiple comparison.

The plant communities significantly differ in all measured environmental variables (Table 4.4).

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northern Ethiopia

Table 4.4 Comparison of environmental variables (mean \pm SE) among the plant communities in Hugumburda forest, northern Ethiopia

Attribute	<i>J. procera</i> — <i>M. senegalensis</i> community (n = 39)	<i>P. stellatum</i> — <i>C. africana</i> community (n = 13)	<i>C. purpurea</i> — <i>O. ficus-indica</i> community (n = 13)	F	P
Distance to the nearest stream (m)	333 (48) ^a	54 (44) ^b	275 (199) ^{ab}	5.60	0.006
Elevation (m a.s.l.)	2387 (22) ^a	2147 (38) ^b	2197 (55) ^b	16.52	< 0.001
Level of disturbance	Moderate	Moderate	High		
Slope (%)	35 (4) ^a	18 (4) ^b	34 (3) ^{ab}	3.27	0.045
Soil depth (cm)	73 (4) ^a	138 (10) ^b	42 (6) ^c	43.6	< 0.001
Wetness index	12.04 (0.34) ^a	15.4 (0.66) ^b	11.65(0.67) ^a	12.64	< 0.001

Letters in superscript indicate significant differences between groups according to Tukey's HSD test

4.3.4 Ordination

For the NMS ordination, the greatest reduction in stress with the fewest number of dimensions was achieved with a three-dimensional solution (McCune and Mefford 1999). The proportion of variance (coefficient of determination R^2 for the correlation between ordination distances and Sørensen distance in the original 40-dimensional space) represented by the three axes were 0.475, 0.225, and 0.183, respectively (cumulative $R^2 = 0.88$). The biplot of the first two NMS axes indicates the partitioning of the three plant communities along the measured environmental gradients (Figure 4.3).

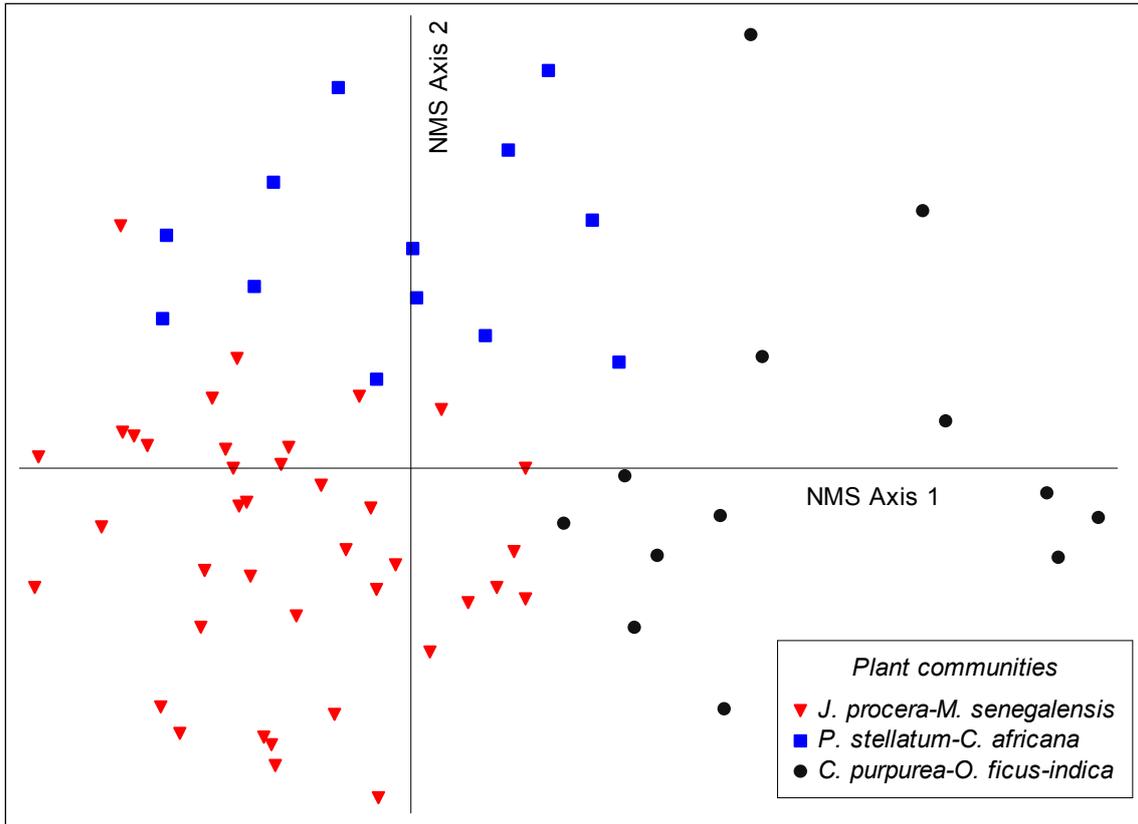


Figure 4.3 Nonmetric multidimensional scaling (NMS) ordination of the 65 plots in Hugumburda forest, northern Ethiopia.

Species distribution along the NMS axes responds to all the environmental variables. Distance to nearest stream, elevation, and slope are negatively correlated to NMS axis 2. Soil depth is positively correlated to NMS axis 2 (Table 4.5). This axis partitions the *Pterolobium stellatum*—*Celtis africana* community from the other two communities.

Table 4.5 Spearman rank correlation (r_s) between NMS axes scores and environmental variables in Hugumburda forest, northern Ethiopia

Attribute	NMS axis 1		NMS axis 2	
	r_s	P	r_s	P
Distance to nearest stream (m)	-0.043	0.731	-0.475	< 0.001
Elevation (m)	-0.503	<0.001	-0.567	< 0.001
Level of disturbance	0.531	<0.001	-0.127	0.313
Slope (%)	0.096	0.446	-0.472	< 0.001
Soil depth (m)	-0.339	0.006	0.580	< 0.001
Wetness index	-0.063	0.619	0.634	< 0.001

The *Pterolobium stellatum*—*Celtis africana* community dominantly found at the lower elevation, which is characterized by a gentle slope, deep soil, and is closer to streams with higher soil moisture, while the other communities dominantly occur on gently to steep slopes at middle and upper elevations with medium to shallow soil depths (Figure 4.4). The level of disturbance is significantly correlated to NMS axis 1, which partitions the *Cadia purpurea*—*Opuntia ficus-indica* community from the other communities. The NMS axis 3 is correlated to disturbance only.

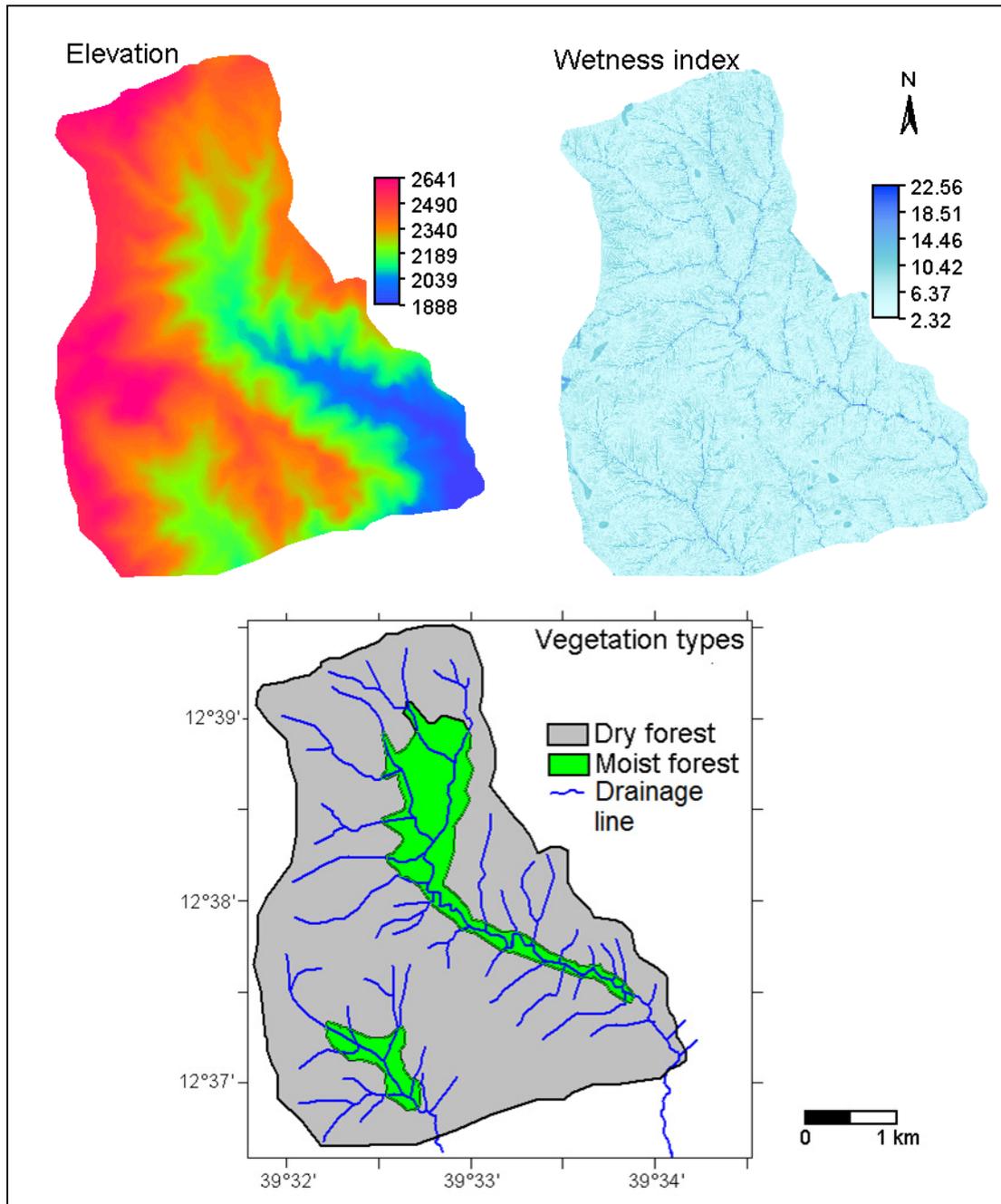


Figure 4.4 Map showing the digital elevation model, topographical wetness index, and vegetation types in Hugumburda forest, northern Ethiopia.

4.3.5 Natural regeneration and diameter class distribution

A total of 39 seedling species belonging to 30 families was recorded. The overall seedling density ranges from 100 to 46,400 seedlings per ha (mean \pm SE: 9182 ± 1820). Like in the standing vegetation, Fabaceae (represented by four species) is the dominant family in the seedling bank. Anacardiaceae, Apocynaceae, Lamiaceae, Rhizophoraceae,

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Rubiaceae and Sapindaceae are each represented by two species and the remaining 23 families by one species (Table 4.6). The three most abundant species represented in the seedling bank are *Pterolobium stellatum* (27 % of the total individuals), *Celtis africana* (14 %), and *Myrsine africana* (8 %). The seedling bank is dominated by shrub species (53 %), followed by tree (37 %), and herb species (10 %). The similarity between the seedling bank and standing vegetation species composition is modest (Sørensen coefficient of similarity = 0.59). Only 49 % of the species in the standing vegetation are represented in the seedling bank.

Table 4.6 Species identified in the seedling bank in Hugumburda forest, northern Ethiopia

No.	Family	Species	Life form*	Density (seedling ha ⁻¹)	Frequency (%)
1	Fabaceae	<i>Pterolobium stellatum</i> (Forssk.) Brenan	sc	2391	35
2	Ulmaceae	<i>Celtis africana</i> Burm. f	t	1189	21
3	Myrsinaceae	<i>Myrsine africana</i> L.	s	712	26
4	Celastraceae	<i>Maytenus senegalensis</i> (Lam.) Exell	sh	706	55
5	Cupressaceae	<i>Juniperus procera</i> Hochst. ex Endl.	t	606	32
6	Rutaceae	<i>Teclea simplicifolia</i> I. Verd.	t	436	30
7	Sapindaceae	<i>Allophylus abyssinicus</i> Radlk.	t	424	17
8	Oleaceae	<i>Olea europaea</i> L. subsp. <i>cuspidata</i> (Wall ex G. Don.) Cif.	t	318	55
9	Fabaceae	<i>Cadia purpurea</i> Ait.	s	300	21
10	Fabaceae	<i>Calpurnia aurea</i> Benth.	st	248	23
11	Sapindaceae	<i>Dodonaea viscosa</i> Jacq.	s	224	41
12	Flacourtiaceae	<i>Dovyalis verucosa</i> (Hochst.) Warb	st	209	41
13	Melianthaceae	<i>Bersama abyssinica</i> Fresen.	t	121	15
14	Rubiaceae	<i>Psydrax schimperiana</i> (A. Rich.) Bridson	st	112	14
15	Anacardiaceae	<i>Rhus natalensis</i> Bernh. ex Krauss	t	95	33
16	Sterculiaceae	<i>Dombeya torrida</i> (J.F. Gmel.) Bamps	t	91	14
17	Ebenaceae	<i>Euclea racemosa</i> Murray subsp. <i>schimperi</i> (A. DC.) F. White	s	91	21
18	Rhizophoraceae	<i>Cassipourea malosana</i> Alston	t	83	23
19	Apocynaceae	<i>Carissa edulis</i> Vahl	s	68	23
20	Amaranthaceae	<i>Alternanthera nodiflora</i> R.Br.	h	38	2
21	Euphorbiaceae	<i>Clutia abyssinica</i> Jaub. & Spach	s	36	11
22	Fabaceae	<i>Acacia abyssinica</i> Hochst. ex Benth.	t	30	8
23	Apocynaceae	<i>Acokanthera schimperi</i> (A. DC.) Benth. & Hook. f. ex Schweinf.	st	20	3
24	Cactaceae	<i>Opuntia ficus-indica</i> (L.) Mill.	st	20	3
25	Podocarpaceae	<i>Afrocarpus falcatus</i> (Thunb.) C.N. Page	t	17	9

Plant species diversity and natural regeneration in an isolated Afromontane forest,
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Table 4.6 continued

No.	Family	Species	Life form*	Density (seedling ha ⁻¹)	Frequency (%)
26	Malvaceae	<i>Pavonia urens</i> Cav.	hs	17	3
27	Pittosporaceae	<i>Pittosporum viridiflorum</i> Sims	t	17	9
28	Santalaceae	<i>Osyris quadripartita</i> Salzm ex Decne.	s	15	9
29	Lamiaceae	<i>Becium grandiflorum</i> (Lam.) Pic.Serm.	s	14	2
30	Rhamnaceae	<i>Sageretia thea</i> (Osbeck) M.C.Johnst.	s	14	5
31	Euphorbiaceae	<i>Clutia lanceolata</i> Jaub. & Spach	s	12	3
32	Verbenaceae	<i>Clerodendrum myricoides</i> R.Br.	s	11	3
33	Solanaceae	<i>Solanum incanum</i> L.	h	11	3
34	Asparagaceae	<i>Asparagus racemosus</i> Willd.	hs	9	8
35	Crassulaceae	<i>Kalanchoe</i> sp.	s	8	2
36	Rubiaceae	<i>Canthium setiflorum</i> Hiern	s	5	5
37	Anacardiaceae	<i>Rhus glutinosa</i> Hochst. ex A.Rich.	t	5	5
38	Solanaceae	<i>Solanum schimperianum</i> Hochst.	h	5	3
39	Sapotaceae	<i>Spiniluma oxyacantha</i> (Baill.) Aubrev.	st	3	3

^a indicate plant life forms: climber (c), herb (h), shrub (s), tree (t), herb or shrub (hs), shrub or climber (sc), and shrub or tree (st).

The *Pterolobium stellatum*—*Celtis africana* community has the highest seedling density (Table 4.3) and seedling species richness ($F = 7.63$, $P = 0.001$) compared to the other communities, while the *Cadia purpurea*—*Opuntia ficus-indica* community has the lowest seedling density and richness. Seedling density is significantly increased with increasing basal area (Figure 4.5) suggesting that removal of canopy trees influences the natural regeneration.

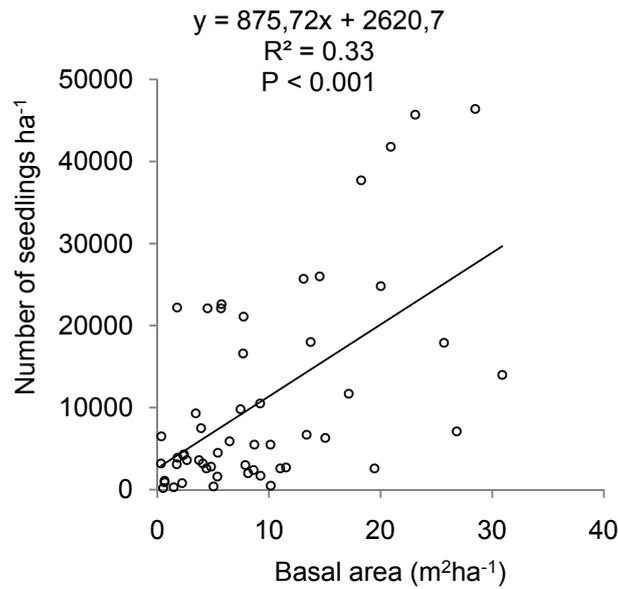


Figure 4.5 Relationship between basal area and seedling density in Hugumburda forest, northern Ethiopia.

Although *Juniperus procera* and *Olea europaea* subsp. *cuspidata* are the most dominant species in the standing vegetation, they are poorly represented in the seedling bank. The diameter distribution of the key native tree species also shows a truncated inverse-J shape (Figure 4.6) indicating that the forest is facing local extinction.

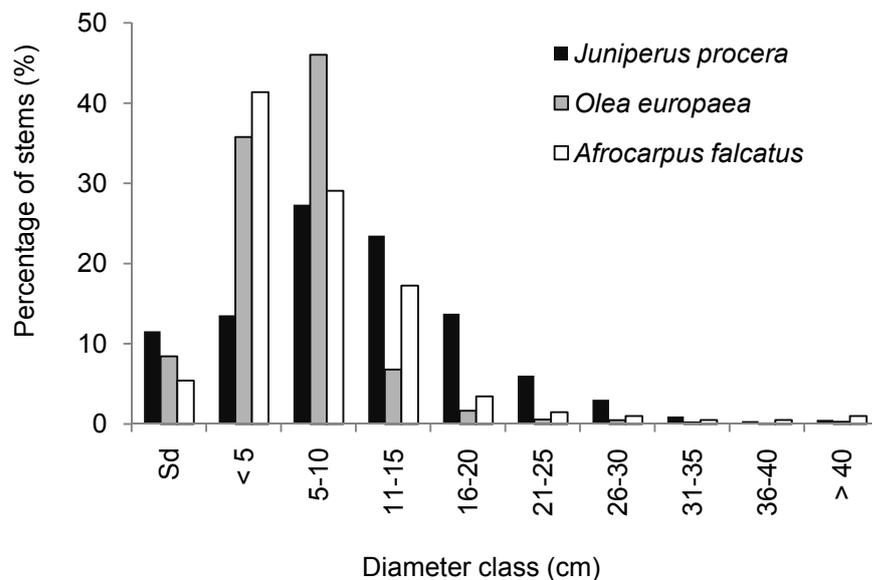


Figure 4.6 Diameter class distribution of the three native tree species in Hugumburda forest, northern Ethiopia. Sd = seedling.

4.4 Discussion

4.4.1 Floristic composition and diversity

Comparison of species richness in tropical and subtropical dry forests is difficult due to the inherent heterogeneity of the forests (Murphy and Lugo 1986). However, to give a general picture of the species richness of Hugumburda forest, the results of the present study are compared with results from other forests in Ethiopia. Accordingly, Hugumburda forest is less species rich, especially in tree species, than many other Afromontane forests, e.g., Wof-Washa (Teketay 1997), Jibat (Bekele 1994), Harena and Berhane-Kontir (Senbeta and Denich 2006), peninsula of Zegie (Alelign et al. 2007), and Yayu (Gole et al. 2008). However, Hugumburda forest is more species rich than small Afromontane forest fragments in Tigray (Aerts et al. 2006c), which may be due to its larger area (Hill and Curran 2003), the relatively higher rainfall (Linder 2001), and lower extent of degradation (Dos-Santos et al. 2007) at Hugumburda forest. Compared to Desa'a forest (Aynekulu et al. 2009), which is another natural forest remnant in Tigray, Hugumburda forest has a higher species density (number of species per unit area). This could be partly due to higher rainfall and less disturbance.

The species-area relationship provides useful information for planning biodiversity conservation (Ney-Nifle and Mangel 2000; Veech 2000). For instance, it can be used to identify patterns of species diversity (Condit et al. 1996; He and Legendre 2002) and to estimate rate of species extinction due to habitat loss (Pimm and Raven 2000). It varies with the diameter classes used (Condit et al. 1996), species resources requirement, competition, and species pool (Tjørve 2003). The species-area relationship at Hugumburda forest is well explained by a power function that is common in many forests (Tjørve 2003). The species-area curve, however, does not show an asymptotic behaviour due to the presence of many rare species, and species with narrow habitat ranges (Condit et al. 1996). The increasing trend in the number of species with increasing area suggests that a reduction in forest area may cause species loss (Ney-Nifle and Mangel 2000).

The stand basal area at Hugumburda forest ($9.23 \text{ m}^2 \text{ ha}^{-1}$) is far less than that of other tropical and subtropical dry forests ($17\text{-}40 \text{ m}^2 \text{ ha}^{-1}$) (Murphy and Lugo 1986), which is evidence for the over-exploitation of the forest especially of tree species. The

stem density at Hugumburda (1218 stems ha⁻¹) forest is slightly higher than at Desa'a forest (741 stems ha⁻¹).

4.4.2 Plant communities

The plant communities in the study site can be broadly classified as dry and moist forest types (Figure 4.4). More specifically, the *Juniperus procera*—*Maytenus senegalensis* community is a dry single-dominant Afromontane forest with *Juniperus procera* and *Olea europaea* subsp. *cuspidata* as dominant species (Friis 1992). Other characterizing species are *Acokanthera schimperi*, *Euclea racemosa* subsp. *schimperi*, *Grewia ferruginea*, and *Rhus natalensis* (Friis 1992). These species also widely occurred in the *Juniperus procera*—*Maytenus senegalensis* community. The *Pterolobium stellatum*—*Celtis africana* forest community belongs to the undifferentiated Afromontane forests, which are moist forests. This forest type is commonly found in the plateaus of Shoa, Wello, Sidamo, Bale, and Hararghe with elevational ranging between 1500 and 2700 m, mean annual rainfall between 700 and 1100 mm, and average annual temperature between 14 and 20 °C (Friis 1992). Elevation, temperature, and rainfall ranges of Hugumburda forest are similar. *Afrocarpus falcatus*, *Allophylus abyssinicus*, *Celtis africana*, and *Bersama abyssinica* are some of the common species in the undifferentiated Afromontane forests (Friis 1992), which are also indicator species of the *Pterolobium stellatum*—*Celtis africana* community (Table 4.2). This plant community is rich in tree species (60 % of the indicator species), which partly represent the pre-disturbance forests in northern Ethiopia (Darbyshire et al. 2003).

