Available online at http://www.journalijdr.com

International Journal of DEVELOPMENT RESEARCH

IJDR

ISSN: 2230-9926

International Journal of Development Research
Vol. 5, Issue, 03, pp. 3745-3754, March, 2015

Full Length Research Article

WOODY PLANT DIVERSITY ALONG DISTURBANCE GRADIENTS IN THE NORTHERN AFRO-MONTANE FORESTS OF THE BALE MOUNTAINS, ETHIOPIA

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ARTICLE INFO

Article History:
Received 22nd December, 2014
Received in revised form
28th January, 2015
Accepted 02nd February, 2015
Published online 31st March, 2015

Key words:
Abundance,
Conservation,
Disturbance,
Diversity,
Gradient,
Invasion,
Woody species.

ABSTRACT

The effects of human disturbances on woody plant species diversity was assessed by comparing species richness, Shannon diversity and evenness, population abundance and composition along three disturbance gradients in the northern Bale Mountains, Ethiopia. Data on woody plant species were collected in six forest patches along three levels of disturbances in 20 by 20 m^{-2} quadrates in each forest patches. Plant species richness peaked at the Moderately Disturbed (MD) site either when trees and shrubs were treated separately or pooled together, but similar between the Low disturbed (LD) and Heavily Disturbed (HD) sites. Overall population density of woody plants was also significantly higher in the MD site, followed by the LD site. The three site groups had distinct species assemblages. Species that contributed most to the differences between the MD and the others were shrubs, which were degradation tolerant; while the difference between LD and HD sites were due to degradation and/or local disappearance of some tree species in the HD site. This result suggest that the consequence of human disturbance on woody plant diversity appeared to be both positive and negative depending on the type and intensities of the disturbances. In comparison to the LD sites, disturbances such as high selective logging and grazing had resulted in increased richness and density of woody plants in the MD sites, while these and crop cultivation and settlement encroachments in the HD site resulted in decreased population abundances. However, the increased diversity in the moderately disturbed site was due to additions of shrub species, which have affinities to disturbed habitats. Since the central goal of conservation is to maintain maximum diversity of native species, but there is a potential of non-native species displacing the native ones in the long-run, and hence the high diversity reported here in the MD site should, therefore, be interpreted cautiously.

INTRODUCTION

Degradation and deforestation of tropical forests due to anthropogenic activities are the major causes of decline in global biodiversity (Heywood, 1995). This is exacerbated in developing countries like Ethiopia where the livelihood of their nations is directly or indirectly linked to the natural resources (van Schaik *et al*., 1997 and Struhsaker *et al.,* 2005). Therefore, in many areasmitigating of the impacts and restoration of disturbed ecosystems is being taken up on a priority basis both for biodiversity conservation and for maintaining ecosystem functions (Bleher *et al*., 2006). This, in turn, requires detailed understanding of the relationship between human activities and biodiversity. Human-induced disturbances such as conversion of forest land to cultivation fields, livestock over grazing, selective logging and settlement encroachments are generally considered to be among the major causes for habitat alterations (Sekercioglu, 2002, Sinclair *et al*., 2002, Millennium Ecosystem Assessment, 2005, Chown, 2010). However**,** research on this subject, particularly in the developing countries, has been limited (Chown 2010) and results are often controversial (Li *et al*., 2004, Chown 2010). Some studies reveal clearly reduced species richness in degraded forests (Parthasarathy 1999; Addo-Fordjou *et al*., 2009), while in other studies it is increased (Kappelle *et al.,* 1995; Fujisaka *et al.,* 1998, Molino

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and Sabatier, 2001, Kumar and Ram 2005, Mishra *et al.,* 2004, Senbeta *et al.,* 2005, Bongers *et al.,* 2009). Of the main reasons for such disparities between the findings is that the impact of disturbance on biodiversity depends on the type, frequency and intensities of disturbances, and biome/ ecosystem concerned (Connell, 1978, Li *et al.,* 2004, Mishra *et al.,* 2004, Bongers *et al.,* 2009). Both theoretic (e.g. Connell, 1978) and empirical studies (Fox, 1979, Kumar and Ram 2005, Mishra *et al.,* 2004, Senbeta *et al.,* 2005) have suggested that increased diversity in response to disturbances is mostly achieved at intermediate level of disturbances. Thus, given such conflicting results have been reported and in view of the growing threat to biodiversity, it is important to see at local-scale how natural communities are affected by anthropogenic disturbances in order to make effective and efficient conservation measures.

In this paper, we report a result of study conducted to determine the impact of human-induced disturbance on woody plant diversity in the northern dry afromonatane forets of the Bale Mountains, south-eastern Ethiopia. The Bale Mountains region contains relatively intact Afromontane forest remaining in the highlands of the country (NH 2004, Williams *et al.*, 2004). It is recognized as a biodiversity hotspot by Conservation International (Williams *et al.,* 2004), and as a center of diversity and endemism, where many of the plant and animal species are also locally endemic to the mountains themselves (see NH 2004, Asefa 2006/08 2011, Largen and Spawls 2011 for more information on biodiversity of the Bale Mountains). The ecological importance of the region was acknowledged by establishment of the Bale Mountains National Park (BMNP) at the heart of these mountains in 1971. The BMNP was proclaimed to conserve the ecological and hydrological systems, and the rare, threatened and endemic floral and faunal species of the region (Hillman 1986, OARDB 2007). However, like so many of Africa's protected areas (Struhsaker *et al.,* 2005), the BMNP and the surrounding areas have been under increasing pressure from an ever-growing human population in the surrounding area and immigrants from other regions (Stephens *et al.,* 2001, NH 2004, Williams *et al.,* 2004, OARDB, 2007).

