BIODIVERSITAS
Volume 16, Number 1, April 2015
Pages: 95-101

ISSN: 1412-033X
E-ISSN: 2085-4722
DOI: 10.13057/biodiv/d160113

Comparison of woody species diversity between managed and unmanaged forests considering vertical structure in Hyrcanian forests, Iran

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Manuscript received: 27 January 2015. Revision accepted: 13 March 2014.

Abstract. *Nouri Z, Zobeiri M, Feghhi J, Amiri GZ, Marvie Mohadjer MR. 2015. Comparison of woody species diversity between managed and unmanaged forests considering vertical structure in Hyrcanian forests, Iran. Biodiversitas 16: 95-101.* Biodiversity conservation is increasingly considered a key to sustainable forest management and understanding biodiversity in forest ecosystems is essential to reveal forest dynamics, so this study aims to compare tree and shrub species diversity and vertical species distribution between two managed and unmanaged forest stands. The study area was consisted of two adjacent districts in which two different management practices were implemented. In 1000 m^2 circular plots, type of species and diameter at breast height (D.B.H) of all trees larger than 2.5 cm as well as type of species of all shrubs and vertical distribution of tree species were recorded. In addition to richness, evenness and heterogeneity indices were calculated for whole tree and shrub species and also for each tree layer. The results showed that tree species diversity indices were significantly greater in the unmanaged area, whereas richness and heterogeneity indices of shrubs were greater in the managed area. Comparing the biodiversity indices indicated that richness index had the greatest value in the understorey and heterogeneity indices were greatest in the middle storey in both regions. Greater amounts of evenness were detected in the middle- and over storey of unmanaged and managed areas, respectively. As forestry operations result in change in various forest characteristics such as species diversity, it is essential to assess and monitor the effect of logging operations on forest diversity Hyrcanian forests of Iran.

Keywords: Forest stories, heterogeneity indices, Iran, species richness, sustainable management.

INTRODUCTION

Sustainable management of forest is one of the recent expressions of sustainability in forestry. It adopts an ecosystem approach to forest management, while operating in an interdisciplinary context (Hahn and Knoke 2010). One of the comprehensive definitions of sustainable forest management is managing forest stands in such a way that their productivity, regeneration, vitality and biodiversity is preserved in accordance with ecological, economic and social functions in local, national and global levels, currently and in the future (Bernasconi 1996). Nowadays, it is increasingly acknowledged that biodiversity, as a main aspect of ecosystem structure and functioning as well as a key issue of sustainable forest management, needs to be considered in forest management plans in conjunction with other environmental and economic criteria (Bertomeu and Romero 2001). Biodiversity has a substantial role in forest ecosystems for the preservation of ecosystem functioning (Bengtsson et al. 2000). Indeed biologically diverse systems serve a variety of human needs; it provides us with a wealth of products and services. There is concern that the loss of biodiversity within forests is jeopardizing these services (Aerts and Honnay 2011).

It is also related to the delivery of many ecosystems services (Balvanera et al. 2006), and results in geomorphological, hydrological, ecological stability in forest ecosystems (Noss 1999). Loss of habitat resulting from human land-use practices is the single largest factor causing the decline of biodiversity (Millennium Ecosystem Assessment 2005; Mönkkönen et al. 2014). Various ecosystem functions might be affected negatively by biodiversity loss, and long term reduction of species numbers may lead to a decrease of the ecosystem’s ability to confront with disturbances (Ishii et al. 2004). As a consequence, any sustainable forest management should be in accordance with environmental policies including biodiversity conservation.

Biodiversity of forest ecosystems encompasses many different aspects, such as species diversity, ecosystem diversity and genetic diversity. Species composition can alter ecosystem properties through functional traits and interactions (Hooper et al. 2005; Schmidt et al. 2015). At the stand level, species diversity is often associated with stand structural complexity (e.g. vertical and horizontal structure and other spatial components), as an appropriate indicator of habitat diversity (Ishii et al. 2004), and has been reported to be a major factor determining forest vegetation (Cardinale et al. 2012).