The *Cadia purpurea*—*Opuntia ficus-indica* plant community can be classified as degraded shrub vegetation. All the indicator species are shrub species. In the degraded parts of Desa'a forest, *Cadia purpurea* occurs in association with *Tarchonanthus camphoratus* (see Chapter 5). The non-occurrence of *Tarchonanthus camphoratus* at Hugumburda forest may be due to the fact that Hugumburda forest is too moist. Thus, the expansion of *Cadia purpurea* in Hugumburda forest can be considered as an indicator of disturbance of the *Juniper-Olea*-dominated forests (Figure 4.7c).

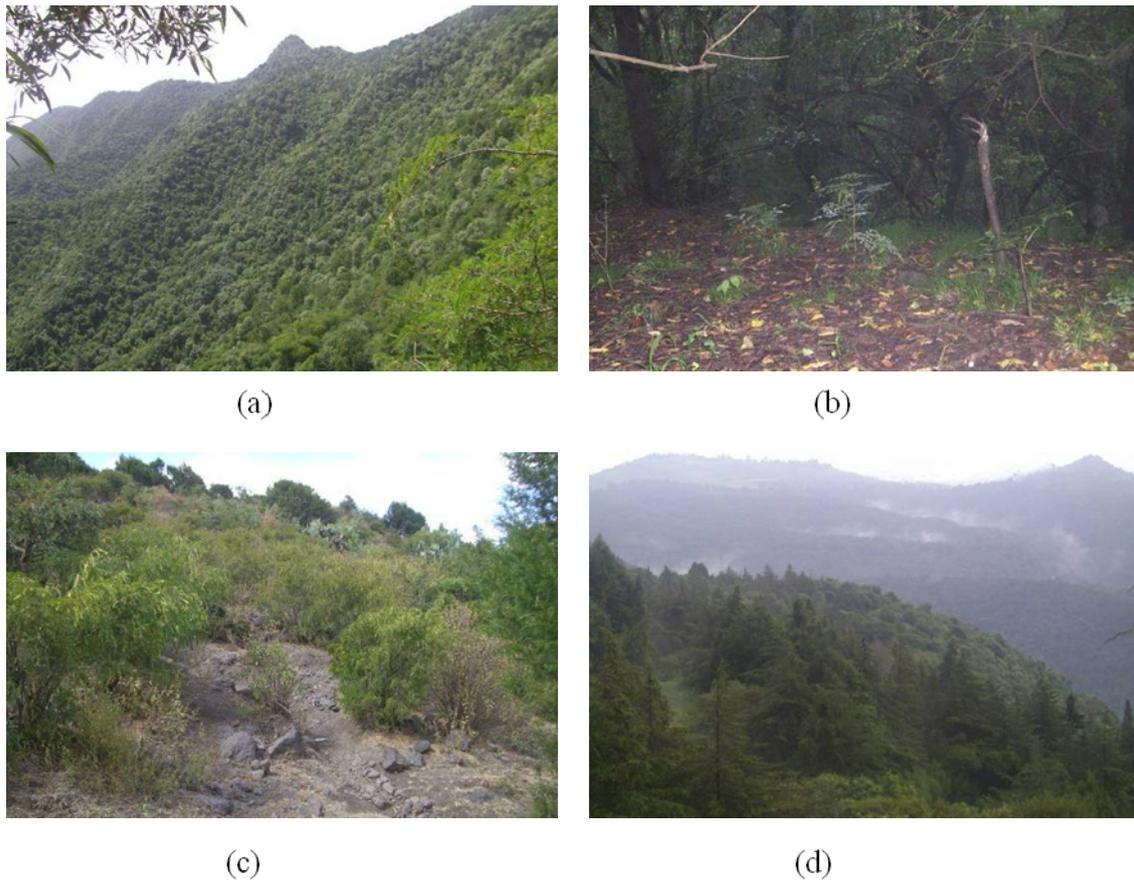


Figure 4.7 Plant communities at Hugumburda forest, (a) *Juniperus procera*—*Maytenus senegalensis*, (b) *Pterolobium stellatum*—*Celtis africana*, (c) *Cadia purpurea*—*Opuntia ficus-indica*, part of the *Cupressus lusitanica* plantation at the western edge of the forest (d) in Hugumburda forest, northern Ethiopia.

4.4.3 Ordination

The NMS ordination bi-plot (Figure 4.3) shows the association of species in three distinctive plant communities along the environmental gradients. The NMS axis 2 is significantly negatively correlated to elevation, slope, soil depth, and distance to the nearest stream, while positively correlated to topographical wetness index (Table 4.5). Generally, the NMS axis 2 interpreted as a moisture gradient that separates the dry (*Juniperus procera*—*Maytenus senegalensis* community) from the moist forest (*Pterolobium stellatum*—*Celtis africana* community). Elevation and slope are important environmental variables partitioning forest communities in Afromontane forests in Ethiopia (Woldu and Ingvar 1991; Bekele 1994; Aerts et al. 2006c; Gole et al. 2008). They do not have a direct effect on species distribution, but indirectly influence other environmental factors (e.g., edaphic and micro-climatic) (Bolstad et al. 1998). The

gentle slope at the lower elevation contributes to the formation of deep soils with a better moisture holding capacity (Hodgson 1978), and here the *Pterolobium stellatum*—*Celtis africana* community occurs (Table 4.4). The positive correlation between wetness index and NMS axis 2 indicates the occurrence of the *Pterolobium stellatum*—*Celtis africana* community in moister parts of the forest. Aerts et al. (2006c) also found a moist vegetation type along drainage lines in Tigray, which makes the riverine habitats important islands of moist forests in the dry-forest dominated landscapes of northern Ethiopia.

The steep slopes surrounding the stream lines may also create a humid microclimate by protecting the area from the dry warm air coming from the lowlands and the cold western highlands. Thus, the higher plant diversity in the *Pterolobium stellatum*—*Celtis africana* community may be due to higher site productivity created by such mild climate and deep and moist soils (Flombaum and Sala 2008) compared to the surrounding slopes where the other communities occur. Thus, the higher level of energy is one explanation for the higher species-richness in this community. A higher energy level stimulates greater biomass that enables more individuals and species to coexist (Gaston 2000).

Juniperus procera—*Maytenus senegalensis* and *Cadia purpurea*—*Opuntia ficus-indica* communities are largely found on the steep slopes, but significantly vary in their species composition. The two communities are clearly separated along the NMS axis 1, which is associated with disturbance. This suggests that the *Cadia purpurea*—*Opuntia ficus-indica* communities may not be an old vegetation type, but a recent succession that gradually replaced the *Juniper-Olea*-dominated forest following forest disturbance. The negative significant correlation between NMS axis 1 and basal area also suggests the influence of disturbance on community composition.

The low level of diversity in the *Juniperus procera*—*Maytenus senegalensis* and *Cadia purpurea*—*Opuntia ficus-indica* communities (Table 4.3) are due to the abundance and dominance of *J. procera* and *C. purpurea* in the two plant communities, respectively. The *Cadia purpurea*—*Opuntia ficus-indica* community has a lower species richness and diversity than the *Juniperus procera*—*Maytenus senegalensis* community, which could be due to the higher disturbance in the *Cadia purpurea*—*Opuntia ficus-indica* community. Disturbance affects species composition

and diversity by affecting certain species and size classes, and by changing the light environment of the understory (Slik 2004; Engelbrecht et al. 2007). The higher species diversity at the *Pterolobium stellatum*—*Celtis africana* community also correlates with the topographic wetness index. The higher species richness in the wetter site can be due to the increase in pH with increasing moisture that stimulates plant diversity (Zinko et al. 2006). The riverine systems are regulated by water and nutrient inputs from the upper slopes, which make them important areas of high species diversity, especially in dry environments.

4.4.4 Natural regeneration

A seedling bank is crucial for old forests because it provides individuals that will eventually influence the composition of future plant communities (Swine 1996). However, most of the seedlings of the native trees species like *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, *Rhus natalensis*, *Allophylus abyssinicus*, *Bersama abyssinica*, *Afrocarpus falcatus*, and *Teclea simplicifolia* are poorly represented in the seedling bank, while some other native species, namely *Erica arborea* and *Hagenia abyssinica* do not occur at all. Similar studies in other dry forest remnants of northern Ethiopia also report poor regeneration of native tree species (Aerts et al. 2006c; Aynekulu et al. 2009), suggesting that some species are experiencing local extinction.

Seedling density is highest in the *Pterolobium stellatum*—*Celtis africana* community (Table 4.2). This may be due to moister soils (Benítez-malvido and Martínez-ramos 2003) and less disturbance (Farwig et al. 2008). *Pterolobium stellatum* has the highest seedling abundance, which might be due to the canopy gaps created in the forest that encourage the spread of the species (Schnitzer et al. 2000). Although such climber species are important in the overall species diversity, they suppress the recruitment of other species (Schnitzer et al. 2000).

In dry tropical forests, tree canopies are favorable for germination and early establishment of seedling (Teketay 1997; Vieira and Scariot 2006; Wassie et al. 2009b). Basal area can be used as a surrogate for canopy cover. The positive correlation between seedling density and basal area (Figure 4.5) thus suggests that a reduction in canopy cover in dry environments may lead to soil desiccation, which hampers regeneration and seedling establishment of native tree species. Hence, a further increase

in canopy gaps in Hugumburda forest may favor the spread of pioneer shrub and herb species like *Cordia purpurea*, which may gradually replace the tree-dominated landscape with encroaching shrubs and herbs.

4.5 Implications for conservation

Three plant communities belonging to dry and moist forests were identified in Hugumburda forest. This indicates that topographical position (e.g., elevation, distance to the drainage line) and disturbance are important determinants of species distribution and community structure. These factors are important and need to be considered in the design of biodiversity conservation programs. The *Pterolobium stellatum*—*Celtis africana* community is more diverse and contains species (e.g., *Afrocarpus falcatus*, *Allophylus abyssinicus*, *Bersama abyssinica*, and *Celtis africana*) that are locally threatened in northern Ethiopia. Furthermore, this community is found in a narrower habitat range (e.g., elevation, slope, soil depth) than the other communities, which makes the rare tree species vulnerable to location extinction. In northern Ethiopia, such a relatively large habitat, rich in diversity and at the same time with rare species is very uncommon. Hugumburda forest at a landscape scale and the *Pterolobium stellatum*—*Celtis africana* community at a local scale are thus important species-rich areas for biodiversity conservation that need conservation priority.

Soil moisture is a major limiting factor for the regeneration of dry forest species. Thus, maintaining a high canopy cover may create a better soil moisture environment for a successful regeneration and seedling establishment. The removal of the canopy species also affects the regeneration of native species while favoring the spread of colonizing shrub and herb species. Poor representation of most of the native tree species in the seedling and sapling stages also suggests that the forest is experiencing extinction. Thus, to conserve such rare and isolated forests, it is important to (1) conserve the standing canopy species, and (2) complement the natural regeneration with enrichment planting.

5 PLANT SPECIES DIVERSITY PATTERN ALONG AN ELEVATIONAL GRADIENT ON THE WESTERN ESCARPMENT OF THE GREAT RIFT VALLEY, NORTHERN ETHIOPIA

5.1 Introduction

Understanding plant species distribution pattern along environmental gradients is crucial for the understanding of ecological processes and managing ecosystems (Naveh and Whittaker 1979; Woldu et al. 1989; Noss 1999; Lovett et al. 2000). The concept of identifying biodiversity-rich areas along environmental gradients has been used, for instance, as a criterion for biodiversity conservation priority setting (Myers 1988; Mittermeier et al. 1998; Breshears et al. 2005). Elevation is a complex environmental factor influencing the distribution patterns of plant species (Perrott and Hamilton 1981; Hegazy et al. 1998; Lovett et al. 2000; Sánchez-González and López-Mata 2005; Zhao and Fang 2006). Accordingly, elevation plays a major role in plant species diversity and floristic formations in Ethiopia (Woldu et al. 1989). Friis (1992) uses elevation as one major criterion for mapping the forests and forest trees of north-eastern tropical Africa.

The elevational pattern of species diversity is a function of ecological and evolutionary processes (Lomolino 2001). Elevation determines species distribution in montane systems by influencing area, climate, geographical isolation of montane communities, and feedback among zonal communities (Lomolino 2001). Larger ranges contribute to diversity by supporting large populations, which enhances speciation while reducing accidental extinction (Rosenzweig 1995). Climate is related to productivity in which diversity commonly peaks at the intermediate level of productivity (Kassen et al. 2000; Lomolino 2001). Elevation has been widely used as a predictor of regional species richness and diversity (Kreft and Jetz 2007) due to its influence on moisture and temperature (Gutierrez et al. 1998; Lovett et al. 2000; Eilu et al. 2004; Sánchez-González and López-Mata 2005). High-elevation habitats are more isolated from other similar habitats, which increases the rate of extinction. Species diversity peaks at the transition zone between two habitats and the respective plant communities (Lomolino 2001).

Studies have shown that response of plant species distribution to elevation varies among ecosystems (Hegazy et al. 1998; Kessler 2000; Lovett et al. 2000; Sánchez-González and López-Mata 2005; Grytnes and Beaman 2006). Furthermore,

different life forms may respond similarly (e.g., Sánchez-González and López-Mata 2005) or differently (e.g., Ren et al. 2006) to elevation. The response of species richness to elevation is also affected by the scale of the study, a hump-shaped pattern is commonly found when data is taken from an entire elevation range (Nogues-Bravo et al. 2008). With decreasing scale, a monotonic pattern is common. Generally, the hump-shaped species distribution pattern is more common than the monotonic decline with increasing elevation (Rahbek 1995). Besides the environmental factors, anthropogenic disturbance affect species diversity. According to the intermediate disturbance hypothesis (Connell 1978), intermediate disturbance promotes species diversity by facilitating regeneration of many species (Denslow 1980; Bongers et al. 2009). However, it is often difficult to determine the influence of the existing environmental factors and forest history on species assemblage (Mutke and Barthlott 2005).

The study site covers large parts of Desa'a forest. Desa'a forest is an important habitat for *Dracaena ombet*, which is listed on the IUCN endangered plant species list (World Conservation Monitoring Centre 1998), and locally rare tree species like *Erica arborea*. Desa'a forest is also an important bird habitat. It is the only habitat in Ethiopia for *Emberiza cineracea* (Bird Life International 2008), which is a migratory bird listed on the IUCN Red List as a Near Threatened species (IUCN 2009). According to Conservation International's (2007) lists of global biodiversity hotspots, the study site is located in the Eastern Afromontane hotspot (Tigray highlands) and the arid Horn of Africa hotspot (Afar lowlands).

Despite the high conservation value, the natural forest remnants in northern Ethiopia are poorly studied (Friis 1992; Aerts et al. 2006c), and information necessary for effective biodiversity conservation is meager (Aerts et al. 2006c). Therefore, the present study examines patterns of alpha and beta diversity, and community composition along an elevational gradient.

5.2 Material and methods

5.2.1 Study site

The study was conducted in the western escarpment of the Great Rift Valley that stretches from the highlands of Tigray to the lowlands of the Afar region in northern Ethiopia (Figure 5.1). Two transects were taken along the mesic Tigraean plateau to the

xeric Afar lowlands. The first transect stretches from Agoro village (Tigray highland, 2400 m a.s.l.; 13°40' N, 39°46') to Shaigubi village (Afar low land, 1000 m a.s.l.; 13°40' N, 39°52' E), and the second transect from Esot village on the Tigrean plateau (2760 m a.s.l., 13°56' N, 39°48' E) to Koneba town of the Afar region at its lower end (1400 m a.s.l.; 13°56' N, 39°51' E). Both transects cross Desa'a forest, which is one of the 58 national forest priority areas in Ethiopia. Unlike mountainous landscapes, the upper limit of the study area is a plateau, where land area per bioclimatic belt has no impact on vegetation distribution (Körner 2007).

Based on the classification of the forests and forest trees of northeast tropical Africa (Friis 1992), Desa'a forest is categorized as a dry single-dominant Afromontane forest, which is characterized by a dry climate (annual precipitation less than 1000 mm) with *Juniperus procera* and *Olea europaea* subsp. *cuspidata* as dominant species. A large part of the study area is formed on shale, limestone, and sandstone of the Tertiary and Mesozoic era (TFAP 1996). The diverse geological formations have led to soil variability, and the dominating soil types in the study region are Leptosols, Cambisols, Vertisols, Regosols and Arenosols (TFAP 1996). The study area receives a mean annual rainfall of 532 mm (Abegaz 2005). The climate of the study area is influenced by elevation in which the decline in rainfall and the increase in temperature from the upland plateau to the eastern slopes are sharp (Degefu 1987).

Plant species diversity pattern along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia

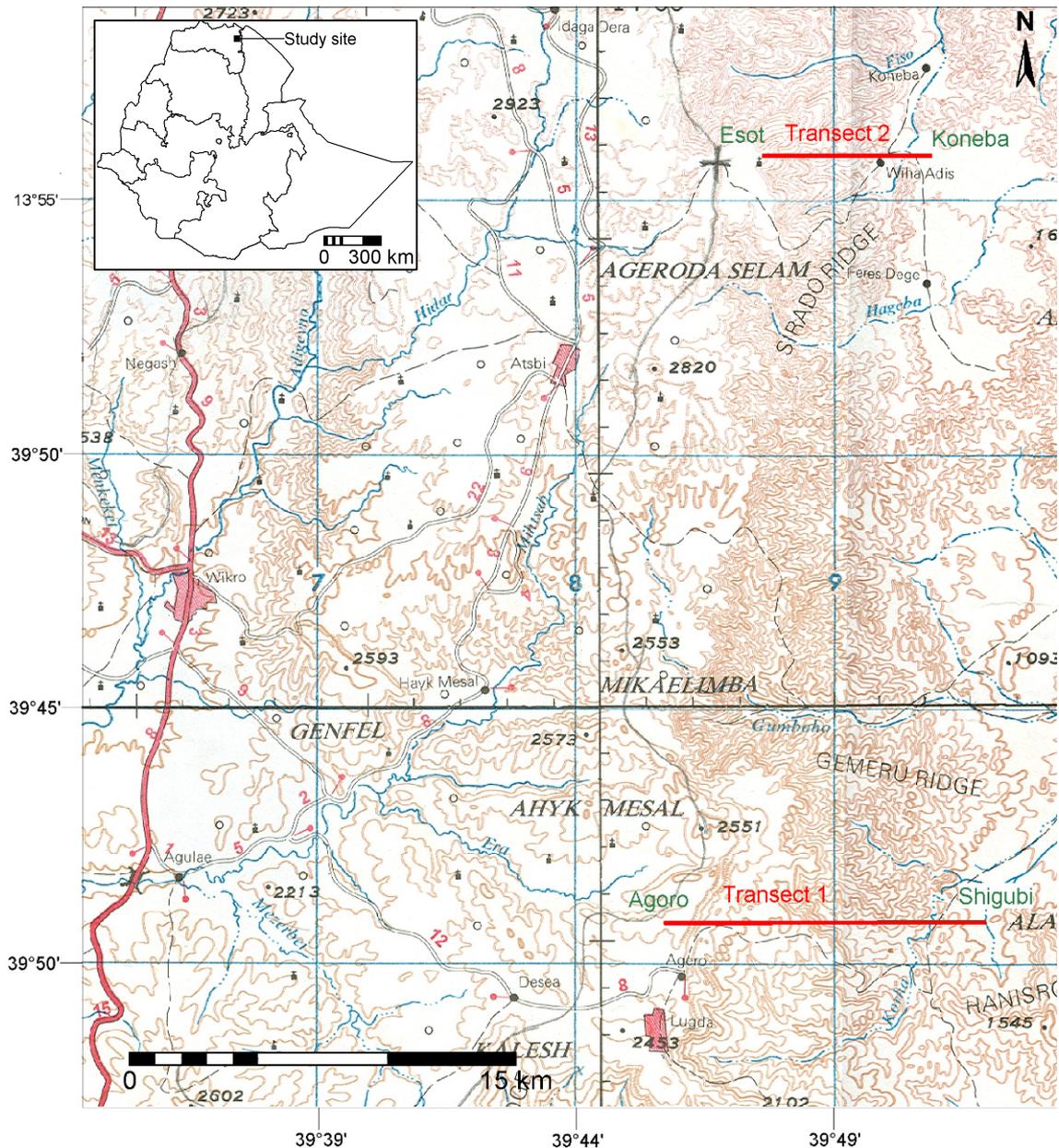


Figure 5.1 Location of the two studied transects on the western escarpment of the Great Rift Valley, northern Ethiopia.

5.2.2 Data collection

Data on the diversity of vascular plant species were collected from July to November 2007 in 29 plots (50 m × 50 m) established at 100-m elevation intervals, i.e., 14 plots in transect 1 and 15 plots in transect 2. However, species outside the 29 plots were also recorded to give a more complete list of species occurring in the study area. The sampling points were identified using 1:50000 topographic maps (EMA 1998), and the

transect layout and coordinates of the plots were identified using ILWIS GIS software (ITC 2001). Plots were identified in the field using a GPS device.

All individual plants were enumerated, and stand density and basal area per hectare for all trees with a height > 1.5 m and diameter > 2 cm at breast height (DBH) were calculated for each sampling plot. Species were identified in the field and at the National Herbarium, Addis Ababa University.

5.2.3 Data analyses

Species diversity

Species diversity (α -diversity) is determined using the Shannon diversity index. In this study, Whittaker's (1972) β -diversity (β_w) is used as a general indicator of species turnover (Eq. 5.1) and pair-wise comparisons of species turnover among plant elevational gradients and communities were determined using the Wilson and Shmida's (1984) β -diversity (Eq. 5.2).

$$\beta_w = \frac{Sc}{s} - 1 \quad (5.1)$$

where β_w is Whittaker's β -diversity, Sc is the total number of species in the composite sample (i.e. gamma diversity), and s is the average number of species found in the plots.

$$\beta_T = \frac{b+c}{2a+b+c} \quad (5.2)$$

where β_T is Wilson and Shmida's beta diversity, a is total number of species that occur in both communities, b is the total number of species in the second community but not in the focal one, and c is the number of species in the focal community but not in the second one.

Cluster analysis and ordination

Plant communities along the elevational gradient were identified using the multivariate hierarchical clustering and Nonmetric Multidimensional Scaling (NMS) (see section 4.2.3).

5.3 Results

5.3.1 Species composition and diversity along the elevational gradient

A total of 130 species belonging to 59 families was recorded (Table 5.1). Of these, 26 % are tree species, 55 % shrub species, 16 % are herb species and 3 % liana species. The 5 most species-rich families are Fabaceae (15 species), Lamiaceae (7 species), Euphorbiaceae, Solanaceae, and Tiliaceae (6 species each), while 33 families (56 %) are represented by one species. No species is distributed over the entire elevation range. The dominant tree, shrub and herb species with wider elevational ranges are *Olea europaea* subsp. *cuspidata* (1400—2760 m), *Cordia purpurea* (1100—2500 m) and *Aloe camperi* (1200—2760 m), respectively. The three most abundant species in the study area are *Cordia purpurea* (13 %), *Juniperus procera* (11 %) and *Olea europaea* subsp. *cuspidata* (7 %), which in total constitute 29 % of the total abundance.