Consequently, settlement, subsistence cultivation, fire, livestock grazing and selective logging have been increasingly threatening biodiversity and ecosystems within the Bale Mountains (Hillman, 1986, Miehe and Miehe, 1994, Stephens *et al.,* 2001, OARDB, 2007, Asefa, 2008, Abera and Kinahan 2011, Teshome *et al.,* 2011). The dry Afromonatane forests of the Bale Mountains occurs in the northern slope of the mountains and represents one of the few remnant forest of this type persisting in the country (Demissie, 2007, OARDB, 2007). It holds, *inter alia*, about two-third of the entire total population of the globally endangered endemic mountain nyala (*Tragelaphusbuxtoni*; Refera and Bekele, 2004). This forests cape has been impacted by settlement, agriculture, livestock grazing and selective logging (OBARD, 2007). However, the consequences of such impacts on flora of the area have been less examined (Asefa 2013).Previous studies examining human impact on these forests were mainly focusing on land cover/land use changes (Demissie, 2007, Teshome *et al.,* 2011). Research on the effect of human disturbance on species composition of the forests has been lacking. The objectives of this study were, therefore, to examine whether differences in woody species diversity exist among forest patches with different types and levels of disturbances in the northern dry ever green Afromontane forest of the Bale Mountains of Ethiopia.

METHODS

Study area

The Bale Mountains region is located 400 km southeast of Addis Ababa, the capital of Ethiopia. It covers 22,176 km^{-2} of which 2 200 km^{-2} designated as the BMNP at 6° 30'- 7° 10' north, and 39° 30'- 39° 55' east (Fig. 1). The area experiences two rainy seasons, the small rains from March to June and the heavy rainy season from July to October, with a dry season from November to February; mean annual rainfall is 1219 mm. Five broad vegetation zones occur in the Bale Mountains eco-region, namely the northern grasslands (flat area at altitude of 3000m *asl.*), the northern dry ever green Afromontane forest (2900-3400 m *asl.*), ericaceous forest (3400-3800m *asl.*), the Afroalpine moorland and grassland (3800-4377m*asl.*), and the southern Harenna forest (1500-3200 m *asl.*; Hillman 1986, Miehe and Miehe 1996, NH, 2004, OARDB, 2007).

This study was undertaken in the northern dry ever green Afromontane forest which occurs in six isolated patches (Fig. 1). Due to the spatial location of these forest patches relative to protected area infrastructure and manpower, such as amount of patrolling activities, some of these patches are under great pressure due to human activities than others (Hillman, 1986, OARDB, 2007, Teshome *et al.,* 2011, Yosef *et al.,* 2012, Mitiku, 2013). Three patches (Adellay, Boditti and Dinsho Hill) are inside the protected BMNP and are relatively well protected than the other three patches (Angesso, Shaya and Darkina) which are partly outside the park. Although all the patches are impacted by human use (mainly through agriculture, settlement, grazing and logging), nature and intensities of disturbances vary among them (Asefa, 2013).

Sampling

Using previous disturbance data collected by Mitiku (2013) in each forest patch, the six forest patches were classified in to one of three categories of disturbance gradients (based on the forms and severities of these disturbances recorded at each of them) as: little disturbed (hereafter referred to as LD), moderately disturbed (MD) and heavily disturbed (HD) sites. LD sites are those forest patches where there were no settlement and crop cultivation, and with relatively low level of logging and grazing; MD sites are those where there were no to low (< 5% cover) crop cultivation and settlement (<3 houses ha^{-1}), but relatively with high levels of logging and grazing; and HD sites are those where crop cultivation and settlement are common (> 65% coverage), and logging and grazing are relatively high level. Accordingly, the protected three patches (Adellay, Boditti and Dinsho Hill) were classified as LD sites, Shaya and Angesso as MD disturbed and Darkina as HD sites (for detail see Mitiku, 2013). This site category was used for subsequent vegetation data analysis. In each forest patch, five line transects of 1km long were randomly placed parallel to each other along on an altitudinal gradient (between 2900 to 3400m *asl*.) and spaced a minimum of 300 m from each other. The exception was that only two transects were sampled in Angessodue to logistic constraints, and, thus, these were pulled together with Shaya forest transects for analysis as these two forests occur in contiguous and are under similar land use types (Mitiku 2013). On each transect four 20 m × 20 m quadrates were established to collect data on tree species abundances (individuals with dbh> 2.5 cm). For shrubs and lianas, this was done by dividing each quadrat in to four 10 m × 10 m sub-quadrates (Newton, 2007). Species identification was carried out at field by expertise and aided by a floral guidebook of Adi and Fichtl (1994). Specimens were also collected and further confirmed by comparing with existing herbarium specimens and deposited at the BMNP research museum.