Forest structure is directly related to the habitat of many different animal and plant species (Kint 2000) and the alterations in forest structure through the intervention of man and natural disturbances can affect the conditions needed for the survival of many species (Guner 2002). Moreover, natural and human disturbances influence different components of biodiversity in many communities by their direct impact on species and stand structural diversity (Huston 1994; Robert and Gilliam 1995; Lindgren and Sullivan 2001). Species diversity as well as its vertical differentiation within stands may thus be used as indicators of disturbances regime in forest ecosystems (Larsson and Danell 2001).

Over the last 300 years, the world population has increased considerably. This rapid development brings increased, widened and varied demands for timber and non-timber products (Baskent 2000). Timber extraction is one of the most important disturbances occurring in forests throughout the world, and there is an increasing debate over the global effect of forest management for timber production on biodiversity (Siitonen 2001). At the local scale, unmanaged forests in general are said to contain more species than managed forests (Okland et al. 2003), but the results of some studies failed to confirm this idea for particular taxa (Graae and Heskjaer 1997; Bobiec 1998). Hyrcanian (Caspian) forests located in the north of Iran comprise a narrow band of temperate deciduous forests and are contiguous to a larger forest block extending across eastern Turkey and Caucasia. These forests cover the north-facing slopes of the Elborz Mountain, and extend from the Northwest to the Northeast of Iran with a total area of about 1.9 million hectares. Most parts of the forests within this range are managed for timber production as these forests are the only source of wood production in Iran and the main revenue of forest management plans is the income of logging (Forest and Rangelands Organization of Iran 1997). We hypothesize that the intensive logging in Hyrcanian forests has considerably decreased the species diversity in managed stands compared to natural forest relicts. Therefore this study aims at analyzing tree and shrub species diversity and comparing vertical species distribution between two managed and unmanaged forests using different diversity indices.

MATERIALS AND METHODS

Study area

This research was conducted in the Kheyrud Forest Research Station of University of Tehran (KFR), an 8000 hectare forest which is a portion of Hyrcanian uneven-aged forest, located approximately 7 km east of Nowshahr (or Noshahr) (51°32′N, 36°27′E), Mazandaran Province, within the Elborz mountain range, northern Iran (Figure 1).