Table 5.1 List of species and their occurrence along the elevational gradients in the western escarpment of the Great Rift Valley, northern Ethiopia

Species/Elevation (m a.s.l.)	LF	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600	2700	2760
<i>Abutilon longicuspe</i> Hochst. ex A.Rich.	s										x	x	x	x	x					
<i>Acacia abyssinica</i> Hochst. ex Benth.	t	x			x	x	x	x		x					x	x	x			
<i>Acacia asak</i> (Forssk.) Wild.	t		x			x														
<i>Acacia etbaica</i> Schweinf.	t				x	x	x	x	x	x			x		x					
<i>Acacia mellifera</i> Benth.	t	x	x	x	x	x														
<i>Acacia orfota</i> Schweinf.	t	x																		
<i>Acacia polyacantha</i> Willd.	t	x	x																	
<i>Acacia senegal</i> Willd.	t		x																	
<i>Acacia tortilis</i> Hayne	t			x																
<i>Acokanthera schimperi</i> (A.DC.) Benth. & Hook.f. ex Schweinf.	st				x	x	x	x	x	x	x	x	x	x	x	x	x	x		
<i>Adenia</i> sp.	st					x			x											
<i>Aerva lanata</i> (L.) Juss. ex Schult.	h						x													
<i>Aloe camperi</i> Schweinf.	h			x	x	x	x	x	x	x	x	x		x				x		x
<i>Alternanthera nodiflora</i> R.Br.	h																x	x		
<i>Asparagus racemosus</i> Willd.	hs										x	x	x	x	x		x			
<i>Balanites rotundifolius</i> Blatt.	t	x	x	x		x	x													

Plant species diversity pattern along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia

Table 5.1 continued

Species/Elevation (m a.s.l.)	LF *	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600	2700	2760
<i>Barbeya oleoides</i> Schweinf.	t																x			
<i>Becium grandiflorum</i> (Lam.) Pic.Serm.	s										x	x	x	x	x				x	
<i>Berchemia discolor</i> Hemsl.	st	x																		
<i>Boscia salicifolia</i> Oliv.	t								x		x									
<i>Cadia purpurea</i> Ait.	s		x		x	x	x	x	x	x	x	x	x	x	x	x				x
<i>Calpurnia aurea</i> Benth.	st							x	x	x	x	x	x	x	x	x	x			
<i>Canthium oligocarpum</i> Hiern	st				x	x	x			x	x	x	x	x	x	x	x		x	x
<i>Canthium setiflorum</i> Hiern	s										x	x	x	x	x					
<i>Capparis cartilaginea</i> Decne.	s		x																	
<i>Caralluma acutangula</i> N.E.Br.	h				x	x														
<i>Carissa edulis</i> Vahl	s								x	x		x	x	x	x	x	x			
<i>Clematis sinensis</i> Lour.	sc								x				x	x	x					
<i>Clerodendrum myricoides</i> R.Br.	s									x	x	x	x	x	x	x	x			
<i>Clutia abyssinica</i> Jaub. & Spach	s	x	x		x	x	x	x	x	x	x	x	x							
<i>Clutia lanceolata</i> Jaub. & Spach	s												x		x	x	x	x	x	x
<i>Combretum molle</i> R.Br. ex G. Don	st						x	x	x	x					x					
<i>Commicarpus plumbagineus</i> Standl.	s							x		x	x									
<i>Cordia monoica</i> Roxb.	st					x			x											
<i>Cordia sinensis</i> Lam.	st						x	x	x	x										
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	st		x					x	x	x	x									
<i>Diospyros mespiliformis</i> Hochst. ex A.DC	t							x	x	x	x	x	x							
<i>Dobera glabra</i> Juss. ex Poir.	t	x	x	x																
<i>Dodonaea viscosa</i> Jacq.	s									x	x		x	x		x	x	x		
<i>Dombeya torrida</i> (J.F. Gmel.) Bamps	t						x		x	x	x	x	x	x		x	x			
<i>Dovyalis abyssinica</i> (A.Rich.) Warb.	st															x	x	x		x
<i>Dovyalis verrucosa</i> Warb.	st															x	x	x		
<i>Dracaena ombet</i> Kotschy & Peyr.	t					x	x	x	x	x										
<i>Ekebergia capensis</i> Sparrm.	t								x		x	x	x		x					
<i>Euclea racemosa</i> Murray subsp. <i>schimperii</i> (A. DC.) F. White	s					x				x	x	x	x	x	x	x	x			
<i>Erica arborea</i> L.	st																			x
<i>Euphorbia polyacantha</i> Boiss.	s					x														
<i>Ficus palmata</i> Forssk.	st										x	x	x							
<i>Ficus thonningii</i> Blume	st											x					x	x		
<i>Ficus vasta</i> Forssk.	t								x											
<i>Grewia ferruginea</i> Hochst.	st				x	x		x	x	x	x	x	x							
<i>Grewia schweinfurthii</i> Burret	st				x	x														
<i>Grewia tenax</i> (Forssk.) Fiori	s					x	x		x	x			x							

Plant species diversity pattern along an elevational gradient on the western escarpment of
the Great Rift Valley, northern Ethiopia

Table 5.1 continued

Species/Elevation (m a.s.l.)	LF *	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600	2700	2760
<i>Heliotropium cinerascens</i> Steud. ex DC.	s				x		x	x	x		x	x								
<i>Indigofera caerulea</i> Roxb.	s		x		x	x														
<i>Jasminum abyssinicum</i> R.Br.	sc										x		x	x	x					
<i>Juniperus procera</i> Hochst. ex Endl.	t									x	x	x	x	x	x	x	x	x	x	x
<i>Laggera tomentosa</i> Sch. Bip. ex Hochst.	s									x	x	x	x			x	x	x	x	
<i>Lantana viburnoides</i> Vahl	s											x				x				
<i>Lavandula dentata</i> L.	h																			x
<i>Lawsonia inermis</i> L.	st		x																	
<i>Leucas abyssinica</i> Briq.	h								x	x	x	x	x	x	x		x			
<i>Lycium shawii</i> Roem. & Schult.	s				x	x	x	x	x											
<i>Maerua</i> sp.	sh						x													
<i>Maytenus senegalensis</i> (Lam.) Exell	st									x	x	x	x	x	x	x	x	x		x
<i>Mimusops laurifolia</i> (Forssk.) Friis	t		x	x	x	x														
<i>Myrsine africana</i> L.	s																x			
<i>Nuxia congesta</i> R.Br.	sh																x	x	x	x
<i>Olea capensis</i> L. subsp. <i>macrocarpa</i> (C.H. Wright) I. Verd.	t																x	x	x	x
<i>Olea europaea</i> L. subsp. <i>cuspidata</i> (Wall. ex G. Don) Cif.	t					x	x			x	x	x	x	x	x	x	x	x	x	x
<i>Osyris quadripartita</i> Salzm. ex Decne.	s										x	x	x		x	x	x	x		
<i>Otostegia fruticosa</i> Schweinf. ex Penz.	sh										x			x	x	x				
<i>Pappea capensis</i> Eckl. & Zeyh.	t		x				x	x	x	x	x									
<i>Pittosporum viridiflorum</i> Sims	t											x	x	x		x				
<i>Plectranthus ornatus</i> Codd	h														x			x	x	x
<i>Premna resinosa</i> Schauer	s	x	x			x	x	x	x	x		x								
<i>Psiadia punctulata</i> Vatke	h								x	x	x	x	x	x		x				
<i>Psydrax schimperiana</i> (A. Rich.) Bridson	st								x	x	x	x	x	x	x	x	x			
<i>Pterolobium stellatum</i> (Forssk.) Brenan	sc								x		x	x	x	x						
<i>Pyrostria phyllanthoidea</i> (Baill.) Bridson	s							x		x										
<i>Rhus natalensis</i> Bernh. ex Krauss	t					x	x	x	x	x	x	x	x	x	x	x	x			
<i>Rhus</i> sp.	t																x	x		x
<i>Ricinus communis</i> L.	st							x	x		x	x								
<i>Rumex nervosus</i> Vahl	h								x	x	x	x	x					x		
<i>Sageretia thea</i> (Osbeck) M.C.Johnst.	s											x								
<i>Salvadora persica</i> L.	st	x		x	x		x		x											
<i>Sansevieria ehrenbergii</i> Schweinf. ex Baker	h									x										
<i>Sarcostemma viminale</i> Wall. Ex Decene.	c				x	x		x		x	x	x	x							
<i>Solanum adoense</i> Hochst. ex A. Braun	h										x	x								
<i>Solanum schimperianum</i> Hochst.	h							x		x	x	x	x	x	x	x	x	x	x	x
<i>Spiniluma oxyacantha</i> (Baill.) Aubrev.	st											x	x	x	x	x				

Plant species diversity pattern along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia

Table 5.1 continued

Species/Elevation (m a.s.l.)	LF *	1000	1100	1200	1300	1400	1500	1600	1700	1800	1900	2000	2100	2200	2300	2400	2500	2600	2700	2760
<i>Sterculia africana</i> (Lour.) Fiori	t				x		x													
<i>Tarchonanthus camphoratus</i> L.	sh						x			x	x	x	x	x	x	x	x			
<i>Tephrosia interrupta</i> Hochst. & Steud.	s				x				x	x										
<i>Withania somnifera</i> (L.) Dunal	s							x	x		x		x							
<i>Ziziphus mucronata</i> Willd.	st	x	x		x				x											
<i>Ziziphus spina-christi</i> Willd.	st							x												
Species identified outside the plots																				
<i>Abutilon pannosum</i> (G.Forst.) Schltld.	hs														x	x	x			
<i>Aeonium leucoblepharum</i> Webb ex A. Rich.	s														x					
<i>Agave americana</i> L.	h																			x
<i>Bersama abyssinica</i> Fresen.	t																			x
<i>Capparis tomentosa</i> Lam.	st		x																	
<i>Cassia occidentalis</i> L.	h						x													
<i>Cassipourea malosana</i> Alston	t																			x
<i>Commelina</i> sp.	s											x								
<i>Commiphora</i> sp.	t			x																
<i>Cyathula cylindrica</i> Moq.	h											x		x		x				x
<i>Cynanchum gerrardii</i> (Harv.) Liede	c															x				x
<i>Discopodium penninervium</i> Hochst.	st																			x
<i>Echinops giganteus</i> A.Rich.	sh														x		x			x
<i>Euphorbia abyssinica</i> J.F. Gmel.	t															x	x			x
<i>Euphorbia tirucalli</i> Forssk..	st						x	x								x				
<i>Ferula communis</i> Heuff.	h																x			x
<i>Grewia kakothamnus</i> K.Schum.	s					x			x	x	x	x					x			
<i>Grewia bicolor</i> Juss.	st						x		x		x									
<i>Grewia mollis</i> Juss.	st						x	x		x										
<i>Gymnosporia senegalensis</i> Loes.	s														x	x	x			x
<i>Indigofera arrecta</i> Hochst. ex A.Rich.	s																			x
<i>Meriandra bengalensis</i> (Roxb.) Benth.	s																x	x		x
<i>Opuntia ficus-indica</i> (L.) Mill.	st										x	x	x	x	x	x	x			x
<i>Otostegia integrifolia</i> Benth.	s																			x
<i>Phytolacca dodecandra</i> L'Hér.	s									x	x	x	x							
<i>Rhamnus staddo</i> A.Rich.	st																			x
<i>Rhus retinorrhoea</i> Steud. ex Oliv.	t															x	x			x
<i>Rosa abyssinica</i> R.Br.	s																			x
<i>Sansevieria forskaliana</i> (Schult.f.)Hepper & J.R.I.Wood	h									x	x	x	x	x						
<i>Sida schimperiana</i> Hochst. ex A.Rich.	s																			x
<i>Solanum incanum</i> L.	h				x	x		x	x	x	x	x	x	x	x	x	x			
<i>Vernonia amygdalina</i> Delile	st																			x

* LF = Life form: climber (c), herb (h), shrub (s), tree (t), herb or shrub (hs), shrub or climber (sc), and shrub or tree (st)

The mean stem density is 548 stems ha⁻¹ and basal area is 10.73 m² ha⁻¹. Stem density and basal area increase with increasing elevation (Figure 5.2).

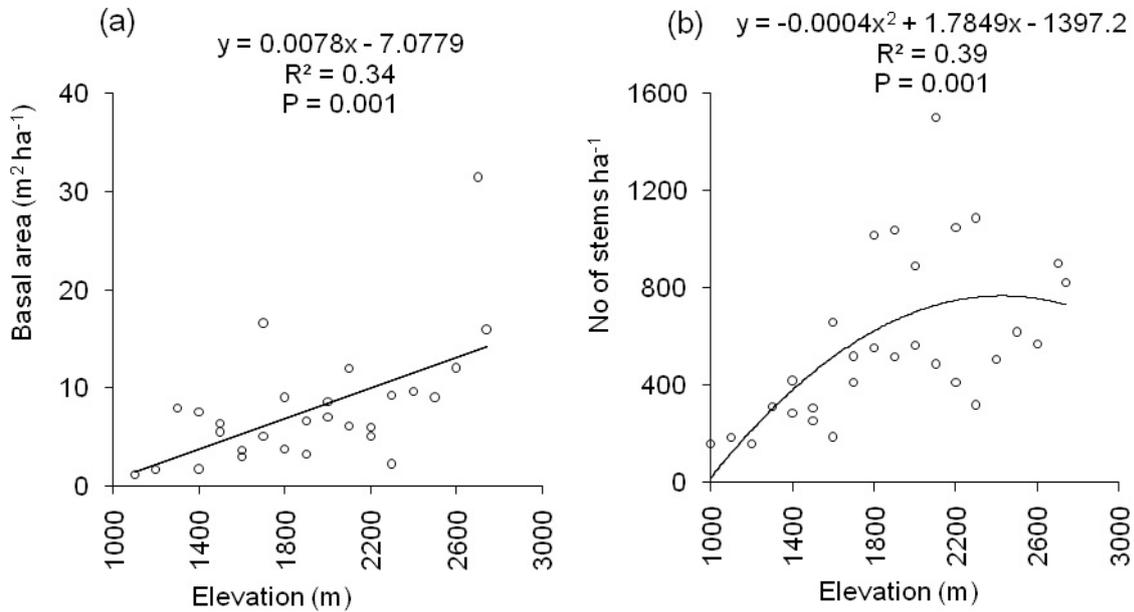


Figure 5.2 Patterns of stem density (a) and basal area (b) along elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia.

The minimum species richness (7 species per plot) was recorded at the lower elevation (1200 m), whilst the highest (42 species per plot) was recorded at the upper mid elevation (1900 m). The Shannon diversity index ranges from 0.80 to 3.08 (average = 2.32) at 2760 and 2100 m, respectively. Species evenness is highest at the lower elevation (1000–1300 m a.s.l), while values are lowest at high elevations (> 2600 m a.s.l).

Total species richness and diversity follow a hump-shaped distribution pattern along the elevational gradient, which is best explained by second-order polynomial models (Figure 5.3).

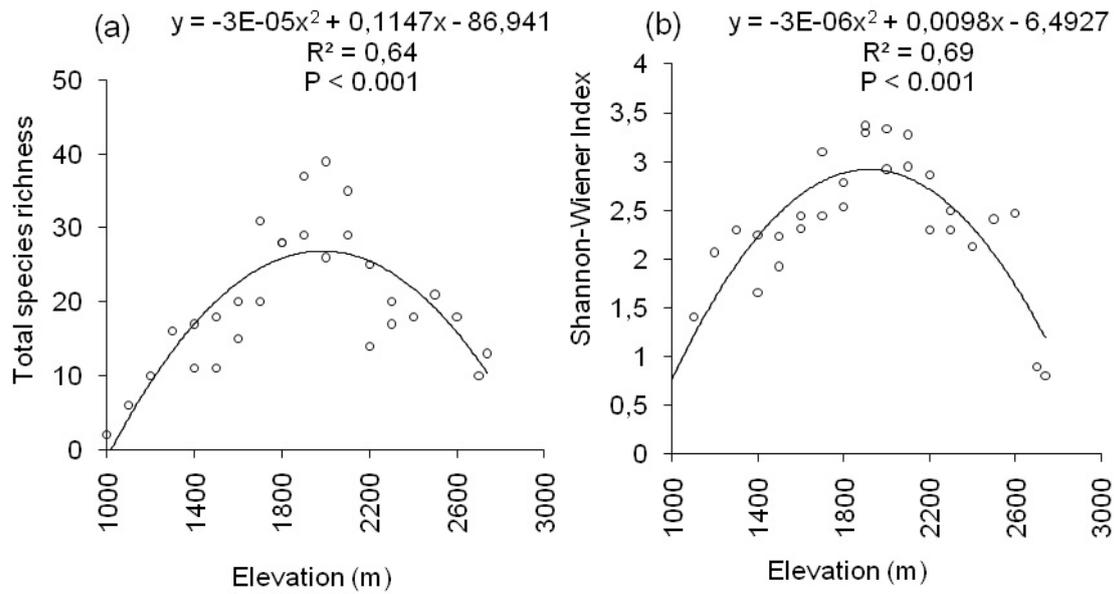


Figure 5.3 Patterns of species richness (a) and diversity (b) along an elevational gradient in the western escarpment of the Great Rift Valley, northern Ethiopia.

5.3.2 Species turnover along an elevational gradient

The Whittaker's ($\beta_w = 2.7$) and the mean Wilson and Shmida's ($\beta_T = 0.6$) β -diversity values indicate medium species turnover along the elevational gradient (Wilson and Shmida 1984). Wilson and Shmida's β -diversity ranges from 0.18 to 1.0, which indicates the highest and lowest species turnover, respectively (Table 5.2). The lowest β diversity is between extreme elevation pairs (e.g., between 1000 and 2760 m a.s.l.) where a 100 % species replacement was recorded.

The values of β -diversity indicate that none of the elevational zones have all identical species composition. The lowest β -diversity ($\beta_w = 0.18$) is between 1900 and 2100 m where α -diversity is maximum. This suggests that the maximum species richness found at mid elevation is partly due to low species turnover. Similarly, the highest diversity of plant families is between 1900 and 2100 (Figure 5.4). The highest β -diversity at the lower elevation indicates poor floristic similarities between adjacent sites, which contribute to poor species richness.

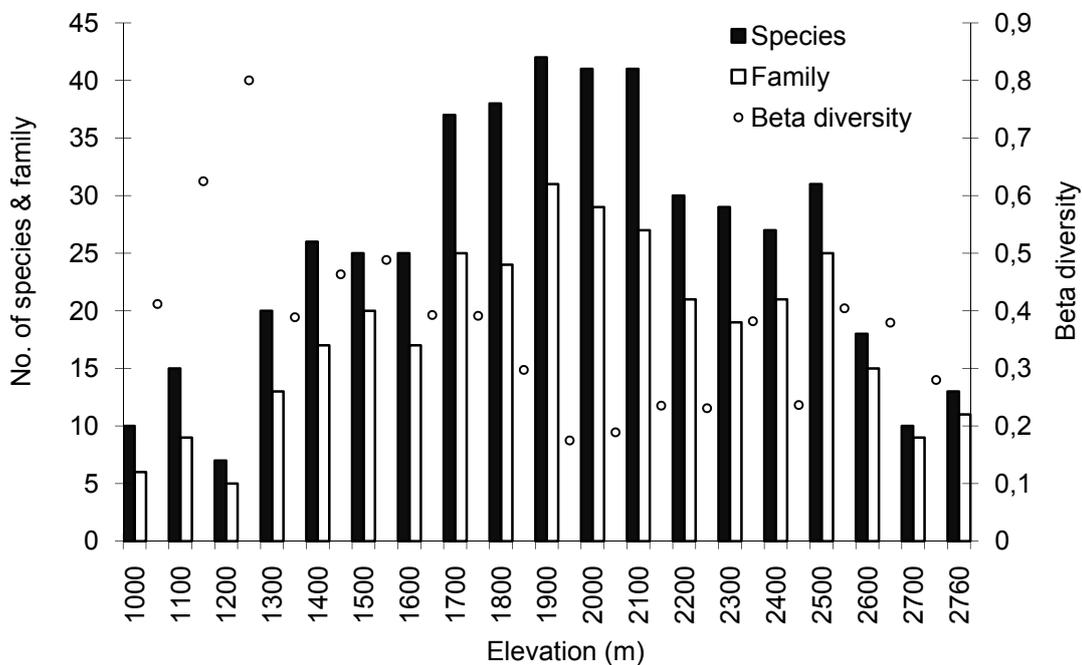


Figure 5.4 Trends in α - and β -diversities along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia. Species turnover between adjacent elevations is based on the Wilson and Shmida's β -diversity.

5.3.3 Plant communities

The cluster and indicator species analyses yield four plant communities (Figure 5.5). The MRPP test indicates a significant difference in the floristic compositions among the four plant communities ($T = -8.97$, $P < 0.001$). The homogeneity within-groups (Chance-corrected within-group agreement, A) is 0.25. In community ecology, values

for *A* are commonly below 0.1, while values exceeding 0.3 are considered as fairly high (McCune and Grace 2002).

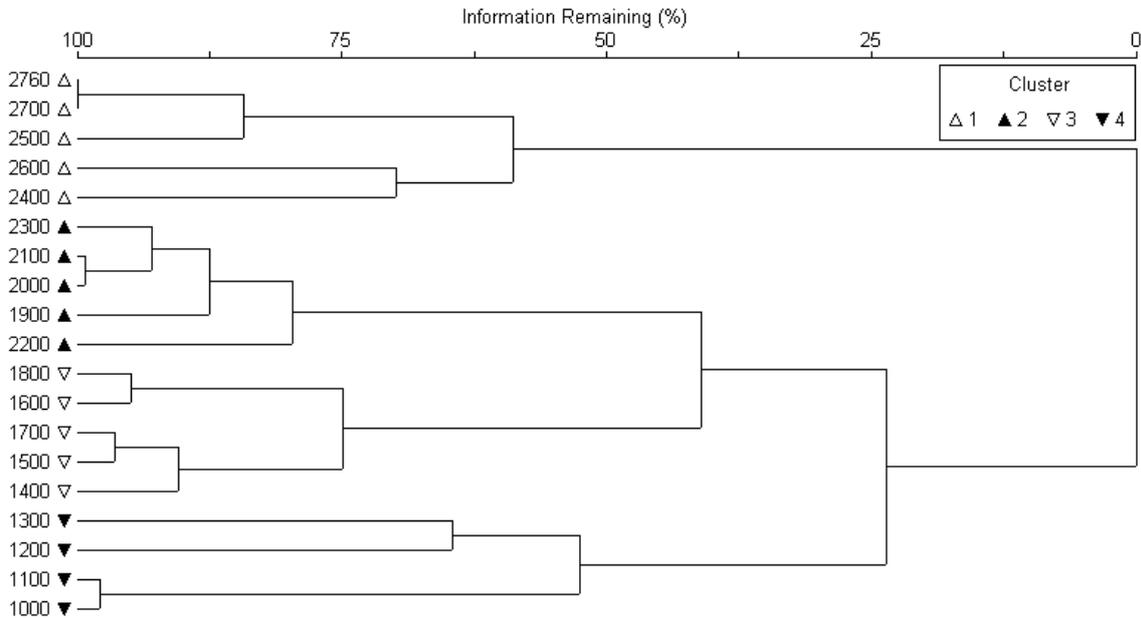


Figure 5.5 Dendrogram of the hierarchical cluster analysis of sampling points taken along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia. By cutting the dendrogram at the 53 % information remaining level, four distinctive plant communities along the 1760 m elevation gradient were identified (C1: 2760, 2700, 2600, 2500, 2400; C2: 2300, 2200, 2100, 2000, 1900; C3: 1800, 1700, 1600, 1500, 1400; C4: 1300, 1200, 1200, 1100).