Data analysis

Species diversity of each site group was assessed using four biodiversity measures: sample-based rarefaction curves (i.e. estimating species density, or number of species per unit area), individual-based rarefaction curves (i.e. estimating species richness, or number of species of a particular site), exponential Shannon diversity index (evenness of relative abundances) and Shannon diversity index (combination of richness and evenness) in Estimate S software (Colwell 2009; http:// viceroy.eeb.uconn.edu/estimates). Sample-based rarefaction curves were computed using a Mao Tau moment-based interpolation method. The sample-based data were rescaled by the number of individuals to compute individual-based curves using the Coleman method (Colwell and Coddington, 1994, Colwell, 2009, Colwell, 2009). All these analyses were conducted allowing a randomization of 500 without sample replacement (Colwell, 2009) separately for trees, shrubs (lianas were treated with shrubs as they were fewer in numbers) and combination of trees and shrubs (hereafter referred to as woody plants). Thereafter, for each comparison of species density, richness and diversity examined, the curves were rarefied to the lowest number of sample (quadrates for sample-based, or individuals for individual-based) recorded in a given site (Gotelli and Colwell 2001, Colwell 2009).

Further, differences in mean species density (based on raw data of number of species recorded per sample unit) and mean population density (number of individuals ha^{-1}) of trees, shrubs and woody plants were also separately compared between the site groups using One-way Analysis of Variance in SPSS version 20 software (IBM Corporation, 2011). Multiple mean comparisons were made using Tukey's Post hoc tests (Quinn and Keough, 2002). ANOSIM (Analysis of similarity) was implemented using PRIMER software (Clarke and Gorley, 2006) to assess variations in species composition of trees, shrubs and all woody plant species among site categories using abundance data obtained for every species at each sampling point. A Bray-Curtis similarity index was used to calculate similarities in composition among assemblages; data were square-root transformed beforehand to down-weight common species relative to those that are rare (Clarke and Gorley, 2006). Global R values were used to determine the degree of similarity among treatments. This is a non-parametric permutation procedure applied to rank similarity matrices underlying sample ordinations (Clarke and Gorley, 2006). The closer the value of R value is to 1, the more dissimilar species assemblages are. In addition, similarity percentage analysis (SIMPER) was conducted in PRIMER software to calculate the percentage contribution each species made to the dissimilarities between each pair of the three assemblages using overall woody species data (Clarke and Gorley 2006).

RESULTS

Species density, richness and diversity

A total of 23 woody species (eight tree and 15 shrub/liana species), belonging to 17 plant families, were recorded across all sites (Table 1). Of these, 16 (70% of the total), 19 (83%) and 12 (52%) of the woody species, six, seven and three of the tree species, and 10,12 and eight of the shrub species were from the LD, MD and HD sites, respectively (Table 2). When the sample-based (Mao Tau) curves were rarified to the smallest sample size sampled in the HD site (n = 22), the MD site contained the highest species density (i.e. number of species per unit area) for all the three plant functional groups (i.e. woody species, trees and shrubs) than the LD and HD sites. However, a difference in rarefied species density between the LD and HD sites was revealed only for trees, which was higher in the LD sites (Table 3, Fig.2). Similar results were found when the out puts of the rarefied individual-based sampling curves (i.e. species richness) were compared except that equal tree species richness between the LD and HD site groups (Table 3).

ANOVA indicated that mean number of species per ha (based on raw data) varied significantly for trees ($F_{1,24}$= 8.514, $P <$ 0.005), shrubs ($F_{1,24}$: 30.829, $P < 0.005$) and woody plants ($F_{1,24}$ = 31.506, $P < 0.005$; Table2). The MD sites had significantly greater mean species density than the other two site groups for all plant functional groups, except equal mean number of tree species with the LD sites. However, no significant difference was found between the LD and HD site groups for all plant functional groups (Table 2). Both Shannon diversity and exponential (i.e. evenness) indexes also revealed diversity of all plant functional groups were highest in the MD sites followed by LD and HD, except that similar diversity and evenness of shrubs between LD and HD sites (Fig.3).

Population density and species composition

Significant variations on mean population densities were found among sites for shrubs ($F_{2,107}$= 24.501, $P < 0.05$) and woody plants ($F_{2,107}$ = 34.030, $P < 0.05$), but not for trees ($F_{2,107}$ = 1.316, $P > 0.05$, Table 2). Pair-wise comparison of sites showed that shrub population density was significantly higher in the MD sites compared to the LD and HD sites, which themselves were similar. Mean population density of woody plants was significantly highest in the MD site and lowest in the HD site (Table 2). Species composition of the three assemblages differed significantly from each other when either trees or shrubs were examined separately or combined (for each pair of comparison made: R = 0.112-0.958; P< 0.05; Table 4, Fig.4). Species that contributed most to the dissimilarities between the MD and LD, and between