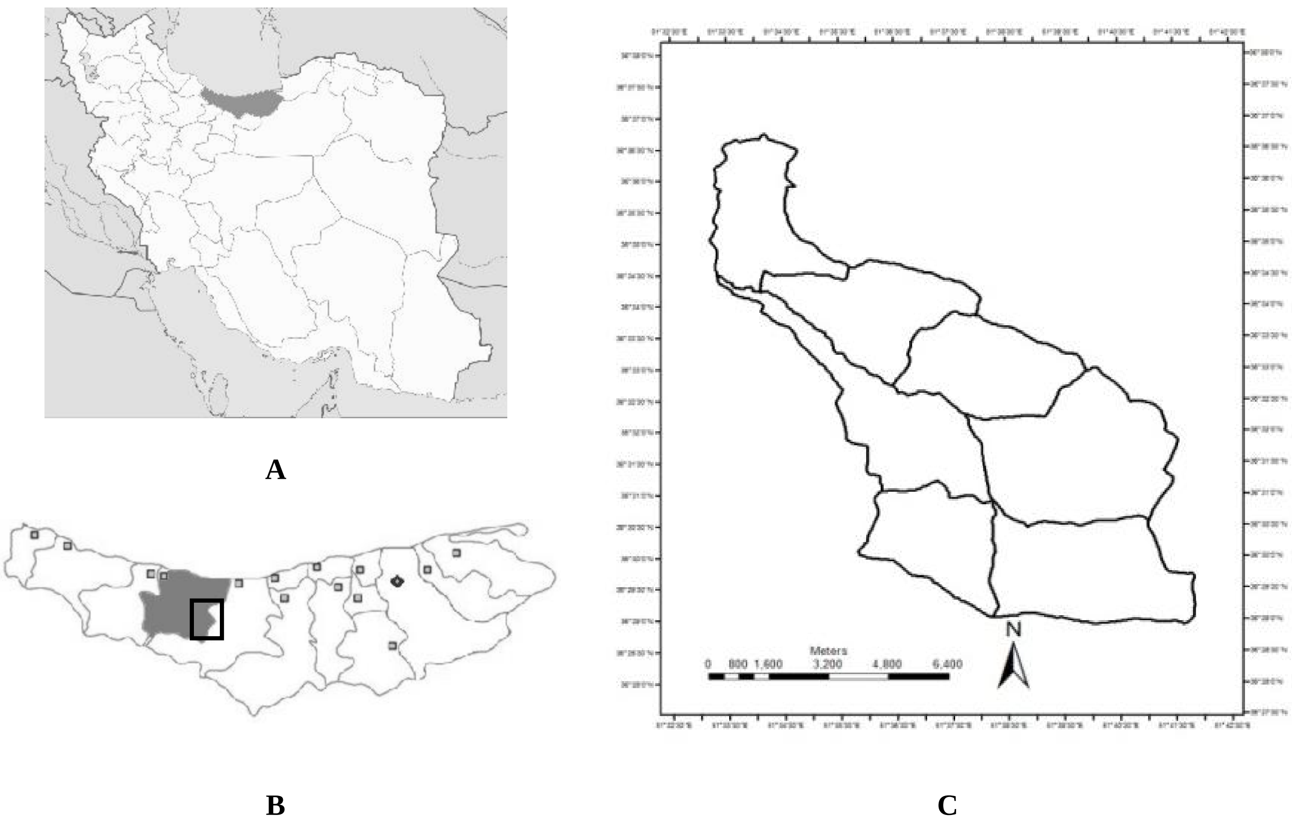

Figure 1. Study site in the Kheyrud Forest Research Station of University of Tehran (KFR) (C), east of Nowshahr (B), Mazandaran Province, northern Iran (A).

The elevation in the region ranges from 50 to 2200 m above sea level, composed of mostly broadleaved species. The climate of the area, according to the Emberge climate system, is wet with cold winters. The mean annual temperature is 15.9°C, the highest mean monthly temperature of 29 °C occurs in June and July and the lowest of 7.1 °C in February. The mean annual precipitation is 1354.5 mm, with maximum and minimum amounts in September and June, respectively. KFR is divided into 7 districts; however, only the first district, Patom, was surveyed. After field inspection, two adjacent areas characterized by the same soil type, plant community and site quality were selected. The southern area which is a protected forest has never been harvested and characterized as a reference forest for sustainable forest management, whereas in the northern area, logging is performed.

Procedures

Using systematic random sampling method, 40 0.1 ha circular sampling plots were laid out in each study area. Within each plot, D.B.H of all trees larger than 2.5 cm and the crown cover of all shrubs were recorded.

Considering that Hyrcanian forests consist of three stories (understorey, middle storey and overstorey), vertical layers were determined by visual estimation. Slope, altitude and aspect were measured for each plot using a clinometer, altimeter and compass, respectively.

Data analysis

Many different indices have been proposed for the evaluation of species diversity. During their historical development, the indices have been separated into three categories: indices of (i) species richness: the oldest and the simplest understanding of species diversity expressed as a number of species in an ecosystem, (ii) species evenness: a measure of the equality in species composition in a community, and (iii) species heterogeneity: a characteristic encompassing both species richness and evenness (Ludwig and Reynolds 1988; Krebs 1989). In this study, species richness S is the number of species recorded at each sampled plot (Magurran 1988). For species heterogeneity Shannon (Shannon 1949) and Simpson (Simpson 1949) diversity indices were used, as these are successful tools for the evaluation and quantification of plant diversity (Dale et al. 1994).

Shannon's index was calculated as:

$$H' = \sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

Where p_i is the relative abundance of species *i*.

Simpson's index (*D*), a diversity index heavily weighted towards the most abundant species in the sample while being less sensitive to species richness, was calculated as:

$$D = \sum_{i=1}^{s} \left(\frac{n_i(n_i-1)}{N(N-1)}\right)$$

Where n_i is the number of individuals in the i^{th} species and *N* the total number of individuals. When *D* increases, diversity decreases and therefore Simpson's index is usually expressed as $1.D^{-1}$ this expression (i.e. $1.D^{-1}$) was also used in this study. Two indices of evenness, Smith and Wilson and Simpson's (*E*), were used. The Simpson's evenness index (*E*) is calculated as the ratio of the Simpson's diversity index *D* to the maximum possible index of diversity, given *S* species and *N* individuals.