The *Juniperus procera*—*Clutia lanceolata* community (C1) is found on Tigrean plateau, the *Abutilon longicuspe*—*Calpurnia aurea* plant community (C2) and the *Dracaena ombet*—*Acacia etbaica* plant community (C3) are found on escarpment, and the *Acacia mellifera*—*Dobera glabra* is found on the low plains of the Afar area (Figure 5.6).

Plant species diversity pattern along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia

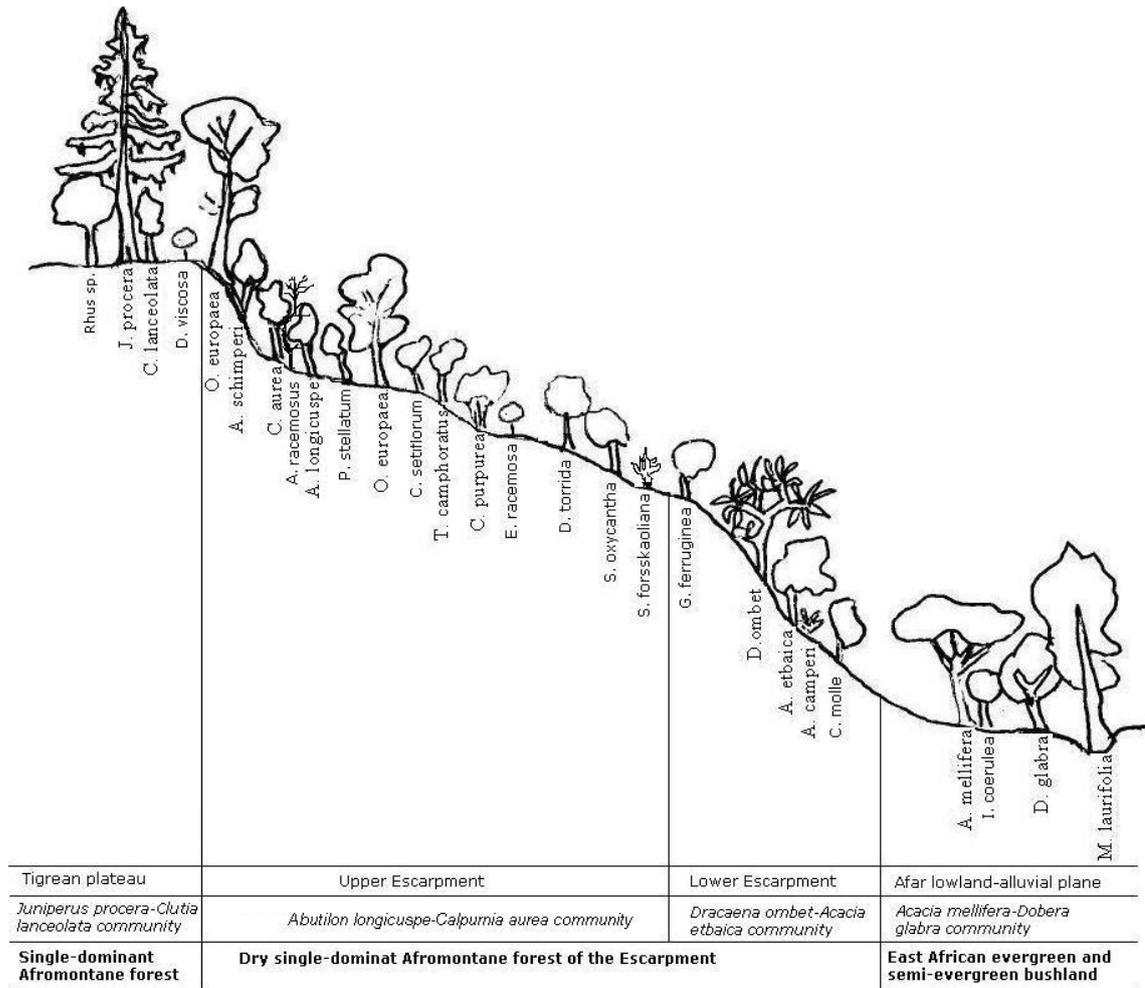


Figure 5.6 Vegetation profile along elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia.

The *Juniperus procera*—*Clusia lanceolata* plant community (C1) contains 42 species and 9 species have significant indicator values ($P < 0.05$) (Table 5.3). *Juniperus procera* is the dominant canopy tree species (Figure 5.7a), while *Clusia lanceolata* dominates the understory. *Cordia purpurea* and *Juniperus procera* constitute 51 % of the total abundance in the community. The *Juniperus procera*—*Clusia lanceolata* community contains 29 families. Lamiaceae and Fabaceae are the dominant families represented by 5 and 3 species, respectively. Seven families were represented by 2 species and the remaining 20 species are represented by one species.

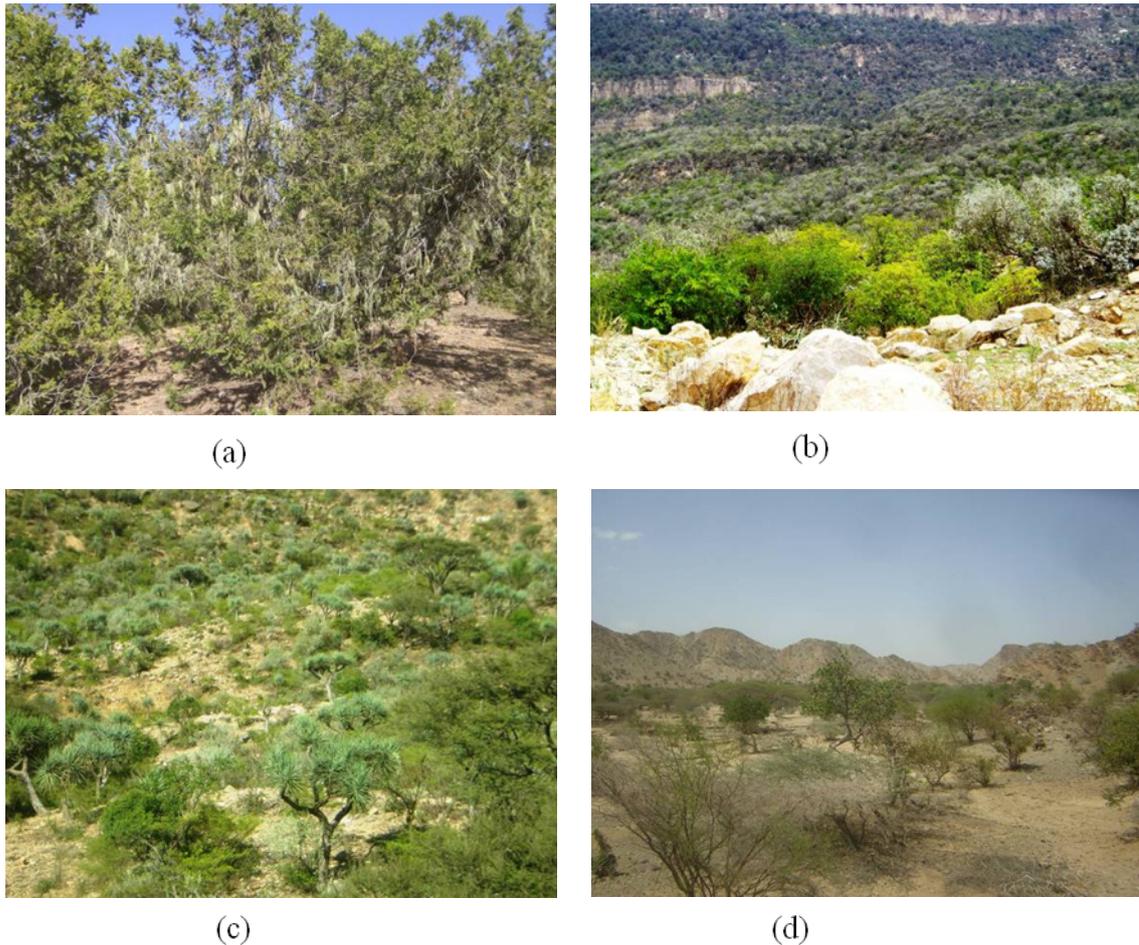


Figure 5.7 Pictures showing the four plant communities: *Juniperus procera*—*Clusia lanceolata* (a), *Abutilon longicuspe*—*Calpurnia aurea* (b), *Dracaena ombet*—*Acacia etbaica* (c), and *Acacia mellifera*—*Dobera glabra* (d) identified on the western escarpment of the Great Rift Valley, northern Ethiopia.

The *Abutilon longicuspe*—*Calpurnia aurea* plant community (C2) is represented by 56 species belonging to 32 families. The dominant tree species in this plant community is *Olea europaea* subsp. *cuspidata*, which is one of the dominant species in the dry Afromontane forests of Ethiopia. The plant community includes many shrub and herb species. *Cordia purpurea* and *Tarchonanthus camphoratus* are abundant shrubs colonizing many of the degraded sites (Figure 5.7b). Fabaceae and Lamiaceae are represented by 6 and 5 species, respectively. Three families are represented by 3, and 9 families by 2 species, while the remaining 18 families are represented by one species.

The *Dracaena ombet*—*Acacia etbaica* plant community (C3) is represented by 64 species belonging to 35 families. Except for a few scattered *Acacia etbaica* trees, this plant community is dominated by shrub and herb species (Figure 5.7c). *Dracaena ombet* is listed on the IUCN endangered species list (World Conservation Monitoring Centre 1998). The species is confined to a small area along the escarpment on shallow soils and has been widely used for fibre and beehive production as well as for household utensils. The Fabaceae is the dominant family represented by 10 species. Six and 8 families are represented by 3 and 2 species, respectively, while the remaining 20 species are represented by one species.

The *Acacia mellifera*—*Dobera glabra* plant community is represented by 31 species belonging to 18 families. This plant community has indicator species like *Dobera glabra*, which is an evergreen tree on the low lying Afar plains, and *Mimusops laurifolia* which is commonly found along major drainage lines. Floristically, the plant community is dominated by *Acacia mellifera*, which constitutes 31 % of the total species abundance (Figure 5.7d). Fabaceae is the dominant family represented by 12 species (39 %). Salvadoraceae and Tiliaceae are represented by 2 species while the remaining 15 families are represented by one species.

The *Dracaena ombet*—*Acacia etbaica* plant community is more species rich than the other communities. However, the *Abutilon longicuspe*—*Calpurnia aurea* community has a higher Shannon index value, which is due to a higher evenness of species composition. Although there is little difference in species richness between the *Juniperus procera*—*Clutia lanceolata* and the *Acacia mellifera*—*Dobera glabra* communities, the latter is more species rich.

The species turnover rates between C1—C2, C2—C3, and C3—C4 is 0.50, 0.35, and 0.47, respectively. This indicates that the species turnover between *Abutilon longicuspe*—*Calpurnia aurea* and *Dracaena ombet*—*Acacia etbaica* is lower than between any other pair of the plant communities.

Plant species diversity pattern along an elevational gradient on the western escarpment
of the Great Rift Valley, northern Ethiopia

Table 5.3 Summary statistics for the indicator species of the four plant communities on
the western escarpment of the Great Rift Valley, northern Ethiopia.

Species	Indicator Value (%)				P
	C1	C2	C3	C4	
<i>Juniperus procera</i>—<i>Clutia lanceolata</i>					
community (C1) (2400-2760 m)					
<i>Juniperus procera</i>	82	18	0	0	0.002
<i>Clutia lanceolata</i>	81	8	0	0	0.002
<i>Dovyalis abyssinica</i>	80	0	0	0	0.004
<i>Nuxia congesta</i>	80	0	0	0	0.005
<i>Olea capensis</i> subsp. <i>macrocarpa</i>	80	0	0	0	0.005
<i>Rhus</i> sp.	80	0	0	0	0.004
<i>Dovyalis verrucosa</i>	60	0	0	0	0.040
<i>Meriandra bengalensis</i>	60	0	0	0	0.040
<i>Rhus retinorrhoea</i>	56	1	0	0	0.031
<i>Abutilon longicuspe</i>—<i>Calpurnia aurea</i>					
community (C2) (1900-2300 m)					
<i>Abutilon longicuspe</i>	0	100	0	0	< 0.001
<i>Calpurnia aurea</i>	0	97	2	0	< 0.001
<i>Canthium setiflorum</i>	1	97	0	0	< 0.001
<i>Asparagus racemosus</i>	5	88	0	0	< 0.001
<i>Tarchonanthus camphoratus</i>	1	87	5	0	< 0.001
<i>Becium grandiflorum</i>	3	84	0	0	0.001
<i>Clerodendrum mxicoides</i>	0	82	3	0	0.001
<i>Jasminum abyssinicum</i>	0	80	0	0	0.004
<i>Pterolobium stellatum</i>	0	78	1	0	0.006
<i>Leucas abyssinica</i>	0	77	9	0	0.002
<i>Ekebergia capensis</i>	0	77	1	0	0.004
<i>Solanum schimperianum</i>	16	77	1	0	0.008
<i>Euclea racemosa</i> subsp. <i>schimperi</i>	2	73	8	0	0.001
<i>Psydrax schimperiana</i>	10	72	1	0	0.007
<i>Cadia purpurea</i>	0	71	27	1	0.002
<i>Canthium oligocarpum</i>	16	71	4	1	0.007
<i>Psiadia punctulata</i>	1	66	6	0	0.011
<i>Olea europaea</i> subsp. <i>cuspidata</i>	33	64	2	0	0.019
<i>Solanum incanum</i>	7	63	14	0	0.005
<i>Sansevieria forskaliana</i>	0	63	4	0	0.018
<i>Opuntia ficus-indica</i>	0	60	0	0	0.037
<i>Dombeya torrida</i>	3	57	12	0	0.026
<i>Acokanthera schimperi</i>	0	54	37	2	0.028
<i>Spiniluma oxyacantha</i>	7	54	0	0	0.029
<i>Dracaena ombet</i>—<i>Acacia etbaica</i> community (C3)					
(1400-1800 m)					
<i>Dracaena ombet</i>	0	0	100	0	< 0.001
<i>Acacia etbaica</i>	0	1	97	0	< 0.001

Plant species diversity pattern along an elevational gradient on the western escarpment
of the Great Rift Valley, northern Ethiopia

Table 5.3 continued

Species	Indicator Value (%)				P
	C1	C2	C3	C4	
<i>Premna resinosa</i>	0	0	82	8	0.002
<i>Cordia sinensis</i>	0	0	80	0	0.006
<i>Lycium shawii</i>	0	0	75	2	0.012
<i>Aloe camperi</i>	1	11	71	4	0.020
<i>Grewia tenax</i>	0	2	71	0	0.009
<i>Combretum molle</i>	0	3	69	0	0.012
<i>Pappea capensis</i>	0	2	65	3	0.009
<i>Grewia ferruginea</i>	0	8	62	2	0.024
<i>Grewia mollis</i>	0	0	60	0	0.035
<i>Clusia abyssinica</i>	0	15	59	13	0.007
<i>Acacia mellifera</i>—<i>Dobera glabra</i> community (C4)					
(1000-1300 m)					
<i>Acacia mellifera</i>	0	0	0	98	< 0.001
<i>Dobera glabra</i>	0	0	0	75	0.003
<i>Ziziphus mucronata</i>	0	0	3	65	0.017
<i>Mimusops laurifolia</i>	0	0	4	58	0.016
<i>Acacia polyacantha</i>	0	0	0	50	0.034

Ordination

In the NMS ordination, the greatest reduction in ‘stress’ (McCune and Mefford 1999) is achieved with a three-dimensional solution. The proportion of variance (coefficient of determination R^2) for the correlation between ordination distances and Sørensen distance in the original 40-dimensional space represented by the two axes is 0.545 and 0.231, respectively (cumulative $R^2 = 0.776$). The NMS axis 1 is strongly correlated with elevation (Spearman rank correlation = 0.98, $P < 0.001$), which clearly partitions the four plant communities (Figure 5.8).

Plant species diversity pattern along an elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia

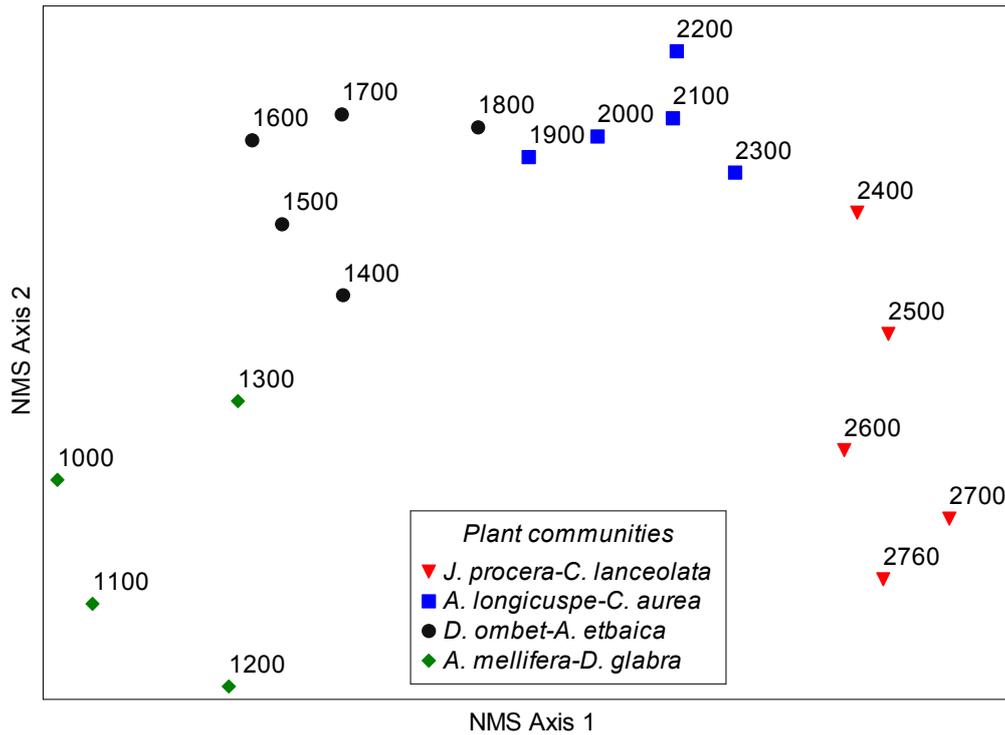


Figure 5.8 Nonmetric multidimensional scaling (NMS) ordination bi-plot showing the composition of plant communities along elevational gradient on the western escarpment of the Great Rift Valley, northern Ethiopia. Numbers indicate elevations labeled into the four groups derived by cluster and indicator species analyses.

NMS axis 1 exhibited positive linear relationship with elevation (Figure 5.9) suggesting that the distribution pattern of plants on the western escarpment in northern Ethiopia is strongly associated with elevation.

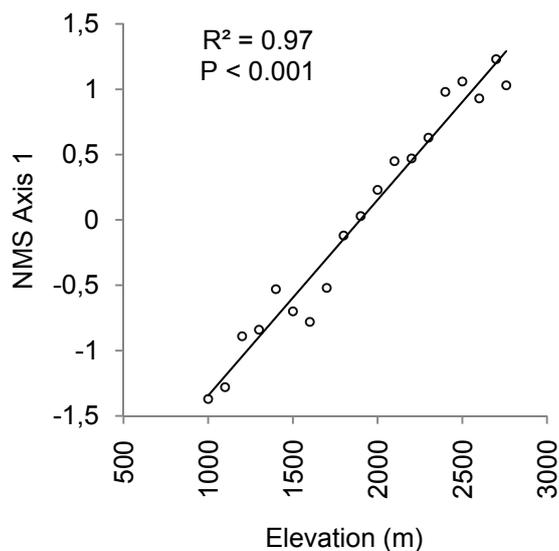


Figure 5.9 Relationship between elevation and NMS axis 1, on the western escarpment of the Great Rift Valley, northern Ethiopia.

5.4 Discussion

5.4.1 Species composition and diversity along an elevational gradient

The vegetation cover in the study site is dominated by shrub and herb species. One reason for the observed low tree species diversity is selective logging of some useful tree species (Gebreegziabher 1999). *Erica arborea*, for instance, used to be logged for its good fuelwood value, and currently it is one of the rare tree species in the highlands of Tigray. Many *Acacia* species in the lowlands have been also extensively logged for fuelwood and charcoal production. Such anthropogenic induced changes in the abundance and spatial distribution of species affect diversity (Hillebrand et al. 2008). Furthermore, the widening of canopy gaps that arises from deforestation and livestock pressure in the study area has hampered the regeneration and recruitment of shade-loving tree species (Aynekulu et al. 2009), which has led to a high diversity of pioneer species (Runkle 1982; Bongers et al. 2009).

The hump-shaped pattern of species diversity along the elevational gradient is partly evidence for a wider range of elevational gradient covered in the study (Mittelbach et al. 2001; Nogues-Bravo et al. 2008). As reviewed by Mittelbach et al. (2001), the hump-shaped distribution of species richness along an elevational gradient is the most frequent pattern (41-45 %). Elevation influences species distribution through its influence on precipitation and temperature (Lovett et al. 2000; Whittaker et al. 2001; Sánchez-González and López-Mata 2005; Zhao and Fang 2006). Such relationship

between diversity and climate is often associated with productivity (Whittaker et al. 2003). The decrease in species richness at higher elevations may be due to the decrease in temperature, which may reduce productivity (Rahbek 1995). Soil moisture is also another limiting factor in species richness and diversity in dry forests (Engelbrecht et al. 2007). Hence, the higher diversity of plants recorded at the mid elevation is likely due to the optimum climatic conditions that allow many species to coexist (Oommen and Shanker 2005; Hemp 2006). Besides environmental variables, the distribution of a species across different habitats also depends on species requirements, tolerances, and their efficiency in utilizing environmental resources (Dansereau 1951). The lower Shannon index at higher elevation was due to the higher abundance of *Juniperus procera*, which reduces the evenness of species distribution.