Table 1. List of plant species recorded from the study areas

Scientific name	Family	Local name (in Afan Oromo)
Asparagus africanus Lam.	Asparagaceae	Seriti
*Carissa spinarum*L.	Apocynaceae	Harangma
*Clematis hirsuta*Perr. &Guill.	Ranunculaceae	Fittii
*Crotolaria agatiflora*Schweinf. Sub.sp. *Erlangeri*Bak. F.	Fabaceae	Shashamane
*Discopodium eremanthum*Chiov.	Solanaceae	Merero
Echinops macrochaetus	Asteraceae	Kabaricho
Euphorbia dumalis S. Carter	Euphorbiaceae	Gurii
Hagenia abyssinica (Bruce) J.F. Gmel.	Rosaceae	Hexxo
Hypericum revolutum Vahl.	Hypericaceae	Garamba
Inula confertiflora A. Rich.	Asteraceae	Haxxawii
Juniperus procera L.	Cuprussaceae	HindesaAdi
Leonotis ocymifolia (Burm.f.) Iwarsson	Lamiaceae	Bokolu
Maytenus arbutifolia (Hochst. ex A. Rich.) Wilztek	Celastraceae	Kombolcha
Myrsine africana	Myrsinaceae	Qachamo
Olea europaesubsp.Cuspidata	Oleaceae	Ejersa
Osyris quadripartita Decn.	Santalaceae	Karo
*Phytolacca dodecandra*L'H´erit.	Phytolaccaceae	Handode
Rapanea melanophloeos	Myrsinaceae	Tulla
Rosa abyssinica Lindley	Rosaceae	Gora
Rubuss teudneri Schwienf.	Rosaceae	Gora
Scheffler avolkensii (Engl.) Harms	Araliaceae	Ansha
*Solanum anguivi*Lam.	Solanaceae	QoreWorabesa
*Solanum marginatum*L.f.	Solanaceae	Hiddi

Table 2. Mean number of species (number of species per ha) and of population density (number of individuals per ha) of plants recorded in the different site groups

Plants	Site*	n	S	N	S (mean ± S.E.)**	N (mean ± S.E.)**
	LD	22	6	719	3.60 ± 0.91^{a}	8.67 ± 1.12^{a}
Trees	MD	31	7	263	4.71 ± 0.95^{ab}	7.06 ± 1.16^{a}
	HD	66	3	114	2.40 ± 1.14^{ac}	6.44 ± 1.16^{a}
	LD	22	10	569	3.40 ± 1.18^{a}	7.77 ± 1.15^{a}
Shrubs	MD	31	12	1360	8.43 ± 1.51^{b}	31.94 ± 1.20^{b}
	HD	66	8	117	3.20 ± 2.17^{a}	6.31 ± 1.24^{a}
	LD	22	16	1288	7.00 ± 1.77^{a}	16.23 ± 1.13^{a}
Woody plants	MD	31	19	1623	13.14 ± 1.77^{b}	43.45 ± 1.15^{b}
	HD	66	12	231	5.60 ± 2.41^{a}	6.75 ± 1.19^{c}

n, number of quadrats; S, total number of species density; N, total number of individuals; S.E., standard error
* LD, low disturbed; MD, moderately disturbed; HD, heavily disturbed
**Different letters denote Tukey's*Post hoc* mean differences at $P < 0.05$.

Table 3. Overall and rarefied species density [based on number of species observed (Sobs)] and species richness (Coleman) of trees, shrubs and woody plants across the site groups (Sites abbreviations as defined on Table 2)

	Tree			shrub			Woody species		
Estimator	LD	MD	HD	LD	MD	HD	LD	MD	HD
Sobs (Overall)	7	8	5	10	12	8	18	20	12
Coleman (Overall)	7	9	5	11	12	8	18	20	12
Sobs (Rarefied)	6	9		9	12		14	20	
Coleman (Rarefied)	5	9		10	12		12	18	

Table 4. R-statistics values of the ANOSIM result of plant assemblages (trees, shrubs and woody plants) in the protected and unprotected sites in the Afromontane forest of the BMNP. R represents measures of dissimilarity between assemblages; the closer significant values of Rare to 1, the larger the differences between assemblages (in all case P < 0.05, except for trees between LD and MD sites; Sites abbreviations as defined on Table 2)

	Trees		Shrubs		Woody plants	
Sites	LD	MD	LD	MD	LD	MD
MD	0.112		0.735		0.662	
HD	0.334	0.930	0.660	0.850	0.709	0.958

Table 5. SIMPER analyses for woody plant abundance between LD and MD (a), LD and HD (b) MD and HD (c) areas (only those species that contributed 60%-70% to the average dissimilarities are listed). Group/site description as defined on Table 2; Av. abund. = average abundance, Av.Diss = average dissimilarity, Cum. % = cumulative percentage of similarity

a) Groups: LD vs. MD					
	Group LD	Group MD			
Species	Av.Abund	Av.Abund	Av.Diss	Contrib%	Cum.%
Rubus steudneri	0.53	7.06	9.91	15.08	15.08
Inula confertiflora	0.00	5.63	7.94	12.08	27.16
Carissa spinarum	0.00	4.00	5.99	9.12	36.28
Clematis hirsuta	0.95	3.58	4.43	6.74	43.02
Solanum marginatum	3.31	1.40	4.38	6.66	49.68
Euphorbia dumalis	2.78	4.21	4.29	6.53	56.21
Rapanea melanophloeos	3.15	4.05	3.65	5.55	61.76
b) Groups: LD vs. HD					
	Group LD	Group HD			
Species	Av.Abund	Av.Abund	Av.Diss	Contrib%	Cum.%
Hypericum revolutum	3.15	0.00	9.39	13.40	13.40
Rapanea melanophloeos	3.15	0.49	8.60	12.27	25.67
Euphorbia dumalis	2.78	0.00	8.34	11.91	37.58
Solanum marginatum	3.31	0.94	7.65	10.92	48.49
Discopodium penninerum	0.34	2.85	7.53	10.75	59.24
Juniperus procera	3.27	3.21	5.54	7.90	67.15
c) Groups: MD vs. HD					
	Group MD	Group HD			
Species	Av.Abund	Av.Abund	Av.Diss	Contrib.%	Cum.%
Rubus steudneri	7.06	0.00	11.97	15.59	15.59
Inula confertiflora	5.63	0.55	8.52	11.10	26.69
Euphorbia dumalis	4.21	0.00	6.99	9.11	35.80
Carissa spinarum	4.00	0.00	6.94	9.05	44.85
Rapanea melanophloeos	4.05	0.49	6.22	8.10	52.95
Clematis hirsuta	3.58	0.00	5.96	7.77	60.72