Smith and Wilson (1996) proposed an index of evenness based on the variance in abundance of the species. According to Smith and Wilson, this is the best index of evenness because it is independent of species richness and is sensitive to both rare and common species in the community, the index calculated as:

$$E_{Var} = 1 - \left(\frac{2}{®}\right)\left[\arctan\left\{\frac{\sum_{i=1}^{s}\log_e(n_i) - \sum_{j=1}^{s}\log_e(n_j)/S}{S}\right\}^2\right]$$

Where, E_{var}= Smith and Wilson's index of evenness

n_i= Number of individuals in species *i* in sample (*i = 1, 2, ..., s*)

n_j= Number of individuals in species *j* in sample (*j = 1, 2, ..., s*)

S = Number of species in entire sample

The indices were calculated for tree and shrub species separately, as well as for vertical tree layers within each plot. If the number of trees *N* is used, the size of the tree is neglected for calculating species diversity indices, while using the basal area, the tree size is taken into account through its diameter, or more precisely by the square of its diameter (Merganic and Smelko 2004). The sum of basal area of all individuals for each species in sample plots was used instead of species number in calculating evenness and heterogeneity indices of trees. Ecological Methodology software package was employed for calculating diversity indices. The normality of calculated indices for shrub and tree species was examined by using Kolmogorov-Smirnov test. Since some geomorphological features like elevation, aspect and slope were different between the two studied areas and might influence the diversity indices, these features were considered as covariates and an Analysis of Covariance (ANCOVA) was applied for removing their effects and then comparing indices between logged and unlogged areas and also among vertical layers. Significant differences among treatment averages for different parameters were tested at $p \leq 0.05$.

RESULTS AND DISCUSSION

There were only a few shrub species and 15 tree species in this study area. Among the species, four tree species and one shrub species were only found in the unlogged area. *Carpinus betulus* L., *Diospyros lotus* L., *Parrotia persica* (Dc.) C.A.M., *Acer velutinum* Boiss., *Fagus orientalis* Lipsky, *Quercus castaneifolia* C.A.M., *Acer cappadocicum* Gled., *Alnus subcordata* C.A.M., *Ulmus glabra* Huds., *Cerasus avium* (L). Moench, *Rhamnus frangula* and *Tilia begonifolia* Stev., *Ulmus carpinifolia* Borkh., *Ficus carica* L., and *Sorbus torminalis* (L.) Crantz were only recorded in the unlogged area. Tree species, stem density and basal area were common species in both areas, whereas of all tree species in both areas are presented in Table 1. *Crataegus microphylla* C. Koch and *Mespilus germanica* L. were common shrub species in both forest sand *Prunus divaricata* Ledeb was only observed in the logged area (Table 2).

Comparison of indices between two areas and among tree layers using ANCOVA showed that diversity indices were not significantly influenced by geomorphological features. The *p*-values related to covariates in all tests were ≥ 0.05. Since community, climatic and edaphic conditions were similar in two regions and geomorphological characteristics did not show significant influence on diversity indices, it seems the difference between diversity indices of two areas were the output of management practices.

Tree species diversity indices

Species richness

The comparison between both study areas showed that species richness of trees was significantly higher in unlogged area (Table 3). Species richness values calculated for vertical layers were also greater in unlogged area, but the difference was only significant in the middle- and understorey (Table 3). Species richness indicated significant difference among layers, and the highest species richness was found in the understorey in both areas ($p < 0.05$).

Evenness indices

Both evenness indices showed significant differences between the areas, with higher values for unlogged area. Evenness indices calculated for the overstorey were higher in unlogged area (Table 4), but these differences were not significant. In the middle- and the understorey, evenness indices were significantly higher in the logged area (Table 4). Highest values in the logged region were observed in the middle storey ($p < 0.05$), but in unlogged area evenness values were the highest in the overstorey ($p < 0.05$).

Table 2. Stem density of observed shrub species in the managed and unmanaged areas.

Shrub species	Stem density (per ha)	
	Managed area	Unmanaged area
Crataegus monophylla	145	8
Mespilus germanica	57	6
Prunus divaricata	3	-

Table 3. Mean values ± standard error of richness index and result of statistical tests in both study areas

	Logged area	Unlogged area	*p*-value
Total tree species	3.923 ± 1.156	1.156 ± 0.925	0.000
Overstorey	0.911 ± 2.100	1.196 ±2.575	0.077
Middle storey	0.811 ± 2.020	1.500±3.575	0.000
Understorey	0.811 ± 2.600	1.500 ± 3.950	0.000

Table 6. Mean values of diversity indices of shrubs

Diversity indices		Managed area	Unmanaged area
Richness	S	2.143	1.307
Evenness	Simpson	0.771	0.799
	Smith and Wilson	0.689	0.708
Hetero-geneity	Simpson	0.408	0.332
	Shannon	0.911	0.705

Table 1. Stem density and basal area of observed tree species in the managed and unmanaged areas.