Due to the variation in the environmental conditions and forest disturbance history, it is difficult to compare species response to elevation among sites (Nogues-Bravo et al. 2008). The heterogeneity in sampling techniques used in such ecological studies also makes it difficult to compare studies (Rahbek 1995). The species richness along an elevational gradient in the study area is in agreement with that of the forest and forest trees of northeast tropical Africa, where Friis (1992) observed the highest diversity of species and families between 1523 and 2135 m a.s.l. The species richness and diversity along an elevational gradient in the study area also shows a similar pattern to those studies in Lokapel Turkana, Kenya (Mwaura and Kaburu 2009), Shennongjia Mountain, China (Zhao and Fang 2006), Guandi Mountain, China (Jun-feng and Yun-xiang 2006), and western Himalaya (Oommen and Shanker 2005).

5.4.2 Species turnover along an elevational gradient

The values of β diversity indicate that none of the elevational zones are identical in their species composition. The highest species turnover was recorded between the extreme elevational zones. This is logical that the elevation below 1300 m and above 2000 m are found in a different ecological zones that leads to maximum ($\beta_w=1$) variation in their species compositions. The lower β diversity ($\beta_w = 0.18$) was recorded between 1900 and 2100m where α diversity is maximum. This suggests, the maximum species richness found between 1900-2100, is partly due to high species turnover between these adjacent elevations. Similarly, the highest diversity of plant families was recorded

between 1900—2100 (Table 1). The highest β diversity at the lower elevation indicates poor floristic similarities between adjacent sites which contribute for poor species richness. Contrarily, the β diversity at the higher elevations is high, but the dominance of few species is a reason for the low species richness.

5.4.3 Plant communities

Based on the hierarchical clustering, we found four distinctive plant communities along the elevational gradient. The indicator species that characterize the plant communities are in agreement with the species used in the classification of the forests of northeast tropical Africa (Friis 1992). Accordingly, the plant communities identified in this study belong to the dry single-dominant Afromontane forest, which is a transition between the dry single-dominant Afromontane forest and East African evergreen and semi-evergreen bushland. The *Juniperus procera*—*Clusia lanceolata* community is found on Tigrean plateau (Figure 5.6). The indicator species of this plant community belong to the dry single-dominant Afromontane forests, which are commonly found in the northwest and southeast Ethiopian Highlands (Friis 1992).

The *Abutilon longicuspe*—*Calpurnia aurea* and *Dracaena ombet*—*Acacia etbaica* communities are categorized under the dry single-dominant Afromontane forest of the escarpments, and transition area between the dry single-dominant Afromontane forest of the Tigrean plateau and the East African evergreen and semi-evergreen bushland and thicket of the Afar lowlands (Friis 1992). The lower species turnover in the two communities (Figure 5.4) contributes to the higher floristic similarities. The two plant communities are mainly found on sloping terrain characterized by shallow soils and frequent rock outcrops. This forest type includes a range of physiognomic types, from typical forest to evergreen scrub with dispersed trees. Many of the plant species recorded in the two plant communities are also recorded on steep terrains of Eritrea, Djibouti and Somalia (Friis 1992). Besides anthropogenic reasons, the vegetation on the escarpment is affected by mass tree dieback (see Chapter 6). Such disturbance might create a favorable environment for the regeneration of many species that increase the species richness in this part of the landscape (Denslow 1980; Bongers et al. 2009). The dominance of *Cordia purpurea* and *Tarchonanthus camphoratus* in the *Abutilon*

longicuspe—*Calpurnia aurea* plant community is evidence of the severe forest degradation in the escarpment.

The *Acacia mellifera*—*Dobera glabra* community is dominated by the Fabaceae family and is located at the foot slope of the lower dry Afar lowlands, where the alluvial deposits have led to a thicker soil layer and thus higher soil moisture than on the upper slopes where *Abutilon longicuspe*—*Calpurnia aurea* and *Dracaena ombet*—*Acacia etbaica* communities are located. Based on Friis (1992), the *Acacia mellifera*—*Dobera glabra* community belongs to the East African evergreen and semi-evergreen bushland and thicket.

5.5 Implications for conservation

In developing regions like northern Ethiopia, the conflict between agriculture and forestry makes conserving large forests for their biodiversity values difficult (Margules et al. 2007). Therefore, it is important to prioritize biodiversity conservation sites. Thus, information on diversity of species along environmental gradients plays a key role in conservation planning (Naveh and Whittaker 1979). A large part of the forest remnants are found on the escarpment of the Great Rift Valley, which is less suitable for agricultural activities. This may be an opportunity to obtain more land for biodiversity conservation. Since the concept of biodiversity conservation prioritization is based on species richness, endemism and threat of extinction, further investigations on the degree of overlap among these criteria are recommended (Reid 1998). Conserving a large number of species may provide the opportunity to conserve species that are rare and whose ecosystem regulatory role may not be yet known (Huston and Gilbert 1996). Thus, besides the species-rich zones, conservation programs should also consider plant communities that may not be species rich, but may include endemic and threatened species. This is typically for northern Ethiopia, where church forests and other small forest fragments play a meaningful role in conserving plant diversity. To conserve a large number of species and plant communities, it is worth establishing a biodiversity conservation corridor along elevational gradient that includes the four plant communities. Such conservation approach may provide the opportunity to conserve species like *Dracaena ombet*, which is listed on the Red List of the IUCN as an

endangered species and is found in the *Dracaena ombet*—*Acacia etbaica* community that needs conservation priority.

In this study, we covered the spatial diversity of plant species and communities. Since the vegetation in the study area has been continuously changing (Darbyshire et al. 2003), it is important to study the species composition and distribution patterns over time (Magurran 2007). Recently, the over-exploitation of canopy tree species like *J. procera* and *O. europaea* subsp. *cuspidata* has led to the gradual replacing of the tree dominated landscapes with pioneer shrub species (e.g., *Cordia purpurea*, *Tarconanthus camphoratus*). Such a loss of or change in habitat may also affect the diversity of fauna, epiphytes, and other associated species, which have rarely been studied. Similar to the dry Afromontane forest at Mafai, Tanzania, mosses are commonly found hanging on big trees. these are important for keeping the microclimate cooler during the dry seasons by trapping and maintaining moisture from the atmosphere (Lyaruu et al. 2000). A further deterioration of the remaining forests will seriously affect the socio-economic and environmental conditions of the region. Thus, it is important to define conservation priorities and take urgent action to protect these habitats. Recently, conservation of biodiversity in the dryland ecosystems has received more attention (CBD 1992), and conserving these last natural forest remnants will address local, national, and international conservation goals.

6 EFFECTS OF MASS TREE DIEBACK ON STAND STRUCTURE AND DIVERSITY IN A DRY AFROMONTANE FOREST, NORTHERN ETHIOPIA

6.1 Introduction

Dead standing trees (hereafter snags) of the two keystone species *Juniperus procera* (Cuperessaceae) and *Olea europaea* subsp. *cuspidata* (Oleaceae) were frequently observed in a dry Afromontane forest remnant in northern Ethiopia (Desa'a forest). The local people noticed that mass tree dieback occurred in the study area in the late 1980s. Changes in forest composition and structure may result from periodic, abrupt, and catastrophic environmental impacts (e.g., White 1979) depending on local situation of the forest, including environmental heterogeneity, regeneration success, and competition (e.g., Chen et al. 2004). Forest dynamics range from those that are the result of individual tree senescence and fall, and those that are the result of large disturbances such as windstorms (White 1979). Human disturbance (e.g., Feoli et al. 2002; Darbyshire et al. 2003) and climate change (e.g., Dale et al. 2000; Hansen and Dale 2001; Lingua et al. 2008) are the major driving forces that shape forest ecosystems. Studies in other areas indicate that mass tree dieback affects species composition and diversity by affecting certain species and size classes, and by changing the light environment of the understory (Slik 2004; Engelbrecht et al. 2007).

The occurrence of large number of snags in the dry Afromontane forest is a notable sign of natural forest degradation. However, snags are important ecological components of forest ecosystems (Franklin et al. 1987). Snags also an important source of nutrients (Kueppers et al. 2004), serve as habitats for a wide range of plant and animal species (Ohmann et al. 1994; Harmon et al. 2000) and as carbon storages (Kueppers et al. 2004). In steep terrains like in the study area, snags play important roles in soil and water conservation (Russell et al. 2006). On the other hand, increased snag density makes the forest more vulnerable to fire hazards and forest managers need to pay more attention to sites with high snag densities (Agee and Skinner 2005; Holden et al. 2006). Snags also contribute to the structural diversity of stands (Hennon and McClellan 2003). However, snags have been removed from the studied forest for fuelwood, which is partly due to lack of knowledge on the roles of snags in ecological processes. It is therefore important to provide information to forest managers on the

roles of snags in the ecological process so that they define a standard number of snags to be retained in the forest (Ganey 1999; Marage and Lemperiere 2005).

Understanding the extent of tree dieback and spatial patterns of snags is therefore useful in managing forests (Craig and Friedland 1991; Gitlin et al. 2006). In particular, understanding the spatial distribution of snags in forests provides useful information to plan assisted regeneration and to investigate the role of snags in maintaining habitats for wildlife, soil protection, and other ecosystem services. However, the status of snags in the tropics has been less studied (Grove 2001). Although a few studies exist on the ecology of dry Afromontane forest remnants in northern Ethiopia (e.g., Aerts et al. 2006c; Aynekulu et al. 2009), they are largely focused on anthropogenic-related disturbance and did not take tree dieback into consideration.

With a rapid development of remote sensing, it is possible to address a number of ecological questions using remotely sensed data. Vegetation indices, for instance, have been widely used to examine the biological and abiotic components of forest ecosystems at different scales (Huete et al. 2002). ASTER imagery has a 16-days revisit time with 15-m spatial resolution in the visible and near infrared bands and has been used in many ecological studies (Clark et al. 2004; Muukkonen and Heiskanen 2005; Buhe et al. 2007; Rivero et al. 2007; García et al. 2008; Yüksel et al. 2008). It is therefore hypothesized that the normalized difference vegetation index (NDVI) from ASTER imagery can estimate the extent of mass tree dieback of *J. procera* and *O. europaea* subsp. *cuspidata*.

Thus, the objectives of this study are to investigate (i) the extent and spatial patterns of mass tree dieback of *J. procera* and *O. europaea* subsp. *cuspidata*, (ii) the applicability of NDVI of ASTER imagery in quantifying the extent of mass tree dieback, and (iii) the influence of mass tree dieback of the two species on the overall stand structure and species diversity in a dry Afromontane forest in northern Ethiopia.

6.2 Material and methods

6.2.1 Study site

The study was conducted in the Desa'a Forest (13°53' - 13°56' N and 39°48' - 39°51' E), which is located on the western escarpment of the Great Rift Valley in northern Ethiopia

(Figure 6.1). The study area lies between the Tigrean plateau (2720 m a.s.l.) and the Afar lowlands (1400 m a.s.l.). Based on the forest classification of northeast tropical Africa (Friis 1992), Desa'a forest is classified as dry single-dominant Afromontane forest with *J. procera* in the canopy and *O. europaea* subsp. *cuspidata* in the understory as dominant species. These are drought-tolerant species (Cuneo and Leishman 2006; Breshears et al. 2009) widely grown from Arabia to the southern Africa. Desa'a forest is a national forest priority area, but illegal logging and free grazing are commonly practiced.

The plateau section of the study site receives a mean annual rainfall of 532 mm (Abegaz 2005). The climate of the study area is influenced by its elevation in which the decline in rainfall and increase in temperature from the upland plateau to the eastern slopes are sharp (Degefu 1987). The geology is characterized by Enticho sandstone and crystalline basement (Asrat 2002). A large part of the study site is characterized by shallow soils and frequent rock outcrops.

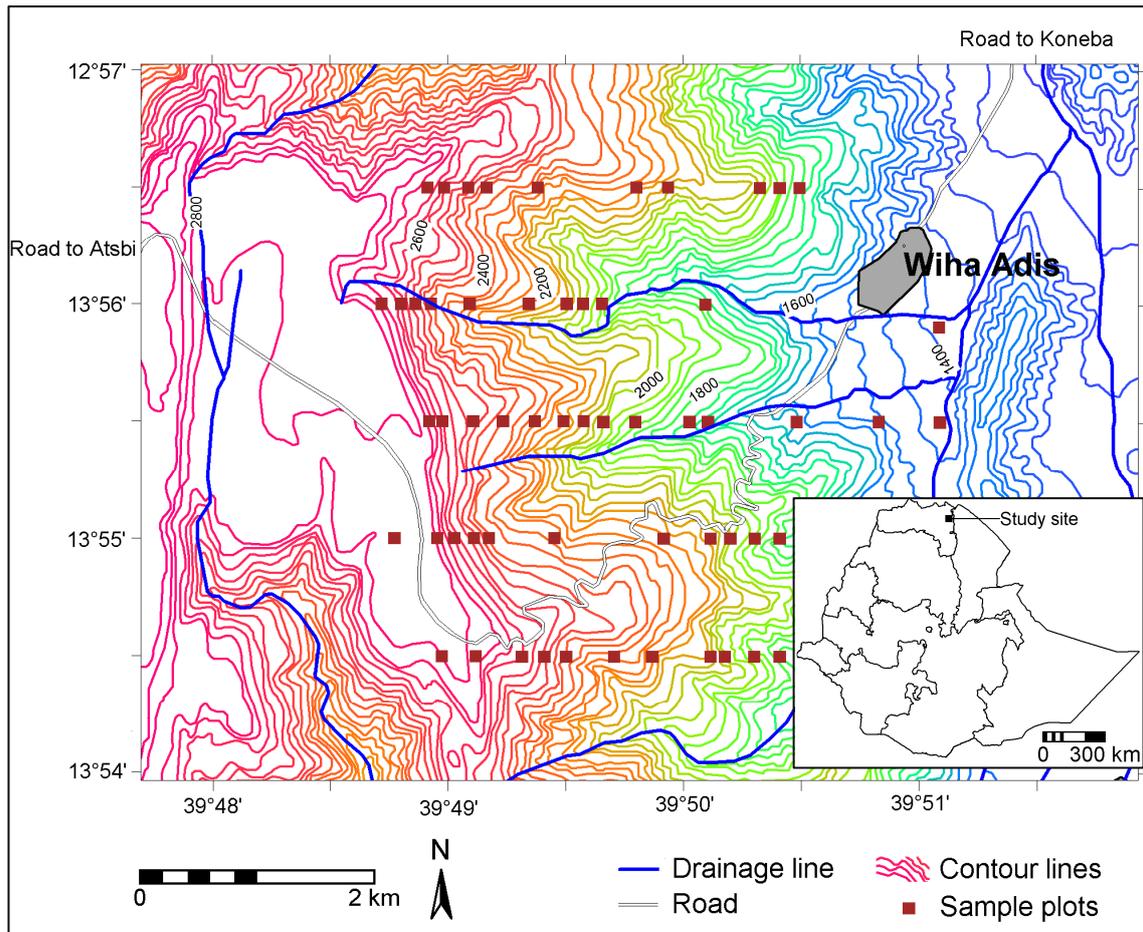


Figure 6.1 Location of the study area indicating the 57 sampling plots on a contour background map.

6.2.2 Data collection

Five transects were established perpendicular to the main slope (W-E) in Desa'a forest in 2008. Vegetation data were collected using 57 plots measuring 50 m × 50 m laid out at 100-m elevation intervals in transects (Figure 6.1). Percentages of snags of *O. europaea* subsp. *cuspidata* were determined in an additional 18 plots along two transects established in a north-south direction in the mid elevation (1800 – 2400 m) of the landscape (Figure 6.5). The percentage of snags for each plot was determined by counting the number of live stems and snags. In each plot, all individual woody plants were enumerated, and stand density and basal area per hectare for all trees including snags with a height > 1.5 m and diameter > 2 cm at breast height (DBH) were determined. Elevation, aspect, and slope were also measured for each plot. In this study, only *J. procera* and *O. europaea* subsp. *cuspidata* are used because they are the

dominant tree species where the effect of mass tree dieback is clearly observed in the field. A topographic map of the study site was used to set the sampling design and collect the coordinates of the plots. A GPS device was used to establish the plots in the field.

6.2.3 Data analyses

The extent and spatial pattern of mass tree dieback along elevation and aspect are analysed in terms of the percentage of snags of the two species, which is calculated as a ratio between the number of dead stems to the total dead and live stems per plot. The effect of mass tree dieback on the population structures of *J. procera* and *O. europaea* subsp. *cuspidata* is summarized using diameter class distributions. In order to quantify the changes in stand structure, stand density, diameter distribution, and basal area with and without snags of the two species are compared. Hill's diversity numbers (Hill 1973) are used to measure species diversity (see section 4.2.3).

An NDVI map is generated from ASTER imagery, which was taken in the dry season of 2006. The NDVI is calculated based on the visible and near infrared bands (Tucker 1979). To match the pixel and plot sizes, the NDVI map was re-sampled to a 50-m pixel value using the nearest-neighbour resampling method (Lillesand and Kiefer 2000). Image processing and mapping are undertaken using the Integrated Land and Water Information System (ILWIS 3.3) remote sensing and GIS software (ITC 2001).

Since most of the data do not follow normal distribution, the non-parametric Kruskal–Wallis ANOVA is used to compare differences in stand structure and species diversity. Linear regression is used to determine the relationship between elevation and percentages of snags of the two species. All tests of statistical significance are decided at $\alpha = 0.05$ level. Statistical analyses are performed in SPSS 13.0 for Windows (SPSS Inc. 2004).

6.3 Results

6.3.1 Extent and spatial patterns of tree dieback

The total mean (\pm SE) live stems and snag densities (*J. procera* and *O. europaea* subsp. *cuspidata*) are 147 ± 28 and 147 ± 23 stems ha^{-1} , respectively. The percentage of snags, which is the ratio of the dead stems to the sum of live and dead stems per plot, of *O.*

europaea subsp. *cuspidata* (60.2 ± 5.4 %) is slightly higher compared to *J. procera* (56.8 ± 7.15 %), but not significantly ($\chi^2 = 0.006$, $P = 0.941$).

The snag densities of both species are significantly reduced above 2500 m (Figure 6.2). A large abundance of live *J. procera* and *O. europaea* subsp. *cuspidata* stems occur above 2600 and 2400 m, respectively.

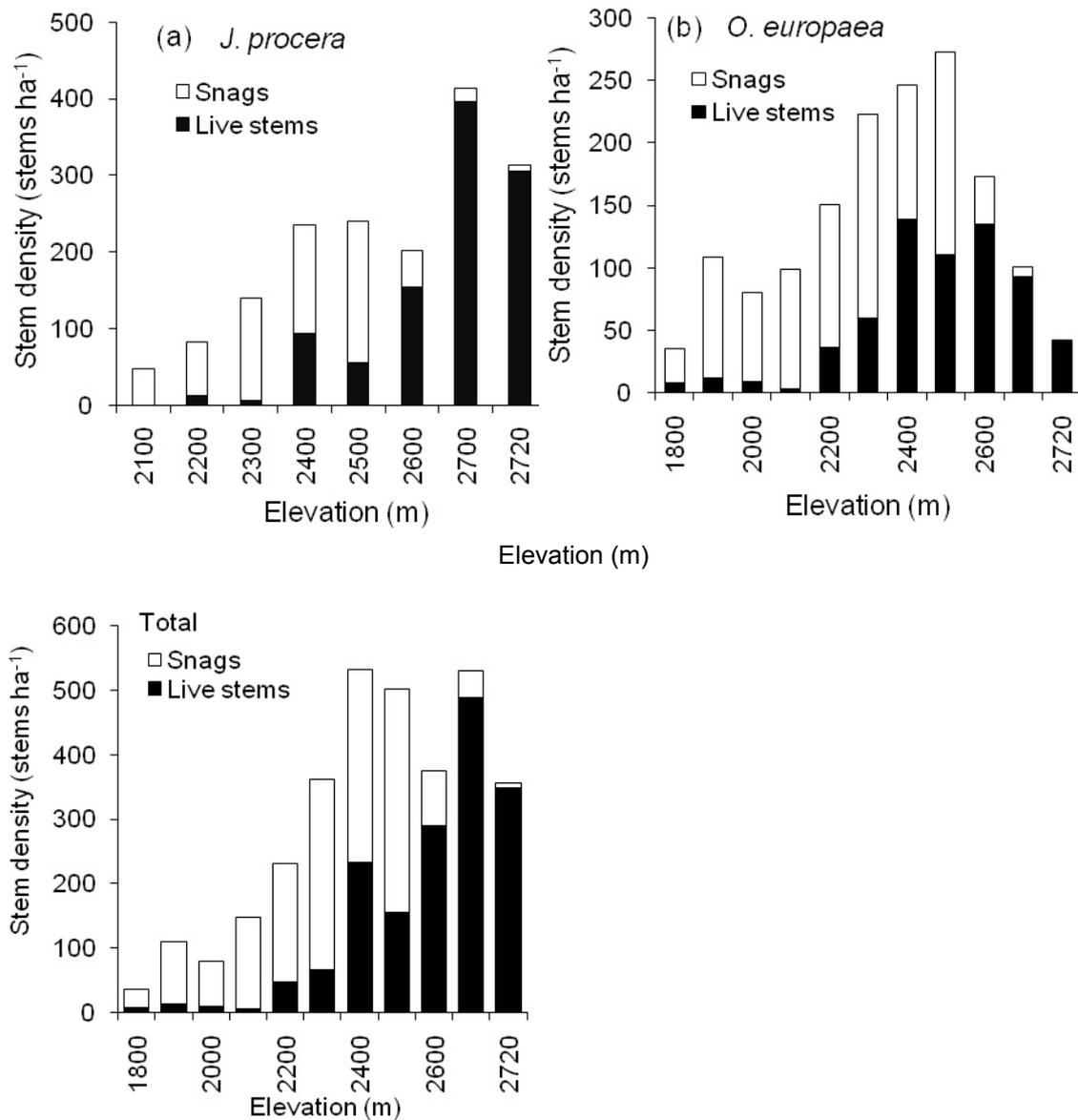


Figure 6.2 Mean densities of live stems and snags of *Juniperus procera*, *Olea europaea* subsp. *cuspidata*, and total (pooled data of the two species) along an elevational gradient in a dry Afromontane forest, northern Ethiopia.

The percentage of snags of both species is significantly related to elevation and the overall percentage of snags ranges from 0 % at higher elevations to 100 % at lower elevations (Figure 6.3; Figure 6.4).