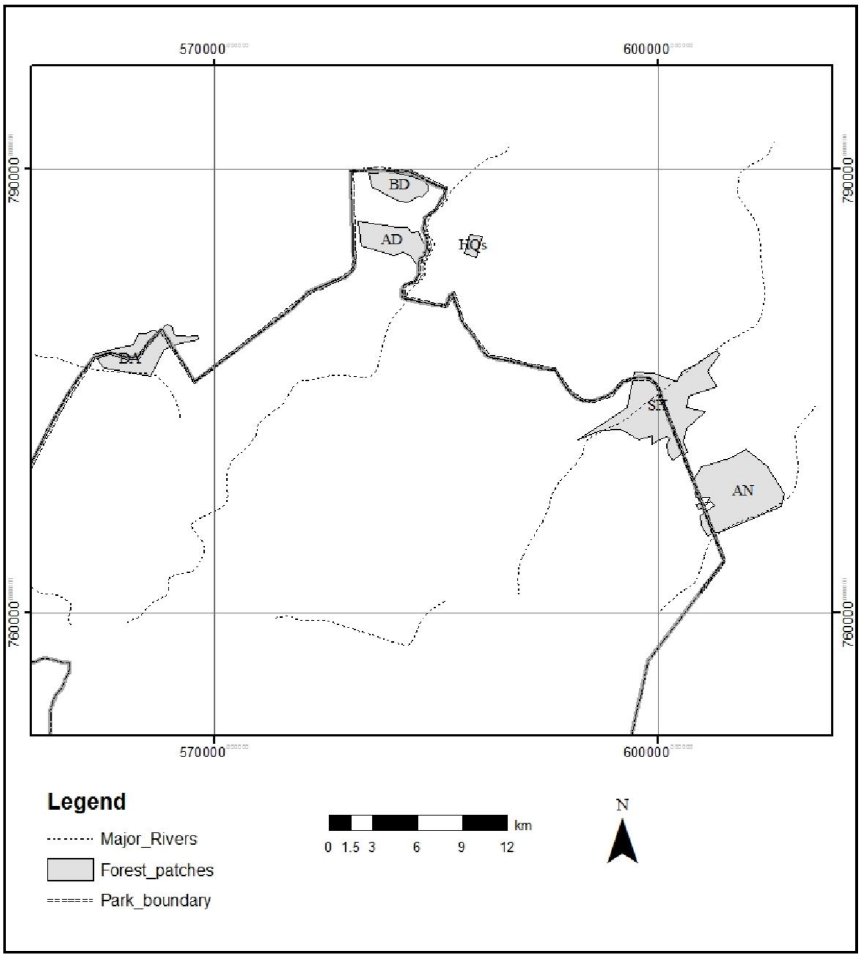


Figure 1. Map of the Bale Mountains National Park (only partly shown) and the six forest patches studied. Abbreviations of the patches: AN = Angesso; SH = Shaya; HQs = Dinsho Hill (BMNP HQs); AD Adellay; BD = Boditti; and DA = Darkina