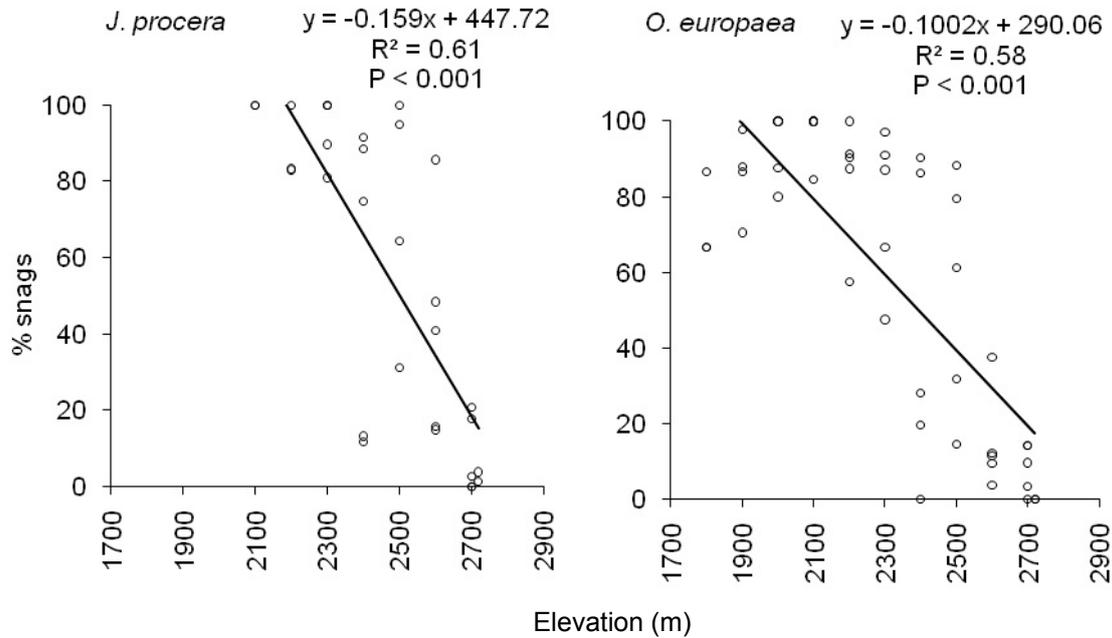


Figure 6.3 Percentage of snags of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* along an elevation gradient in a dry Afromontane forest, northern Ethiopia.

The percentage of snags of *O. europaea* subsp. *cuspidata* in the plots located on the south-eastern aspects (83 ± 6 %) is significantly higher ($\chi^2 = 7.87$, $P = 0.005$) than those located on the north-eastern (47.3 ± 8.4 %). However, snag percentage is not significantly related to slope.



Figure 6.4 Dry Afromontane forest with a) high density of snags at lower elevations, b) no tree die-off at higher elevations (> 2500 m) in a dry Afromontane forest, northern Ethiopia.

6.3.2 Estimation of mass tree die-off using NDVI

The False Colour Composite and the NDVI maps give a visual impression of the alternating pattern of high and low extent of tree die-off across the landscape (Figure 6.5). The percentage of snags per plot ranges from 16 to 100 % and the NDVI values range from -0.08 to 0.18.

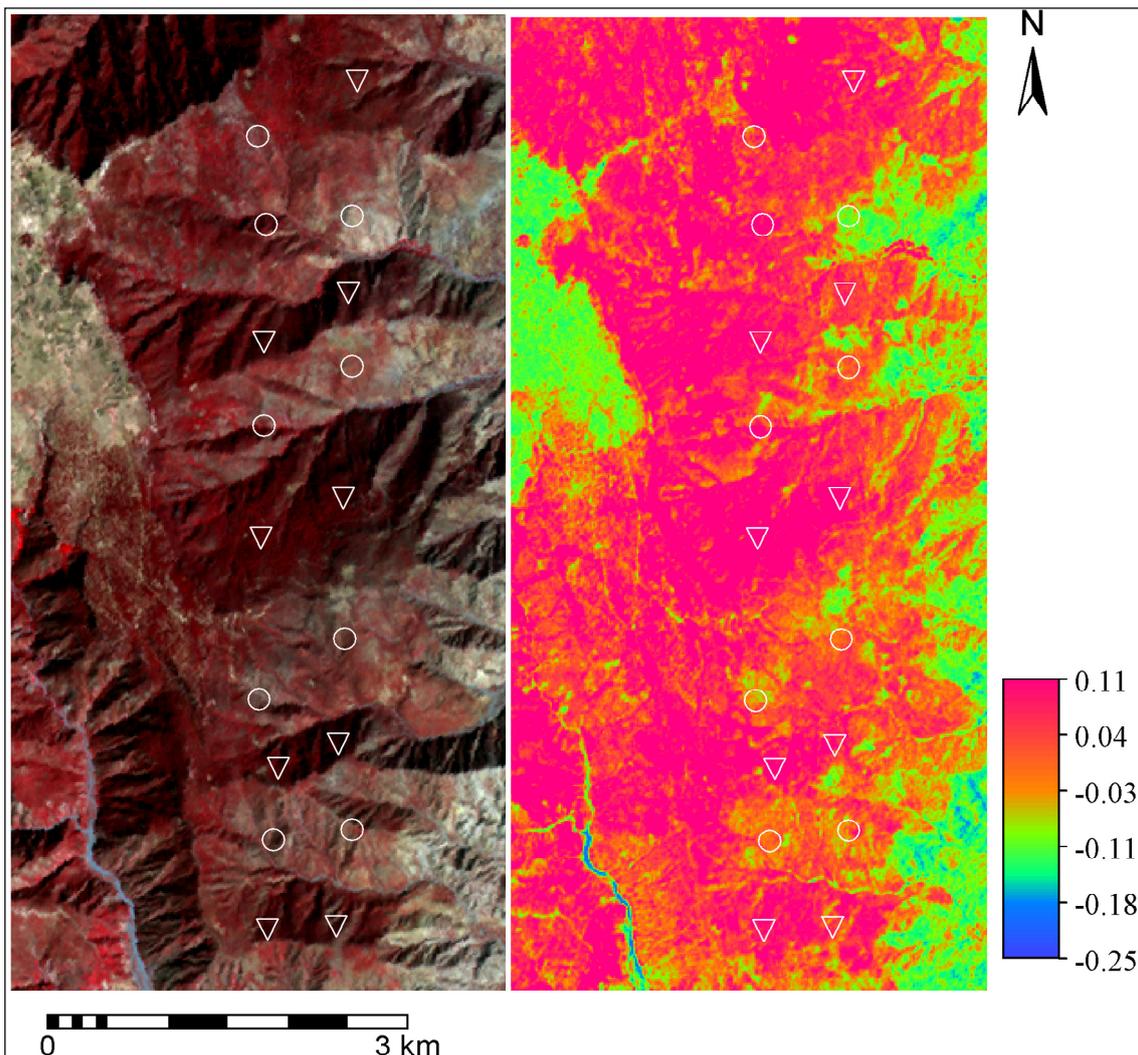


Figure 6.5 False Colour Composite (left) and NDVI map of ASTER imagery (right) showing low (▽) and high (o) extent of tree die-off (percentage snags per plot) along a micro-topography in a dry Afromontane forest, northern Ethiopia.

The extent of tree die-off of *O. europaea* subsp. *cuspidata* in the plots located on the south-eastern exposure is significantly higher ($P = 0.004$) than those located on the north eastern aspect, indicating that micro-topography plays a role in tree mortality. The NDVI of Aster imagery is also found to be good for estimating the tree mortality pattern (Figure 6.6).

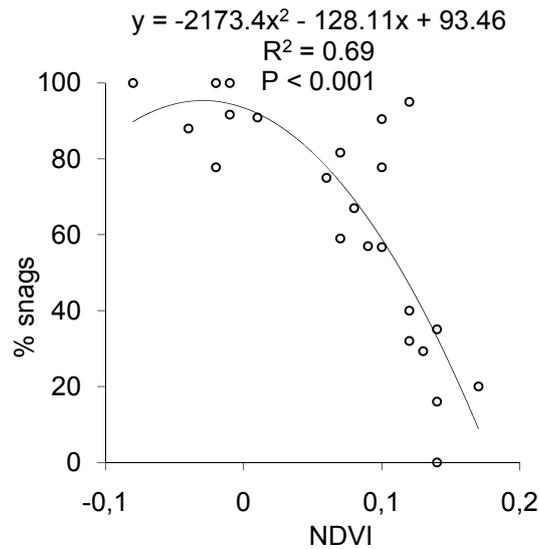


Figure 6.6 Relationship between mass tree dieback (per cent snag per plot) and NDVI along micro-topography in a dry Afromontane forest, northern Ethiopia.

6.3.3 Mass tree dieback, stand structure and species diversity

Stand structure

The mass dieback of the two key species significantly reduced the stem density stand and basal area of live stems in the forest by 30 and 44 %, respectively (Table 6.1). The diameter and height distribution of the two species are also significantly affected by mass tree dieback of the two species (Figure 6.7). The diameter distributions of both species have a truncated inverse-J shape indicating a serious regeneration problem of these keystone species in the study area.

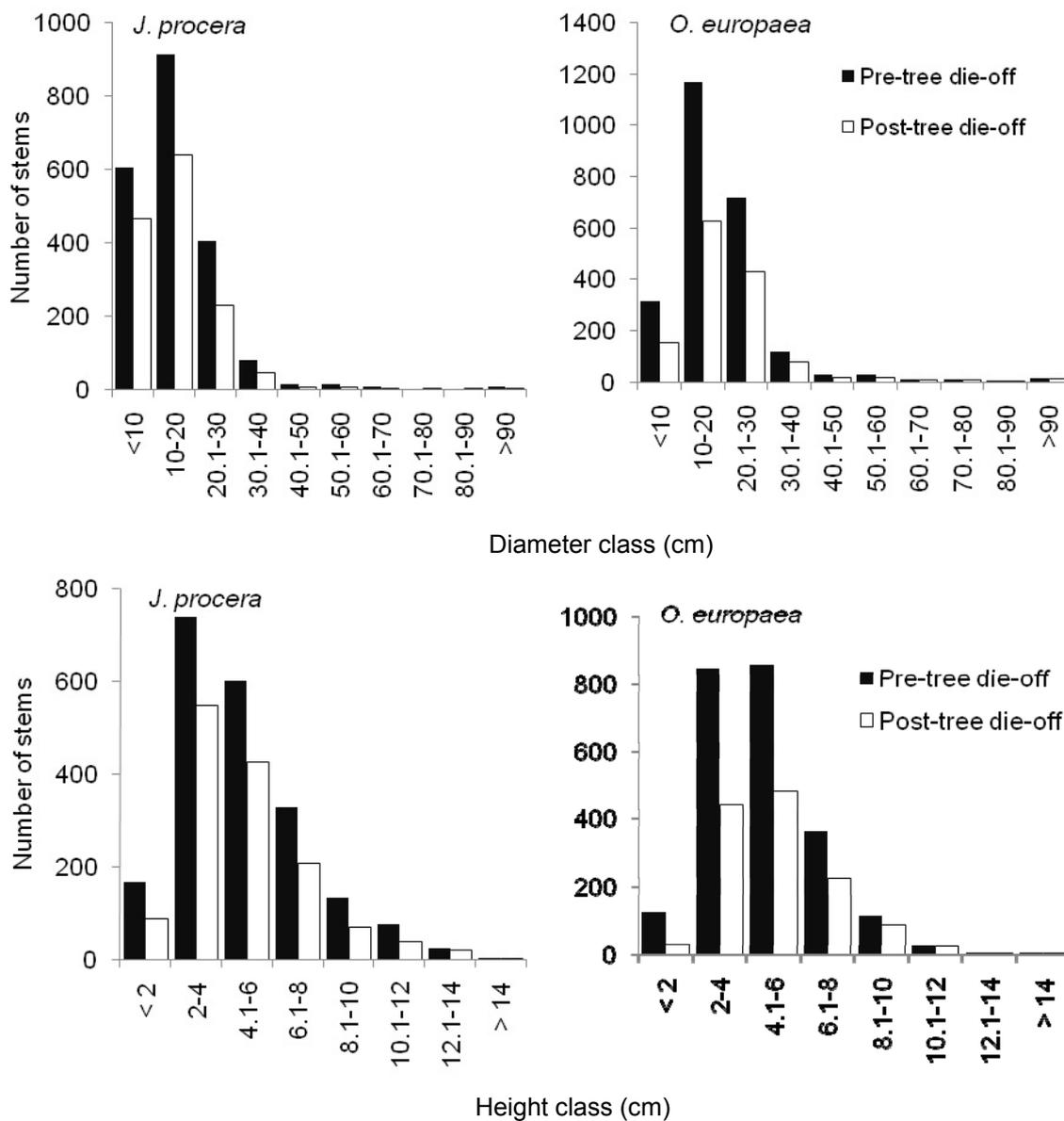


Figure 6.7 Diameter and height distribution of *J. procera* and *O. europaea* subsp. *cuspidata* with snags (pre-tree dieback) and without snags (post-tree dieback) in a dry Afromontane forest, northern Ethiopia.

The mean diameter of snags of *J. procera* (18 cm) is significantly higher ($\chi^2 = 98.23$, $P = < 0.001$) than that of the live stems (13 cm). Similarly, the mean diameter of snags of *O. europaea* subsp. *cuspidata* (18 cm) trees is not much higher ($\chi^2 = 6.68$, $P = 0.01$) than the mean diameter of live stems (17 cm). However, this comparison does not consider the diameter growth of the live stems after the tree death incidence. The percentage of snags is high for large diameter classes (> 40 cm) for *J. procera* (Figure 6.8). Although no clear trend can be observed in the percentage of snags in the different

diameter class of *O. europaea* subsp. *cuspidata*, higher values can be observed for larger trees (40-50cm).

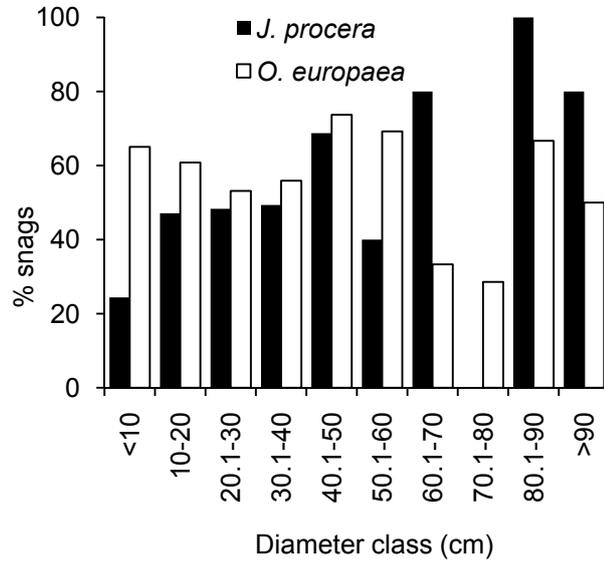


Figure 6.8 Percentage of snags according to stem diameter class in a dry Afromontane forest, northern Ethiopia.

Species diversity

A total of 9632 stems belonging to 83 species and 42 families were recorded in the 57 plots. Fabaceae, Lamiaceae, and Asteraceae are the 3 dominant families represented by 7, 6 and 5 species, respectively. *Juniperus procera* and *O. europaea* subsp. *cuspidata* are the two dominant species with relative abundance of 18 and 20 %, respectively. The mass tree dieback the two species did not influence richness, evenness, and species diversity (Table 6.1).

Effects of mass tree dieback on stand structure and diversity in a dry Afromontane forest, northern Ethiopia

Table 6.1 Stand structure and species diversity in a dry Afromontane forest, northern Ethiopia. Stand condition refers (mean \pm SE) values with and without snags of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* in a dry Afromontane forest, northern Ethiopia

Attribute	Plots (n)	Stand condition		χ^2	P
		With snag	Without snag		
Stem density (stems ha ⁻¹)					
<i>J. procera</i>	31	222 (31)	133 (33)	9.22	0.006
<i>O. europaea</i>	49	154 (15)	63 (10)	11.07	0.001
Stand (all species)	57	792 (47)	553 (30)	16.01	< 0.001
Basal area (m ² ha ⁻¹)					
<i>J. procera</i>	31	6.03 (0.92)	2.90 (0.75)	11.20	0.001
<i>O. europaea</i>	49	5.93 (0.58)	2.55 (0.47)	23.29	< 0.001
Stand (all species)	57	10.41(1.01)	5.79 (0.68)	15.80	< 0.001
Species richness (average per plot)	57	14 (1)	14 (1)	0.08	0.772
Hill's N_0 (total species richness)	57	83	83	-	-
Hill's N_1	57	7.63 (0.43)	7.75 (0.42)	0.06	0.812
Hill's N_2	57	6.08 (0.4)	6.17 (0.4)	0.07	0.79
Hill's E_1	57	0.54 (0.02)	0.55 (0.01)	0.56	0.448

6.4 Discussion

6.4.1 Extent and spatial patterns of tree dieback

The extent of mass tree dieback is high for both species in the study area. The mass tree dieback has significantly affected the abundance and spatial distribution of these dominant species. Canopy tree mortality can determine to a large extent the spatial and temporal scales of forest dynamics (Szwagrzyk and Szewczyk 2001). The effects of forest disturbance on stand structure and diversity is more severe in dry than in mesic tropical forests (Nepstad et al. 2007; Bongers et al. 2009). Changes in stand structure and diversity affect forest-climate interactions by changing canopy structure (Laurance 2004) and reducing the abundance of associated species like epiphytes, which play important roles in ecosystem functioning (Holscher et al. 2004).

The similar decreasing trend in the percentage of snags for both species along an elevation gradient indicates the non-randomness of tree death in the study area. This also suggests that trees at the lower and middle elevation, which are exposed to lower moisture and higher temperature conditions, were more affected. Studies have shown that extent of drought-driven tree death increases following moisture stress gradients

(Hanson and Weltzin 2000; Suarez et al. 2004). Lower elevations have warm temperatures where a slight increase in temperatures or a short drought can cause mass death of trees (Adams et al. 2009). A study on the density of snags in a tropical dry forest in western Mexico also shows a high percentage of snags at the driest site (Segura et al. 2003). A study in northern Arizona reports a decline in tree mortality with increasing elevation (Gitlin et al. 2006). Thus, lower abundance of live trees at lower elevations (Figure 6.3) implies that the distribution of the two species may be shifted 500 m to higher elevation from the lower extremes in the study area.

The percentage of snags of *O. europaea* subsp. *cuspidata* is slightly higher than that of *J. procera*. This is partly because *O. europaea* subsp. *cuspidata* is largely found at lower elevations compared to *J. procera* (Figure 6.3). Tree dieback is more pronounced in large trees, particularly in the case of *J. procera* (Figure 6.8). Similar findings were reported for the Amazon forest (Nepstad et al. 2007), northern Arizona (Mueller et al. 2005), and Indonesia (Slik 2004), where large trees were more affected by drought-triggered mortality. Since large trees use more water per unit time than smaller trees (Meizner 2003), the higher death rate of larger trees following elevated temperatures is probably due to the higher vulnerability of larger trees to xylem cavitations especially during extreme drought conditions (Brodribb and Cochard 2009).

Although there is a clear trend in the percentage of snags along an elevation gradient, some variations along the aspects were observed. Accordingly, percentages of snags are higher in the plots found in the south-eastern aspects. Similarly, mortality of pine and juniper trees is higher on the southern than on the northern aspect in mid-elevation woodlands in Arizona (Gitlin et al. 2006). This can be due to the exposition of south-eastern plots to thermal wind, while plots in north-eastern aspects are protected by micro-topography. Slopes with a south-eastern aspect also receive a higher heat load during the day than slopes oriented to the north-east (McCune and Keon 2002).

The high mortality of larger trees, particularly in the middle and lower elevations of *O. europaea* subsp. *cuspidata*, leads to a high variation in the level of greenness, which makes NDVI very suitable for estimating tree mortality patterns. The same applies to ASTER imagery with its relatively high spatial resolution (15 m). Other studies have also documented the applicability of such remotely sensed data in similar ecological studies. Levin et al. (2007) find NDVI of ASTER imagery useful for

predicting plant cover and species richness in dry environments in Israel. The Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery for estimating insect-triggered tree mortality in a pine plantation in Australia based on NDVI (Verbesselt et al. 2009).

6.4.2 Mass tree dieback, stand structure and species diversity

Stand density, basal area and diameter distribution are significantly affected by the mass tree dieback of *J. procera* and *O. europaea* subsp. *cuspidata*, which indicates the dominance of the two species in the stand. The wider gap created in the diameter distribution (Figure 6.7) due to tree dieback suggests that the stand structure did not recover after the incidence. The return to the pre-disturbance status is less likely due to the slow growth and poor regeneration of the species (Aynekulu et al. 2009; Wassie et al. 2009a). The increase in canopy gaps caused by mass tree dieback might have increased the soil temperature and reduces soil moisture availability, which are major limiting factors for the regeneration of many dry Afromontane tree species (Teketay 1997). Moreover, mass tree dieback may also reduce the availability of nursing trees for a successful establishment of seedlings (Mueller et al. 2005; Aerts et al. 2007). Mass tree dieback (74 % snags) strongly affects the reproductive range (10 - 40 cm) of *Juniperus procera* (Couralet et al. 2005), which may influence the maintenance of a viable plant population.

The openness of the canopies due to tree dieback also changes the understory light conditions and encourages the establishment of pioneer species (Slik 2004). Accordingly, dry Afromontane forests in northern Ethiopia, which were dominated by *J. procera* and *O. europaea* subsp. *cuspidata* prior to disturbance, have been gradually replaced by encroaching light-demanding shrubs and herbs such as *Cadia purpurea* and *Tarchonanthus camphoratus* (Gebreegziabher 1999; Feoli et al. 2002). Thus, mass tree dieback in the dry Afromontane forests in the study area may further lead to a gradual replacement of the high canopy trees by pioneer shrub and herb species.

Despite the massive decline in the abundance of the two dominant species, overall species evenness and diversity are not affected. This is because of the dominance of *J. procera* and *O. europaea* subsp. *cuspidata* in the community even after the tree dieback. A review of studies from 1985 to 1996 concludes that disturbance and

diversity have no strong relationship (Mackey and Currie 2001). Unlike in moist tropical forests, disturbance in dry forests does not create diverse habitats that encourage tree species diversity (Denslow 1980; Engelbrecht et al. 2007). Spatial and temporal variations in gap disturbance regimes may not explain variations in species richness (Engelbrecht et al. 2007). Since data on species richness before the mass tree dieback incidence are not available, there is no evidence on whether some species have disappeared from the community or whether others are new. This implies that species richness may not be a good indicator of community disturbance due to mass tree dieback in this study.

Even if no significant difference in species diversity can be observed, a reduction in the abundance of the two dominant tree species might reduce the net primary productivity of the forests that affects the energy flow and nutrient recycling. Wittebolle et al. (2009) also indicate that the original species evenness plays a key role in stabilizing ecosystem productivity. Moreover, the poor evenness of species distribution in the study site due to the dominance of *J. procera* and *O. europaea* subsp. *cuspidata* also makes the study area poor in species diversity, which may make it less resistant to environmental stress (Wittebolle et al. 2009).

6.5 Conclusions and management implications

The results indicate that mass tree dieback was not a random process, but significantly related to elevation and aspect. The lower elevation and south-eastern aspects are more affected by mass tree dieback. This implies that the distribution of the two species may shift to a higher elevation from the lower extremes. The tree dieback of the two dominant tree species has significantly reduced the stand density and basal area, but has had no effect on species diversity. The population structure of the two species is affected by the mass tree dieback, and both species have smaller seedling and sapling populations than mature individuals. Besides mass tree dieback, continued pressure on the *J. procera* and *O. europaea* subsp. *cuspidata* trees for their economic value is a major concern in the tree-scarce landscapes in northern Ethiopia. Thus, it is important to reduce further anthropogenic pressure on the forest to restore the population of the two species. It is also important to increase their seedling population through assisted

restoration measures. Sites with high snag density should also be carefully managed to reduce potential fire incidents.