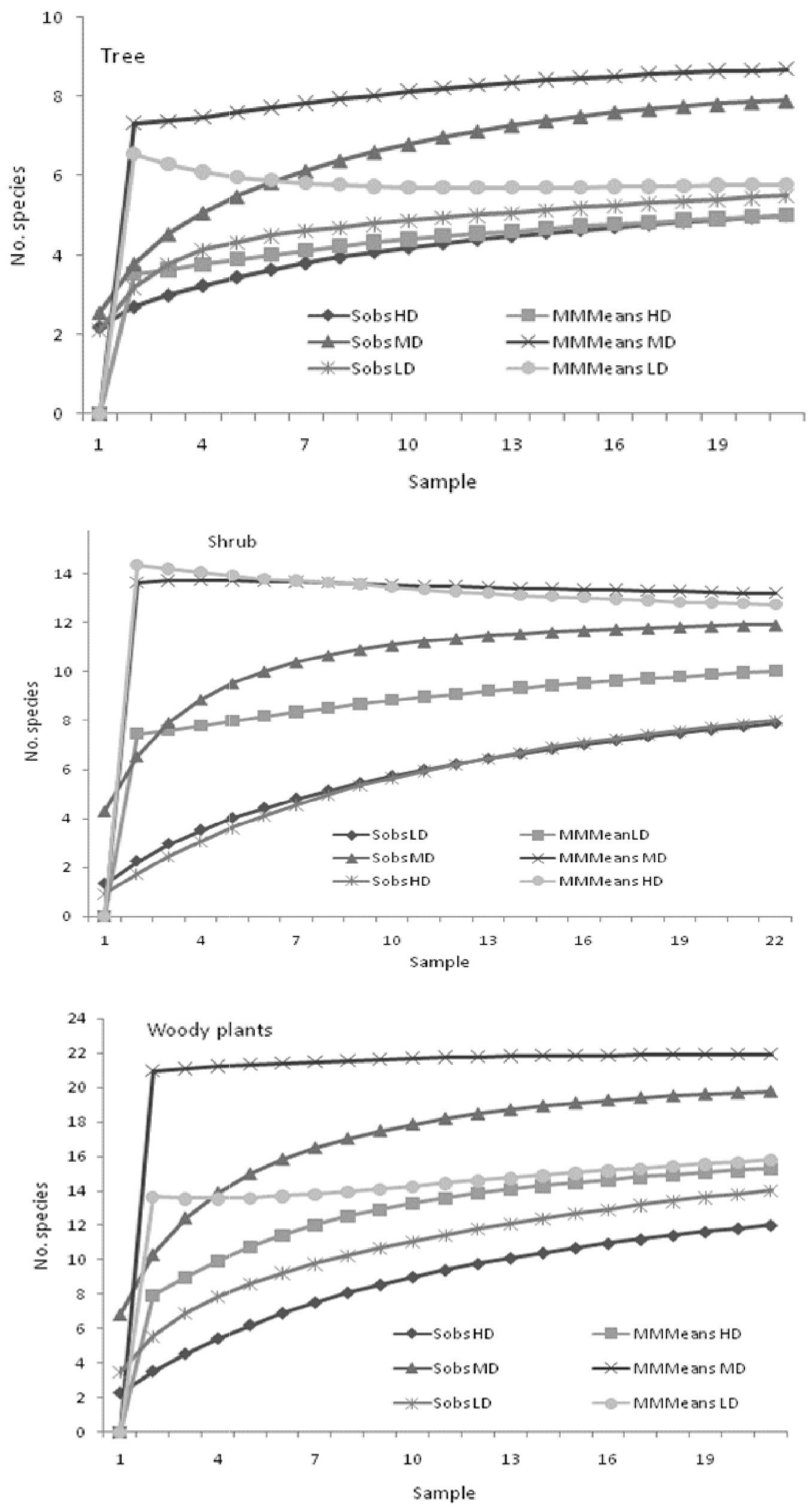


Figure 2. Sample-based (based on the observed number of species (Sobs) and richness estimator (Chao 1 richness estimator) tree, shrub and woody plants species rarefaction curves for the LD, MD and HD sites

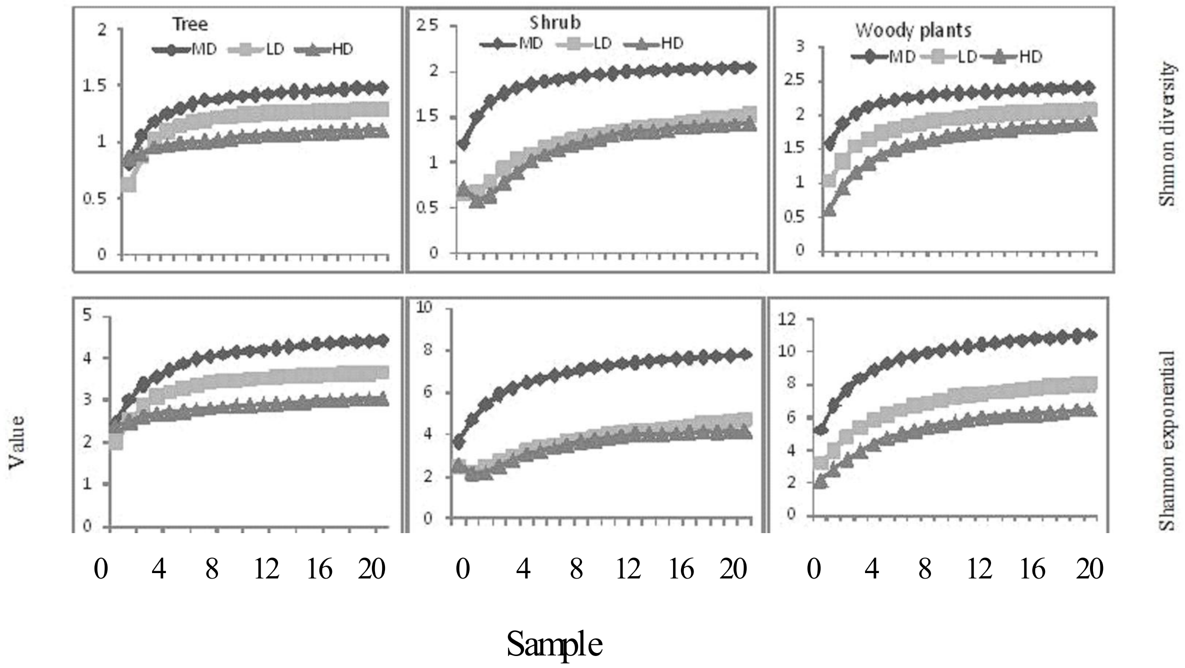
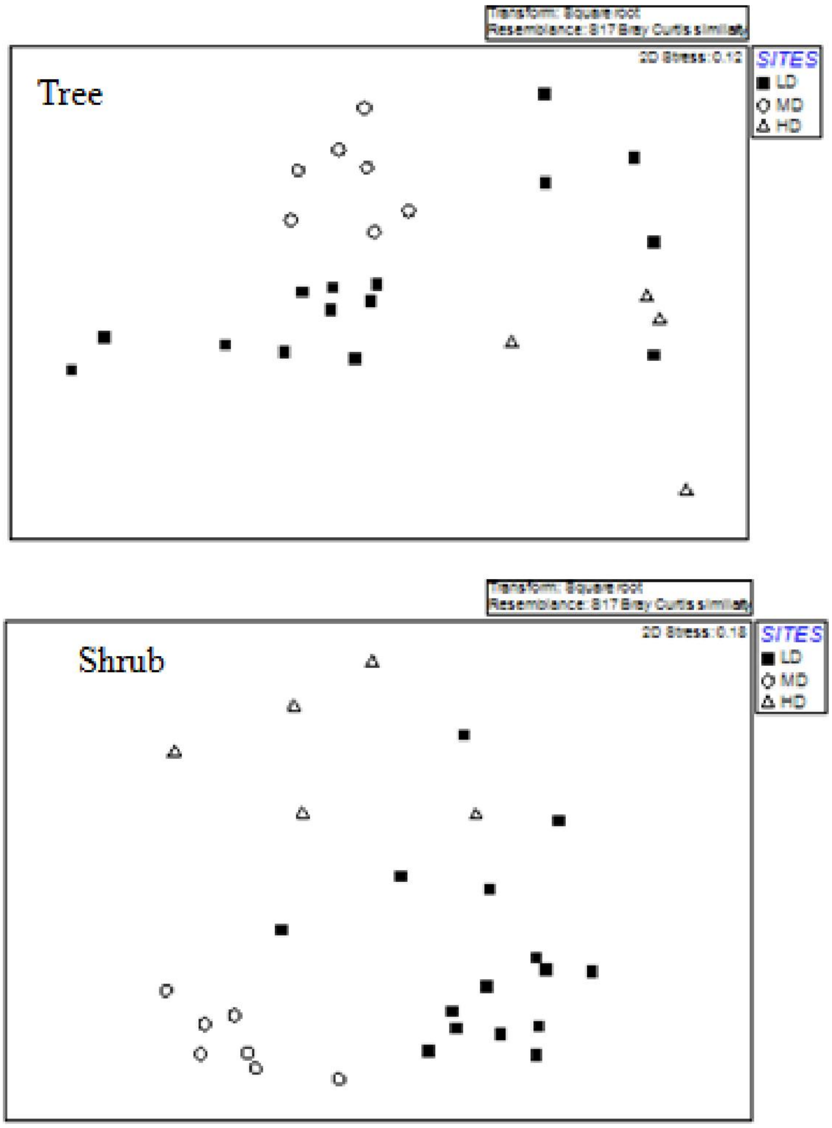


Figure 3. Shannon diversity and exponential Shannon evenness indexes of plant functional groups for each site groups



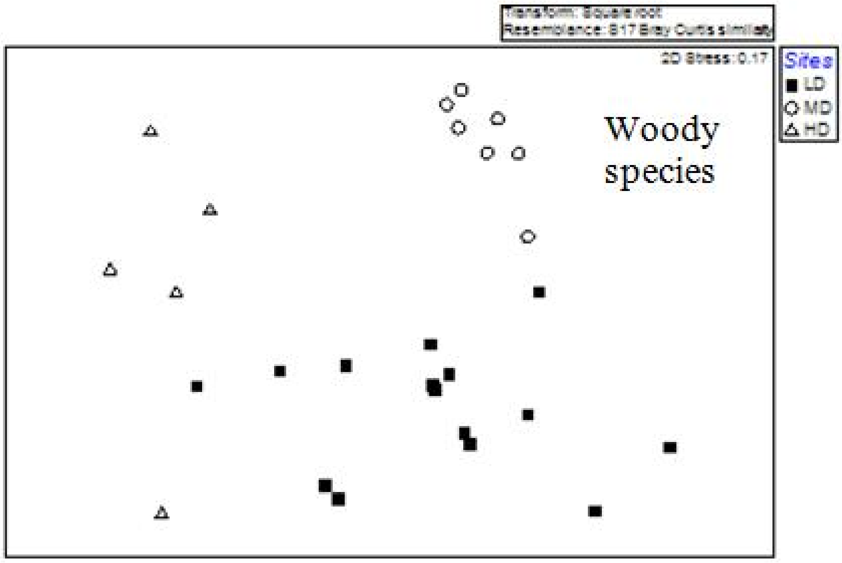


Figure 4. Non-metric multi-dimensional scaling (nMDS) ordination of plant assemblages (trees, shrubs and woody plants) from each sampling trees, shrubs and woody plants point in the protected and unprotected sites in the Afromontane forest of the BMNP. Sites abbreviations as defined in Table 2

the former and HD site were mostly shrubs; namely, *Rubussteudneri, Inulaconfertiflora* and *Carissa spinarum* (Table 5a and b). These species were among the most dominants in the MD site (contributed 49 % to the total abundance of woody plants). However, trees such as *Juniperusprocera* and *Hypericumrevoluteum* were characteristics of the LD sites and distinguished it from the HD site (Table 5c).