Climate-driven mortality is difficult to predict, and the frequency of extreme climatic conditions that greatly affect semi-arid habitats is expected to increase (IPCC 2007), and may cause a further decreases in the habitat range of canopy species. Thus, further degradation of the few natural forest remnants in northern Ethiopia might lead to a change in plant community composition in the long run. Forest managers therefore need to plan for potential climate change.

7 REGENERATION RESPONSE OF NATIVE TREE SPECIES TO EXCLOSURE IN A DRY AFROMONTANE FOREST, NORTHERN ETHIOPIA

7.1 Introduction

In many tropical forests, excessive deforestation has hampered natural regeneration and seedling establishment and affected the diversity and structure of plant communities (Denslow 1980; Runkle 1982; Denslow 1987; Bussmann 2001). Similarly, forests in Ethiopia have been affected by climatic and anthropogenic factors for centuries (Friis 1992; Machado et al. 1998; Tekle and Hedlund 2000; Zeleke and Hurni 2001; Dessie and Kleman 2007). Historically, soil erosion as a result of vegetation clearing in the highlands of Tigray, for instance, took place in the Middle Holocene (Bard et al. 2000; Darbyshire et al. 2003).

The vascular plants of the Afromontane forests of Ethiopia maintain their population through natural regeneration (Teketay 1997; Mamo et al. 2006). However, large-scale degradation of natural forest in Ethiopia has created a major challenge with respect to the regeneration of key native tree species (Wassie et al. 2009a), while favoring shrub and herb species. For instance, Desa'a Afromontane forest, which was dominated by *Juniperus procera* and *Olea europaea* prior to disturbance, has been gradually replaced by encroaching light-demanding shrubs such as *Cordia purpurea* and *Tarchonanthus camphoratus*.

Natural regeneration is a site-specific ecological process, and it is usually difficult to characterize the factors that control regeneration processes (Schupp 1988; Khurana and Singh 2001). Protecting areas from livestock intervention i.e., a practice termed exclosure, is an assisted natural regeneration strategy to restore degraded forests (Parrotta et al. 1997; Shono et al. 2007). Many degraded sites have been managed as exclosures in northern Ethiopia, and attempts have been made to document the regeneration and ecology of the plants in these exclosures. Studies have indicated that vegetation recovery is quick in the younger stages (Mengistu et al. 2005; Abebe et al. 2006). However, exclosures that are older than 8 years do not show significant increases in species diversity and biomass production (Asefa et al. 2003; Yayneshet et al. 2009).

Some studies on vegetation restoration in Ethiopia have suggested that the presence of matured trees as seed sources (Tekle and Hedlund 2000), plantation forests (Senbeta and Teketay 2001; Yirdaw 2001; Lemenih et al. 2004), and minimization of livestock pressure (Aerts et al. 2007) create favorable conditions for the regeneration of native species. Although some studies exist on the regeneration and ecology of *J. procera* and *O. europaea* in the northern Ethiopian highlands (Aerts et al. 2006c; Wassie et al. 2009a) little is known about regeneration in the relatively larger dry Afromontane forest remnants in northern Ethiopia. Thus, the aim of this study is to investigate the response of natural regeneration of *J. procera* and *O. europaea* to a 3-year exclosure in comparison to an open forest management system in a dry Afromontane forest in northern Ethiopia.

7.2 Material and methods

7.2.1 Study site

The study was conducted in Desa'a forest, which is one of the dry Afromontane forest remnants in northern Ethiopia (Friis 1992). The site is located at 13°56' N, 39°49' E at an elevation of 2700 m above sea level (Figure 7.1). The study is located on the Tigrean Plateau, which lies immediately above the escarpment of north western Great Rift Valley. A large part of the site is located on shale, limestone, and sandstone of the Tertiary and Mesozoic era (TFAP 1996). Based on the diverse geological formations, the soils are variable; the dominating soil types in the study region are Leptosols, Cambisols, Vertisols, Regosols, and Arenosols (TFAP 1996).

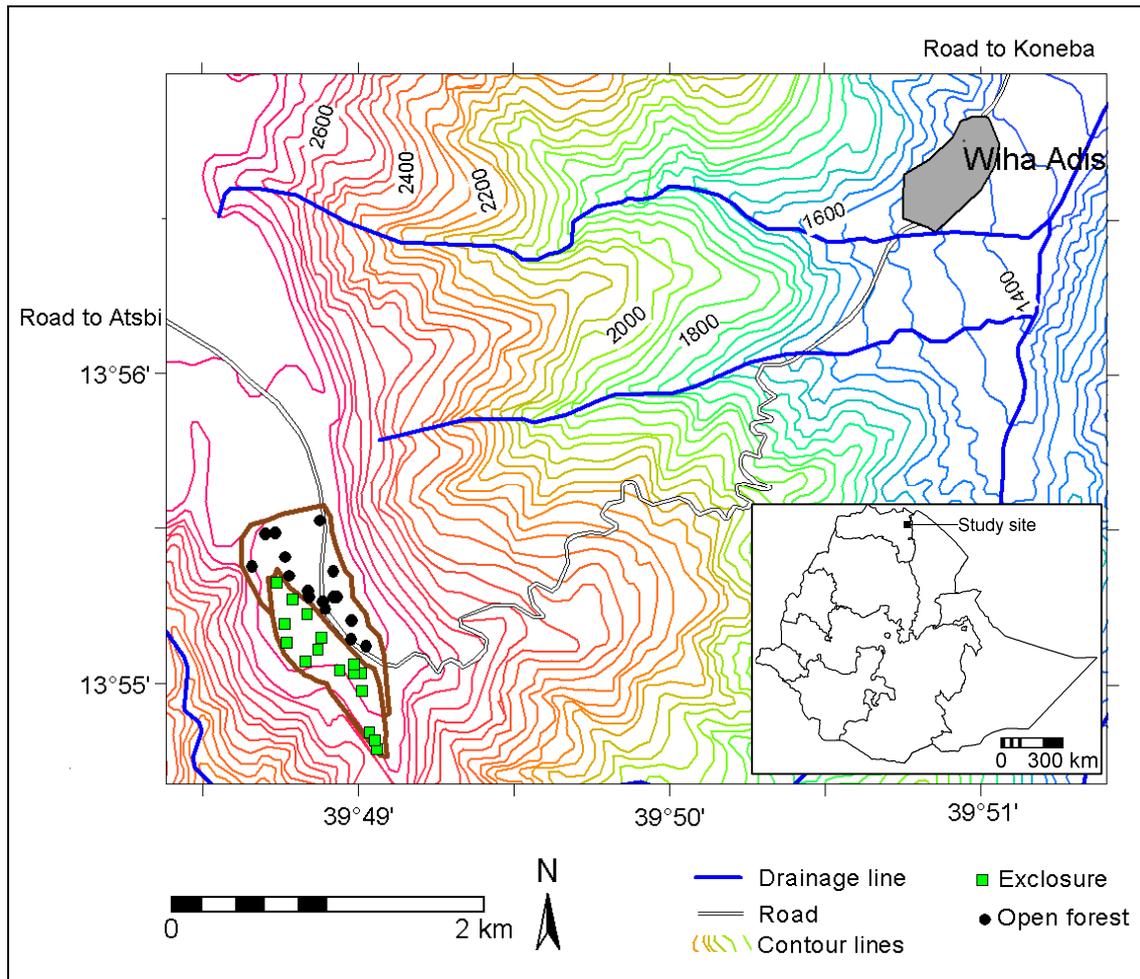


Figure 7.1 Location of the study sites and the distribution of plots in the open forest (circle) and exclosure (squares) in a dry Afromontane forest, northern Ethiopia.

7.2.2 Study species

The forests of eastern and north-eastern Africa are categorized into 9 major floristic groups (see Friis 1992). Accordingly, Desa'a forest is categorized as a dry single-dominated Afromontane forest, which is characterized by a dry climate (annual precipitation less than 1000 mm) and with *J. procera* and *O.europaea* subsp. *cuspidata* as dominant species. *Juniperus procera* is commonly found from Arabia to Zimbabwe (Hall 1981). Due to heavy pressure on this species, the Food and Agriculture Organization (FAO) has listed it as a threatened species that requires in-situ conservation priority beginning 1985–1989 (FAO 1975). James Bruce first documented *J. procera* as a common forest tree species in the highlands of northern Ethiopia during his expedition to trace the origin of the Blue Nile (1768–1773) (Bruce 1790 cited in

Friis 1992). *Juniperus procera* has a slow germination rate (Yirdaw and Leinonen 2002) and low germination capacity, which are mainly attributed to seed dormancy (Tigabu et al. 2007).

The genus *Olea* has 33 species, and *Olea europaea* subsp. *cuspidata* is one of the subspecies that was previously named *Olea africana*. The species is commonly called the African olive and is widely distributed from Arabia to southern Africa. Although it is a useful tree species in its natural habitat, it is categorized as an invasive plant in countries like Australia (Cuneo and Leishman 2006) and Hawaii (Santos et al. 1992). *Olea europaea* subsp. *cuspidata* is a common species in the highlands of Ethiopia.

7.2.3 Sampling design

The exclosure and an adjacent open forest, which is not protected from livestock, were mapped using a global positioning system (GPS) device. Later, the GPS data were transferred to a geographic information system (GIS) environment for further mapping. The exclosure and open forest areas cover 33 and 43 ha, respectively. Data on the floristic and structural compositions of the standing vegetation were collected in 32 randomly selected plots (20 m × 20 m), and nested plots (10 m × 10 m) were used to investigate the seedling bank in the exclosure and the adjacent open forest. Emphasis was placed on the two target species, i.e., *J. procera* and *O. europaea* subsp. *cuspidata*.

7.2.4 Data analysis

The importance of a species is determined using the importance value index (IVI) (see section 4.2.3). Species diversity is determined using the Shannon diversity index and Simpson's Index of diversity given by (Magurran 2004). The generalized linear model (GLM) with quasi-Poisson distribution (with log link) is used to determine the effect of management on seedling abundance of *J. procera* and *O. europaea* subsp. *cuspidata* in R software version 2.7.0 (R Development Core Team 2008). The family quasi-Poisson distribution is used because there were over-dispersions when Poisson distribution was run (Crawley 2007). For a better visualization and consideration of spatial correlations (Webster and Oliver 2001), the spatial distribution of seedling density (number of

seedlings per plot) is mapped using the ordinary kriging interpolation method with the Integrated Land and Water Information System (ILWIS 3.3) GIS software (ITC 2001).

7.3 Results

7.3.1 Floristic composition

In total, 17 vascular plant species (with measured DBH) belonging to 12 families were recorded in the exclosure and the open forest; *J. procera* is the dominant species with the highest relative importance value (Table 7.1). *Juniperus procea*, *Olea europaea* subsp. *cuspidata*, *Solanum schimperianum*, and *Maytenus senegalensis* are the most common species found in more than 75 % of the plots, while *Erica arborea* is among the rare species, recorded only in one plot.

Regeneration response of native tree species to exclosure in a dry Afromontane forest, northern Ethiopia

Table 7.1 List of standing and seedling species recorded in the exclosure and open forest in a dry Afromontane forest, northern Ethiopia

Family	Species	Abundance		Frequency		Dominance		IV (%)	
		Open	Exclosure	Open	Exclosure	Open	Exclosure	Open	Exclosure
Overstorey species									
Cupressaceae	<i>Juniperus procera</i> Hochst. ex Endl.	642	814	100	100	9.53	11.35	161.01	170.54
Oleaceae	<i>Olea europaea</i> L. subsp. <i>cuspidata</i> (Wall ex G. Don.)	57	42	94	81	2.19	2.46	41.71	39.01
Solanaceae	<i>Solanum schimperianum</i> Hochst.	120	268	88	100	0.03	0.06	29.36	45.64
Celasteraceae	<i>Martinius senegalensis</i> (Lam.) Exell.	35	22	88	63	0.13	0.08	21.64	16.5
Sapindaceae	<i>Dondonaea viscosa</i> Jacq.	84	5	19	13	0.12	0.03	13.04	3.43
Anacardiaceae	Ruth species	13	11	25	31	0.35	0.33	8.99	10.3
Euphorbiaceae	<i>Clutia lanceolata</i> Jaub. & Spach	10	16	19	31	0	0	4.66	8.4
Apocynaceae	<i>Carrisa edulis</i> Vahl	14	0	13	0	0.04	0	4.16	0
Fabaceae	<i>Acacia etbaica</i> Schweinf.	1	0	6	0	0	0	1.32	0
Rhizophoraceae	<i>Cassipourea malosana</i> Alston	1	3	6	13	0	0	1.32	3.07
Moraceae	<i>Ficus palmata</i> Forssk.	1	0	6	0	0	0	1.32	0
Rubiaceae	<i>Canthium setiflorum</i> Hiern	1	0	6	0	0	0	1.32	0
Solanaceae	<i>Solanum adoense</i> Hochst. ex A. Braun	1	0	6	0	0	0	1.32	0
Rubiaceae	<i>Canthium oligocarpum</i> Hiern	2	1	5	8	0.01	.02	0.61	0.42
Ericaceae	<i>Erica arborea</i> L.	1	0	0	0	0.01	0	0.5	0
Fabaceae	<i>Cordia purpurea</i> Ait.	3	1	3	4	0.02	0.03	0.4	0.6
Sapindaceae	<i>Pappaea capensis</i> Eckl. & Zey	2	0	1	0	0.01	0	0.31	0

Table 7.1 continued

Family	Species	Abundance		Frequency		Dominance		IV (%)	
		Exclosure	Open	Exclosure	Open	Exclosure	Open	Exclosure	Open
Seedling species									
Oleaceae	<i>Olea europaea</i> L. subsp. <i>cuspidata</i>	498	232	100	100				
Cupressaceae	<i>Juniperus procera</i> Hochst. ex Endl	25	44	63	75				
Celastraceae	<i>Maytinus senegalensis</i> (Lam.) Exell.	33	54	63	69				
Solanaceae	<i>Solanum schimperianum</i> Hochst.	12	0	19	0				
Moraceae	<i>Opuntia ficus-indica</i> (L.) Mill.	1	2	6	6				
Rhamnaceae	<i>Sageretia thea</i> (Osbeck) M.C.Johnst.	2	0	6	0				
Sapindaceae	<i>Dodonaea viscosa</i> Jacq.	11	0	13	0				
Flacourtiaceae	<i>Dovyalis abyssinica</i> (A.Rich.) Warb.	1	0	6	0				
Lamiaceae	<i>Plectranthus ornatus</i> Codd.	1	0	6	0				
Apocynaceae	<i>Carissa edulis</i> Vahl	1	0	6	0				

Species richness and diversity of woody plants are higher in the exclosure than in the open forest (Table 7.2). The stem density of *J. procera* is higher in the open forest than in the exclosure, while the density of *O. europaea* is higher in the exclosure than in the open forest. The average density of all woody plants in the open forest is higher than in the exclosure. The mean basal area in the open forest is slightly higher than in the exclosure.

Table 7.2 Summary of vegetation attributes (Mean \pm SE) of all woody species and densities of *Juniperus procera* and *Olea europaea* in an exclosure and an open management system in a dry Afromontane forest, northern Ethiopia

Attribute	Management	
	Open (n = 16)	Exclosure (n = 16)
Stem density (stems ha ⁻¹)		
<i>J. procera</i>	1272 \pm 170	947 \pm 252
<i>O. europaea</i>	67 \pm 22	87 \pm 19
Stand (all species)	1853 \pm 75	1499 \pm 264
Stand basal area (m ² ha ⁻¹)	21.1	19.4
Species richness	9	14
Shannon Diversity Index (H')	1.08	1.42
Simpson's Index of Diversity (1-D)	0.56	0.63

7.3.2 Structure

The diameter distribution of *J. procera* indicates that the number of individuals in the lower diameter class, including seedlings, is very low (Figure 7.2). The highest numbers of *J. procera* individuals are found in the diameter class of 2- 6.9 cm declining with increasing diameter. Although the number of individuals in the open forest is somewhat higher than in the exclosure, the population structure in both sites follows a similar trend. The seedling population of *O. europaea* is much higher than in the subsequent higher diameter classes. Although the number of individuals is low, more *O. europaea* saplings were recorded in the exclosure than in the open forest.

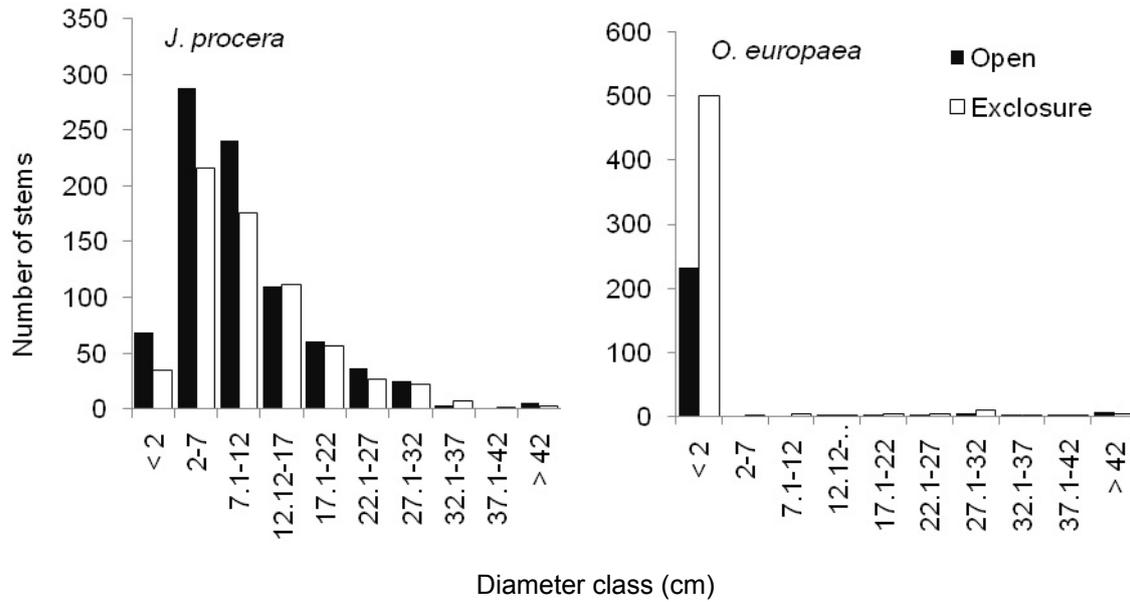


Figure 7.2 Diameter (DBH) class distribution of *Juniperus procera* and *Olea europaea* subsp. *cuspidata* in an exclosure and open forest in northern Ethiopia.

7.3.3 Natural regeneration

A total of 10 species of vascular plants was recorded in the seedling bank. Like in the standing vegetation, *O. europaea*, *J. procera* and *M. senegalensis* seedlings are the most dominant species and are observed in more than 65 % of the plots (Table 7.1). The seedling density of *O. europaea* is significantly higher in the exclosure than in the open forest. The seedling density of *J. procera* is slightly higher in the open forest than in the exclosure, but this is not statistically significant (Table 7.3).

Table 7.3 Seedling density (Mean \pm SE.) of *Juniperus procera* and *Olea europaea* in an exclosure and open forest in northern Ethiopia

Species	Management		<i>F</i>	<i>P</i>
	Open	Exclosure		
<i>J. procera</i>	275 \pm 156	156 \pm 104	2.1	0.16
<i>O. europaea</i>	1450 \pm 929	3113 \pm 1852	7.29	0.01

The spatial distribution of *J. procera* and *O. europaea* seedling densities in the exclosure and open forest (Figure 7.3) indicates that protecting the forest has a different effect on the seedling abundance of the two species.

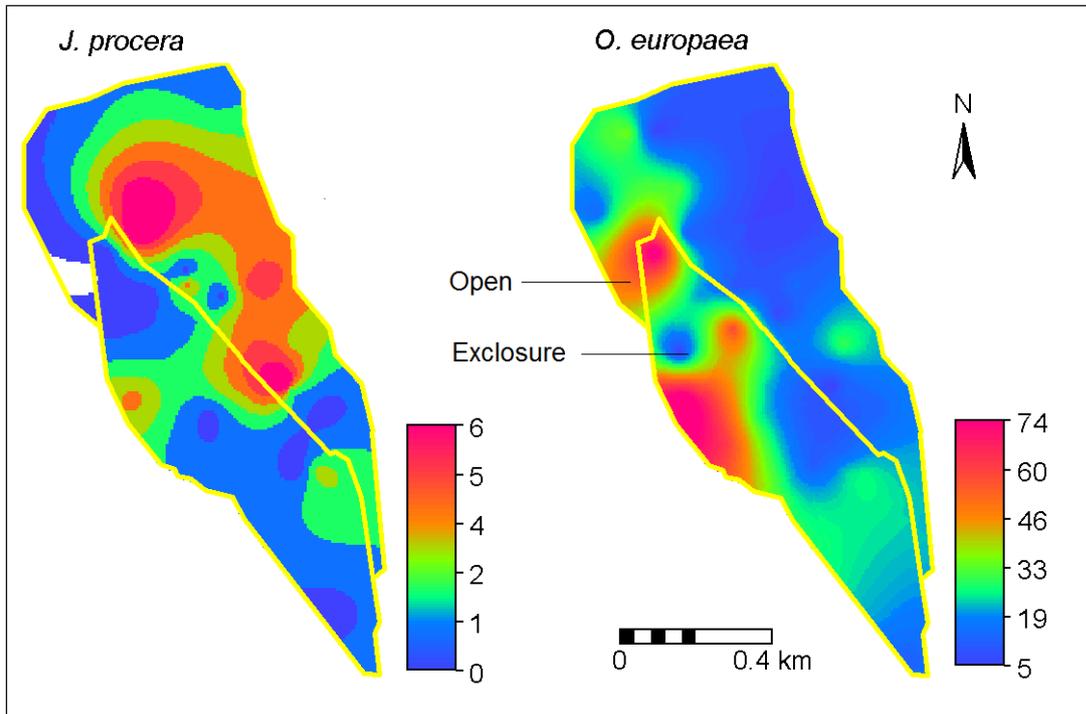


Figure 7.3 Kriged maps showing spatial distribution of seedling density of *Juniperus procera* and *Olea europaea* in the exclosure and in the open-access forest in northern Ethiopia. Numbers in the legend indicate the number of seedlings per plot (10 m × 10 m).

7.4 Discussion

The results show higher species diversity and seedling abundance in the exclosure than in the open forest, suggesting that protection of the forest contributes positively to the restoration of Desa'a forest. Similar findings have been reported for other protected areas in northern Ethiopia (e.g., Mengistu et al. 2005; Yayneshet et al. 2009). Although *J. procera* and *O. europaea* are the dominant species in Desa'a forest, they respond differently to exclosure in terms of regeneration. The seedling abundance of *O. europaea* is significantly higher in the exclosure than in the open forest (Figure 7.3). However, there is no evidence of any direct effects of exclosure on the abundance of *J. procera*, calling for further investigation of other influencing factors. The population structure of *J. procera* (Figure 7.2) also indicates that this species is less represented in the lower-diameter classes, in which higher regeneration and recruitment are needed to attain a viable population of the species.

Although *J. procera* is the most dominant species in the standing vegetation and has higher availability of seeds in the study area, seedling abundance in both

exclosure and open forest is very low. This is also in agreement with the findings of Wassie et al. (2009a) who found lower regeneration of *J. procera* in church forests in northern Ethiopia. Although not statistically significant, regeneration of *J. procera* is higher at the open forest than at the exclosure (Table 7.3). This is in agreement with the findings of Mamo et al. (2006), who found poor regeneration of *J. procera* under field conditions, suggesting a need for additional manipulation. Although some studies have indicated that light may not be a major limiting factor for the germination of *J. procera* (Sharew et al. 1997; Wassie et al. 2009a), the dense grass and herb cover in the exclosure might prevent optimum radiation reaching the forest floor (Yirdaw and Leinonen 2002; Teketay 2005) and thus influence germination (Cabin et al. 2002).

Seed dormancy, which varies depending on the provenance of *J. procera* in Ethiopia (Tigabu et al. 2007), might also influence germination. The thick, less decomposable litter of *J. procera* (Prescott et al. 2000) in the exclosure also prevents seeds from contacting the soil. This might slow down the breaking of seed dormancy, which would ultimately hamper germination (Rotundo and Aguiar 2005; Cierjacks et al. 2008). The thick litter in the exclosure might also have influenced emergence of newly germinated seedlings (Yirdaw and Leinonen 2002; Teketay 2005). Sharew et al. (1997) found that land preparation by raking and burning increased the germination capacity of this species. Hence, the relatively higher abundance of *J. procera* seedlings in the open forest than in the exclosure suggests that other factors such as absence of excessive shade, less litter, low livestock preference, and the breaking of seed dormancy through livestock trampling (Cierjacks et al. 2008) may determine regeneration.

The seedling abundance of *O. europaea* is higher in the exclosure than in the open forest (Table 7.3), indicating that this species is negatively influenced by livestock browsing and other microsite characteristics such as shade. Studies indicate that the establishment and recruitment of *O. europaea* are better under shaded and protected conditions (Fetene and Feleke 2001; Bekele 2005; Aerts et al. 2006c; Aerts et al. 2008). In contrast, Tesfaye et al. (2002) found that *O. europaea* is a light-demanding species in the Harena forest in the south-eastern highlands of Ethiopia, which is wetter than the study site. This indicates that the establishment of *O. europaea* requires shade in drier environments that reduces moisture loss during the dry season (Holmgren et al. 1997).

In line with this, Aerts et al. (2006b) also found successful regeneration of *O. europaea* under *Euclea* shrubs, which create a better moisture regime through thick humus and organic matter accumulation (Descheemaeker et al. 2006) in protected sites in northern Ethiopia. Rey et al. (2000) also found that regeneration of *O. europaea* is much influenced by the availability of moisture. Although mature individuals trees of this species are tolerant to browsing (Dansereau 1951; Dale et al. 2000; Tesfaye et al. 2002; Darbyshire et al. 2003; DeLong et al. 2008), seedlings are sensitive to herbivory (Tefaye et al. 2002). Thus, protection of *O. europaea* seedlings from herbivory in the exclosure contributed to a higher abundance of seedlings than in the open forest. Like the findings of Aerts et al. (2008), coppicing shoots of *O. europaea* subsp. *cuspidata* are commonly observed in the exclosures and can be used to restore Desa'a forest.

Similar to findings elsewhere (Richter et al. 2001; Cabin et al. 2002), the exclosure in Desa'a forest favors grass and herbaceous species (Figure 7.4), which may lead to a gradual shift of the forestland to wooded grassland. Hence, it is important to reduce the grass cover to enhance the regeneration of tree species (Cabin et al. 2002). It is well documented that livestock is an important agent of regeneration (e.g., Cierjacks et al. 2008). However, in degraded environments where there is overgrazing, the impact of livestock with respect to enhancing regeneration is limited. Instead, livestock contribute negatively to the establishment of seedlings through intensive browsing (Wassie et al. 2009b). In such degraded environments, species such as *O. europaea* are frequently browsed in the absence of other feed sources, particularly during the long dry season, which does not allow the species to develop a viable population (Gunderson 2000).



Figure 7.4 Exclosure (a) and open forest (b) in a dry Afromontane forest, northern Ethiopia.

7.5 Implications for conservation and management

The results of many studies concluded that there is a strong need to give priority to conservation of the existing natural forest remnants in northern Ethiopia before they lose their ecological resilience (Nyssen et al. 2004; Aerts et al. 2006c). In this regard, this study reveals that protecting the degraded natural forest contributes positively to the natural regeneration of *O. europaea* but not to *J. procera* in Desa'a forest. The findings of this study, therefore, provide scientific knowledge to support a change from the traditional pattern of exploitation to a targeted management of the species. However, management options or factors seem to influence the natural regeneration of *J. procera* other than protecting this species from livestock. It may also be worthwhile to consider other management options such as enrichment planting and reducing litter accumulation and dense grass cover, especially in the exclosure, as suggested by Yirdaw and Leinonen (2002), in order to maintain a viable population of *J. procera*. Based on the findings of this study, it is concluded that restoration of the degraded dry Afromontane forest remnants in northern Ethiopia through exclosures requires a better understanding of the ecological requirements of the different species involved. Since the objective of forest restoration is to improve the status of native tree species, experience from the exclosures in other areas should be carefully applied when attempting to restore degraded dry forest remnants in northern Ethiopia. This study is based on a 3-year protection period, and thus the results should be interpreted cautiously and extrapolated to other forests with care.

8 FOREST DIVERSITY IN FRAGMENTED LANDSCAPES IN NORTHERN ETHIOPIA: SYNTHESIS, IMPLICATIONS FOR CONSERVATION, AND FURTHER STUDIES

Deforestation and forest degradation in northern Ethiopia has a long history. Following the early settlements in northern Ethiopia, the extent of deforestation and forest degradation in northern Ethiopia is more severe than in other parts of the country. The forests have suffered from anthropogenic and natural disturbance. The forest remnants in northern Ethiopia are part of the eastern Afromontane and Horn of Africa biodiversity hotspots that need conservation priorities. Recently, conservation of biodiversity in the dryland ecosystems has received greater attention. One of the national biodiversity strategies of Ethiopia is conserving forest ecosystems (IBC 2005). This study gives detailed analyses of species diversity, composition of plant communities, natural regeneration, and forest structure in relation to selected environmental factors in Desa'a and Hugumburda forests, which are large natural forest remnants in northern Ethiopia. The findings can provide decision support in the design of such a conservation strategy.

Species diversity and assemblage

Species diversity in the study forests is lower than in many of the natural forests in southern Ethiopia. Floristically, the studied forests are largely (ca. 70 %) composed of shrub and herb species. This indicates that the forest remnants in northern Ethiopia, particularly Desa'a forest, are experiencing a retrogressive succession in which tree species are gradually replaced by shrub and herb species.

Topographic position, which is associated to moisture availability, and forest disturbance explain the species distribution patterns and partitioned plant communities (Chapter 4, 5). The *Pterolobium stellatum*—*Celtis africana* plant community, which is found in Hugumburda forest (Chapter 4) is categorized under a moist forest type while all other plant communities belong to dry Afromontane forests with *J. procera* and *O. europaea* subsp. *cuspidata* as dominant species. This indicates that the riverine plant communities are islands of moist forest in the dry lands of northern Ethiopia that need conservation priority.

Natural regeneration

The results indicate that the standing vegetation is only partly represented in the seedling bank, and many of the rare tree species show poor or no regeneration (Chapter 4, 6). A smaller number of saplings than mature species suggests that locally some tree species are experiencing extinction.

The natural regeneration at the exclosure in Desa'a forest did not significantly contribute to the natural regeneration of native tree species. This implies that closing of the degraded forests to livestock intervention may not guarantee a successful regeneration of tree species in the degraded dry forests especially for *J. procera*. Thus, it is important to complement protected forests with enrichment planting and other assisted regeneration measures like reducing litter accumulation and dense-grass cover while managing exclosures. Since moisture is a limiting factor for regeneration in dry forests (Chapter 4), it is also important to reduce soil desiccation by maintaining adequate canopy cover.

Effects of mass tree dieback on forest structure

The results indicate that mass tree dieback of *J. procera* and *O. europaea* subsp. *cuspidata* has significantly reduced the living stand density and basal area of Desa'a forest (Chapter 6). Mass tree dieback is significantly reduced with increasing elevation, which reduces the elevational range of the key tree species (*J. procera* and *O. europaea*) by nearly 500 m to the higher elevations. This may also cause a shift in the forest-shrub land ecotone to higher elevation. Besides continued pressure on the *J. procera* and *O. europaea* trees for their economic value, mass tree dieback of these species is thus a major concern in the tree-scarce landscapes in northern Ethiopia. Forest disturbance has favored the expansion of herbs and pioneer shrub species e.g., *Cadia purpurea* and *Tarchonanthus camphoratus* (Chapter 4 & 5), which may change the once forest-dominated landscape of the escarpment of the western Rift Valley into a shrub-herb dominated degraded vegetation landscape. Therefore, it is important to reduce further anthropogenic pressure on the remnant forests to restore the population of the tree species.

The ecological importance of snags is less understood and has been overlooked. However, studies show that snags are part of the ecological process in the forest ecosystem that should not be over exploited. To prevent loss of nutrients, soils and water, habitats for birds, etc., in the forest ecosystems it is important to leave the snags in the forest. But, places with high snag density should be also carefully managed to reduce potential fire incidents. Climate-driven mortality is difficult to predict, and the frequency of extreme climatic conditions that greatly affect semi-arid habitats is expected to increase (IPCC 2007). Thus, forest managers need to plan for potential tree dieback.

Conservation strategy

It is important to follow the ecosystem strategy of biodiversity conservation that integrates land, water and living resources. The ecosystem approach of biodiversity conservation provides an opportunity to conserve large numbers of species that are rare and whose ecosystem regulating role might not be yet known. Thus, besides the species-rich zones, conservation programs should also consider plant communities that are not species rich but contain endemic and threatened species. In the study area, to conserve a large number of species and plant communities, it is worth establishing a biodiversity conservation corridor along the Tigrean-Afar ecological zones.

However, with the current socio-economic context in northern Ethiopia, it may be difficult to implement some of the recommendations stated above. The expansion of agricultural lands in Tigray has reached its limits, and there is a serious shortage of grazing land, which increases the pressure on the forests and thus makes conservation of forests for their biodiversity values difficult. Thus, it is important to prioritize conservation sites. The *Pterolobium stellatum*—*Celtis africana* community identified at Hugumburda forest, for instance, contains many rare species experiencing extinction and needs conservation priority. *Dracaena ombet*, which is found in the *Dracaena ombet*—*Acacia etbaica* community in Desa'a forest, is listed under the Red List of the IUCN as an endangered species that needs conservation priority. However, a sustainable forest development in the region can be realised when the pressure on the forests from further expansion of agriculture and high demand for biomass energy is reduced. Therefore, it is indispensable to have a strategy for a sustainable rural development that increases the productivity of the agriculture sector. Shortage of wood has also been a

serious problem in the rural and urban areas, and broader rural-urban solutions like establishing fuelwood plantations to reduce the pressure on the remnant forests are necessary.

Income from forest-related economic activities accounts for the second largest share in the average total household income in Tigray. Thus, it is important to develop the forestry sector to improve the rural livelihoods in northern Ethiopia. It is also important to strengthen the forest institutions from national to local levels, so that appropriate policies can be designed and their implementation monitored. There are many successful community-based soil and water conservation and vegetation restoration programs in Tigray. It is important to also implement community-based forest development programs to develop the existing forest remnants.

In conclusion, the results of the present study clearly show that forest disturbance due to human and natural causes has significantly affected the dry Afromontane forests in northern Ethiopia, which need urgent conservation attention. Thus, the findings can provide important information for researchers, conservationists, policy makers, and other stakeholders for conservation of the remnant forests. The study also addresses the lack of information on the vegetation ecology of the two large forest remnants in northern Ethiopia, which is one of the major limitations for students and researchers.

Further research

- The present study is based on few selected environmental factors that determine species distribution patterns in which further investigations on the influence of soil physical and chemical properties on species distribution is needed.
- No empirical evidence on the time and cause for the mass tree dieback exists, which needs further investigations.
- Natural regeneration of tree species in the fragmented forests, even in protected forests from livestock is poor. Thus, further research on the regeneration ecology of key native tree species is recommended. One major limiting factor for poor sapling population that affects the population structure of many native tree species is lack of recruitment of both natural regenerated and planted seedlings that needs further investigations.

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10 APPENDIX

Appendix 10.1 List of species recorded at Desa'a and Hugumburda forests in northern Ethiopia. Abbreviations in the parantheses indicate speices life form, where [C] is climber, [H] is Herb, [S] is shrub, and [T] is tree. Number indicates the site where the species is recorded, where ¹ is Desa'a and ² is Hugumburda forest

Agavaceae

Agave americana L., [H]¹

Cynanchum gerrardii (Harv.) Liede,

[C]¹

Sarcostemma viminale Wall. Ex

Decene., [C]¹

Aloaceae

Aloe camperi Schweinf., [H]^{1,2}

Asparagaceae

Asparagus racemosus Willd., [HS]^{1,2}

Amaranthaceae

Aerva lanata (L.) Juss. ex Schult., [H]¹

Alternanthera nodiflora R.Br., [H]^{1,2}

Cyathula cylindrica Moq., [H]¹

Asteraceae

Echinops giganteus A.Rich., [H]^{1,2}

Laggera tomentosa Sch. Bip. ex Hochst.

[S]^{1,2}

Anacardiaceae

Rhus glutinosa Hochst. ex A.Rich., [T]²

Rhus natalensis Bernh. ex Krauss, [T]²

Rhus retinorrhoea Steud. ex Oliv., [T]¹

Rhus sp., [ST]^{1,2}

Rhus vulgaris Meikle, [ST]²

Psiadia punctulata Vatke, [S]^{1,2}

Vernonia amygdalina Delile, [ST]^{1,2}

Vernonia auriculifera Hiern, [ST]^{1,2}

Tarchonanthus camphoratus L., [HS]¹

Apiaceae

Ferula communis Heuff., [H]¹

Balanitaceae

Balanites rotundifolius Blatt. [H]¹

Apocynaceae

Acokanthera schimperi (A.DC.) Benth.

& Hook.f. ex Schweinf., [ST]^{1,2}

Carissa edulis Vahl, [S]^{1,2}

Barbeyaceae

Barbeya oleoides Schweinf., [T]¹

Berberidaceae

Berberis holstii Engl., [ST]²

Asciopiadaceae

Caralluma acutangula N. E. Br., [H]¹

Boraginaceae

Cordia monoica Roxb., [ST]¹

Cordia sinensis Lam., [ST]¹

Heliotropium cinerascens Steud. ex DC., [S]¹

Cactaceae

Opuntia ficus-indica (L.) Mill., [ST]^{1,2}

Caesalpiniaceae

Cassia occidentalis L., [H]¹

Capparaceae

Boscia salicifolia Oliv., [S]¹

Capparis tomentosa Lam., [ST]¹

Capparidaceae

Capparis cartilaginea Decne., [S]¹

Maerua sp., [HS]²

Celasteraceae

Maytenus senegalensis (Lam.) Exell., [ST]^{1,2}

Clusiaceae

Gymnosporia senegalensis Loes., [S]^{1,2}

Hypericum quartinianum A. Rich., [H]²

Combretaceae

Combretum molle G. Don, [ST]¹

Commelinaceae

Commelina sp., [S]¹

Crassulaceae

Aeonium leucoblepharum Webb ex A. Rich. [S]¹

Kalanchoe sp., [S]²

Cupressaceae

Cupressus lusitanica Mill., [T]²

Juniperus procera Hochst. ex Endl., [T]^{1,2}

Dracaenaceae

Dracaena ombet Kotschy & Peyr., [T]¹

Sansevieria ehrenbergii Schweinf. ex Baker, [H]¹

Sansevieria forskaliana (Schult.f.)

Hepper & J.R.I. Wood, [H]¹

Ebenaceae

Diospyros mespiliformis Hochst. ex A. DC., [T]¹

Euclea racemosa Murray subsp. *schimperi* (A. DC.) F. White, [S]^{1,2}

Ericaceae

Erica arborea L.; [ST]^{1,2}

Euphorbiaceae

Clutia abyssinica Jaub. & Spach, [S]^{1,2}

Clutia lanceolata Jaub. & Spach., [S]¹

Euphorbia abyssinica J.F. Gmel., [T]¹

Euphorbia polyacantha Boiss., [S]¹

Euphorbia tirucalli Forssk., [ST]^{1,2}

Ricinus communis L., [ST]¹

Fabaceae

Acacia abyssinica Hochst. ex Benth.,

[T]^{1,2}

Acacia asak (Forssk.) Wild., [T]¹

Acacia etbaica Schweinf., [T]^{1,2}

Acacia mellifera Benth. [T]¹

Acacia orfota Schweinf., [T]¹

Acacia polyacantha Willd., [T]¹

Acacia saligna (Labill.) H. L. Wendl.;

[T]²

Acacia senegal Willd., [T]¹

Acacia tortilis Hayne, [T]¹

Cadia purpurea Ait. [S]^{1,2}

Calpurnia aurea Benth., [ST]^{1,2}

Colutea abyssinica Kunth &

C.D.Bouche, [S]²

Dichrostachys cinerea (L.) Wight &

Arn., [TS]¹

Indigofera caerulea Roxb., [S]¹

Indigofera arrecta Hochst. Ex A. Rich.,

[S]¹

Nuxia congesta R.Br., [HS]²

Pterolobium stellatum (Forssk.) Brenan,

[CS]^{1,2}

Tephrosia interrupta Hochst. & Steud.,

[S]^{1,2}

Flacourtiaceae

Dovyalis abyssinica (A.Rich.) Warb.,

[ST]^{1,2}

Dovyalis verrucosa Warb., [ST]^{1,2}

Lamiaceae

Becium grandiflorum (Lam.) Pic.Serm.,

[S]^{1,2}

Clerodendrum myricoides R.Br. [S]^{1,2}

Lavandula dentata L., [H]¹

Leucas abyssinica Briq., [H]^{1,2}

Meriandra bengalensis (Roxb.) Benth.,

[S]¹

Otostegia fruticosa Schweinf. ex Penz.,

[HS]¹

Otostegia integrifolia Benth., [H]¹

Plectranthus ornatus Codd., [H]¹

Premna resinosa Schauer, [S]^{1,2}

Lythraceae

Lawsonia inermis L., [ST]¹

Malvaceae

Abutilon longicuspe Hochst. ex A.Rich.,

[S]^{1,2}

Abutilon pannosum (G.Forst.) Schldl.,

[HS]¹

Pavonia urens Cav., [HS]²

Sida schimperiana Hochst. ex A.Rich.,

[S]

Meliaceae

Ekebergia capensis Sparrm., [T]²

Meliantaceae

Bersama abyssinica Fresen., [T]^{1,2}

Moraceae

- Ficus palmata* Forssk., [ST]^{1,2}
Ficus thonningii Blume, [ST]^{1,2}
Ficus vasta Forssk., [T]¹

Myrsinaceae

- Myrsine africana* L., [S]^{1,2}

Myrtaceae

- Eucalyptus camaldulensis* Dehnh., [T]
^{1,2}

Nyctaginaceae

- Commicarpus plumbagineus* Standl.,
 [S]¹

Oleaceae

- Jasminum abyssinicum* R.Br. [CS]^{1,2}
Olea capensis L. subsp. *macrocarpa*
 (C.H. Wright) I. Verd., [T]^{1,2}
Olea europaea L. subsp. *cupidata*
 (Wall. ex G. Don) Cif., [T]^{1,2}

Oliniaceae

- Olinia rochetiana* A. Juss., [ST]²

Passifloraceae

- Adenia* sp., [ST]¹

Phytolaccaceae

- Phytolacca dodecandra* L'Hér., [S]²

Pittosporaceae

- Pittosporum viridiflorum* Sims, [T]^{1,2}

Podocarpaceae

- Afrocarpus falcatus* (Thunb.) C.N.Page,
 [T]¹

Polygonaceae

- Rumex nervosus* Vahl, [H]^{1,2}

Ranunculaceae

- Clematis sinensis* Lour. [SC]^{1,2}

Rhamnaceae

- Berchemia discolor* Hemsl., [ST]
Rhamnus staddo A.Rich., [ST]
Sageretia thea (Osbeck) M.C.Johnst.,
 [S]^{1,2}
Ziziphus mucronata Willd., [ST]¹
Ziziphus spina-christi Willd., [ST]^{1,2}

Rhizophoraceae

- Cassipourea malosana* Alston, [T]²

Rosaceae

- Hagenia abyssinica* J.F.Gmel., [T]²
Rosa abyssinica R.Br., [S]^{1,2}

Rubiaceae

- Canthium oligocarpum* Heirn, [S]^{1,2}
Canthium setiflorum Hiern, [S]¹

Pyrostria phyllanthoidea (Baill.)

Bridson, [S]²

Psydrax schimperiana (A. Rich.)

Bridson, [ST]^{1,2}

Rutaceae

Teclea simplicifolia I. Verd., [T]²

Salvadoraceae

Dobera glabra Juss. ex Poir., [T]¹

Salvadora persica L., [ST]²

Santalaceae

Osyris quadripartita Salzm. Ex Decne.,

[S]^{1,2}

Sapindaceae

Allophylus abyssinicus Radlk. [T]²

Dodonia viscosa Jacq., [S]^{1,2}

Pappea capensis Eckl. & Zeyh., [T]^{1,2}

Sapotaceae

Mimusops laurifolia (Forssk.) Friis, [T]

¹

Spiniluma oxyacantha (Baill.) Aubrev.,

[ST]^{1,2}

Solanaceae

Discopodium penninervium Hochst.,

[ST]¹

Lycium shawii Roem. & Schult., [H]¹

Solanaceae

Solanum adoense Hochst. ex A. Braun,

[H]¹

Solanum incanum L., [H]^{1,2}

Solanum schimperianum Hochst., [H]^{1,2}

Withania somnifera (L.) Dunal, [S]²

Sterculiaceae

Dombeya torrida (J.F. Gmel.) Bamps,

[T]^{1,2}

Sterculia africana (Lour.) Fiori, [T]¹

Tiliaceae

Grewia bicolor Juss., [ST]¹

Grewia kakothamnos K. Schum., [S]¹

Grewia ferruginea Hochst., [ST]^{1,2}

Grewia mollis Juss., [ST]¹

Grewia schweinfurthii Burret, [ST]¹

Grweia sp., [ST]²

Grewia tenax (Forssk.) Fiori, [S]

Ulmaceae

Celtis africana Burm. f., [T]²

Lantana viburnoides Vahl, [S]^{1,2}

Verbenaceae

Clerodendrum myricoides R.Br. [S]^{1,2}

Vitaceae

Cissus quadrangularis L., [H]²

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