DISCUSSION

Human-induced disturbances are the major causes for changes in forest structure and composition (Kumar and Ram 2005), and the extent of these effects are dependent on the type and severities of the disturbances (Chown, 2011). As expected, the present study demonstrated that vegetation diversity vary along disturbance gradients in the studied forests. Overall woody plant, tree and shrub species richness were generally higher at MD site, but the LD and HD sites had almost similar species richness either when trees and shrubs were analyzed separately or combined. Such increased plant species richness at moderate level of disturbance has been often reported by several authors (e.g. Mishra *et al.,* 2004, Senbeta *et al.,* 2005, Bongers *et al.,* 2009). The authors have suggested that at moderate level of disturbance conditions necessary for germination, establishment and growth is created, leading to co-existence of several species. Similar to richness, population density of woody plants was also highest in the MD and lowest in the HD disturbed sites. The observed differences in terms of richness and population density could be attributed to the underlying differences among the sites in types and level of disturbances. In the MD the main disturbance type are selective logging and livestock grazing, while these and agricultural and settlement expansion in the HD site (Mitiku, 2013). Selective logging creates canopy openings that readily favor the germination and growth of light-demanding plant species, thus, leading to increased diversity and density of woody plants. Herbivory actions, however, has two opposing consequences; the removal of herbaceous cover may be important for the germination and survival of unpalatable weedy species, but for those palatable species it could hinder their regeneration due to up-rooting of seedlings and saplings and removal of meristematic tissues (Tesfaye *et al*., 2002, Bleher *et al.,* 2004, Newton, 2007). In contrast, plough up of land for cultivation removes understory vegetation and younger individuals of woody plants in the HD site, which suppresses the regeneration and recruitment of tree and shrub species. The studied forests differed not only in terms of species richness and population density, but also in their species composition. As revealed from the similarity analysis, the only non-significant difference observed wasin their tree species composition between the LD and MD sites. This shows: (1) the persistence of tree species in MD site which are characteristics of the original landscape (i.e. assuming that the LD sites represent the original landscape), in contrast, local extinction of some tree species (e.g. *Hypericum revoluteum*) in the HD site; and (2) changes in species composition of shrubs in the MD and HD sites.

These facts were clearly demonstrated with the outcome of SIMPER analyses (Table 5a-c). Species that distinguished the MD most from the LD and HD sites were mostly shrub species, such as, *Rubus steudneri, Inula confertiflora* and *Carissa spinarum* (Table 5a and b). These species are considered as characteristics of secondary forests, growing at forest edges and along roadsides, usually indicating disturbances (Adi and Fichtl, 1994). Therefore, the findings that the MD disturbed site contained higher richness and density of woody plants than the LD and HD sites should be interpreted cautiously, as the increased diversity at moderate level of disturbance are due to additions of non-native and/or invasive species in the expenses of the native ones, a phenomenon with paramount ecosystem consequences (Hobbs and Huenneke, 1992, Parker *et al.,* 1999, Richardson *et al.,* 2000, Sala *et al.,* 2000, Stein *et al.,* 2000, Chown, 2010). Contrary to the general supposition that invasive species that are favored by degradation of habitats may be expected to be more abundant in the moderately disturbed habitat, Solanummarginatum L. was found to be one of the most abundant and characteristic of the LD (Table 5),contributing high percentage value to the dissimilarities between the LD site and the other sites. This shrub species has been considered as an invasive weedy plant growing in degraded habitats (Adi and Fichtl, 1994). Previous study showed that mountain nyala (Tragelaphusbuxtoni), an ungulate species with 95% of its total global population restricted to the LD sites (Refera and Bekele, 2004), is one of the seed dispersal agents of this shrub species (Asefa, 2005). Thus, the increased abundance of S. marginatum L. seems to follow the abundance of its seed disperser, mountain nyala. The implication of this finding could be, therefore, in addition to the presence of favorable environmental conditions necessary for the seed germination, seedling growth and establishment of population of such species in degraded habitats, the presence of seed source in the vicinity and arrival of the seeds at the appropriate sites are required.

This study has shown that the consequence of human disturbance on woody plant diversity was both positive and negative depending on the type and intensities of the disturbances. Disturbance had resulted in increased species richness and population density of trees, shrubs and overall woody species in the MD sites compared to the LD sites. The converse was true for the HD site where intensities crop cultivation and settlement encroachments are practiced. However, the increased diversity in the moderately disturbed site was due to additions of shrub species, which are known to have affinities to disturbed habitats. Since the central goal of conservation is to maintain maximum diversity of native species (Hobbs and Huenneke 1992), the high diversity reported in the moderately disturbed site in the present study should, therefore, be interpreted carefully. This is because such non-native species could displace the original species through succession; perhaps, leading to ecosystem alterations. Therefore, the current ranger-based resource protection activities practiced in the LD should be strengthened, and should be extended to the MD and HD sites in order to mitigate the prevailing disturbances in the areas reported here. Alternatively, designating the forests as community-based conservation areas might be useful to ensure a regulated and sustainable natural resource use in the areas. Finally, future studies focusing on the impacts of disturbances on the regeneration and population structure of woody species in the present area would be of paramount to increase our understanding of the subject matter.

Acknowledgments

We are grateful to Jemal Kassim and Usman Abdella for their help during the data collection. This study was funded by the Fitzpatrick Institute of Ornithology Centre of Excellence/ University of Pretoria and Frankfurt Zoological Society-Bale Mountains Conservation Project. We are also thankful to the Ethiopian Wildlife Conservation Authority/Bale Mountains National Park for the study permission given.

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