Tree species	Managed area		Unmanaged area	
	Stem density (per ha)	Basal area ($m^2.ha^{-1}$)	Stem density (per ha)	Basal area ($m^2.ha^{-1}$)
Carpinus betulus	167	26.23	153	11.29
Diospyros lotus	51	0.50	51	0.72
Parrotia persica	42	2.30	490	11.30
Acer velutinum	14	2.04	3	2.50
Fagus orientalis	8	0.94	7	0.90
Quercus castaneifolia	4	1.86	57	6.62
Acer cappadocicum	4	0.45	29	1.79
Alnus subcordata	3	0.28	1	<0.01
Ulmus glabra	3	<0.01	5	0.11
Rhamnus frangula	1	<0.01	1	<0.01
Tilia begonifolia	1	<0.01	17	1.26
Prunus avium	-	-	4	0.13
Ulmus carpinifolia	-	-	1	<0.01
Ficus carica	-	-	1	<0.01
Sorbus torminalis	-	-	1	<0.01

Table 4. Mean values ± standard error of evenness indices and result of statistical tests in both study areas

	Managed area		**Unmanaged area**		***p*-value**	
	Simpson	**Smith and Wilson**	**Simpson**	**Smith and Wilson**	**Simpson**	**Smith and Wilson**
Total tree species	0.438 ± 0.162	0.228 ± 0.215	0.501 ± 0.098	0.236 ± 0.168	0.020	0.000
Overstorey	0.141±0.650	0.538 ± 0.230	0.687 ± 0.141	0.633 ± 0.202	0.147	0.096
Middle storey	0.721 ± 0.164	2.568 ± 0.980	0.167 ± 0.611	0.488± 1.919	0.006	0.007
Understorey	0.175 ± 0.533	0.262 ± 0.350	0.179± 0.424	0.230 ± 0.264	0.004	0.093

Table 5. Mean values ± standard error of heterogeneity indices and result of statistical tests in both study areas

	Managed area		**Unmanaged area**		***p*-value**	
	Simpson	**Shannon**	**Simpson**	**Shannon**	**Simpson**	**Shannon**
Total tree species	0.338 ± 0.186	0.842 ± 0.446	0.628 ± 0.104	1.727 ± 0.406	0.000	0.000
Overstorey	0.181 ± 0.331	0.422 ± 0.809	0.196 ± 0.450	0.528 ± 1.143	0.021	0.010
Middle storey	0.387 ± 0.151	0.899 ± 0.348	0.173 ± 0.482	0.523 ±1.263	0.023	0.003
Understorey	0.174 ± 0.284	0.705 ± 0.390	0.178 ± 0.298	0.441 ± 0.804	0.748	0.331

Shannon's diversity index

The Shannon diversity index for all tree species was significantly higher in unlogged area (Table 5). The same is observed for tree layers, but the difference was not significant in understorey (Table 5). Regarding to vertical structure, this index had the highest value for middle storey, but the difference was only significant difference between layers in unlogged area ($p < 0.05$).

Simpson's diversity index

The Simpson diversity index for tree species showed significant differences between both areas with higher diversity value for unlogged area (Table 5). The same holds for all tree layers, but only in the upper and middle storey the differences were significant (Table 5). Regarding to vertical structure, this index had the highest value in middle storey but only in the unlogged area a significant difference was found between layers ($p < 0.05$).

Shrub diversity indices

Since shrub species were recorded in 35 sample plots in logged area and only in 3 sample plots in unlogged area, the difference of diversity indices of shrub species between two areas were obvious. As presented in Table 6, in contrary to tree species, richness and heterogeneity (Simpson and Shannon) indices of shrubs were greater in the logged area but evenness indices values were greater in unlogged area.

Discussion

Considering overall tree species diversity indices, all species richness, evenness and heterogeneity indices showed significant differences between unlogged and logged areas with greater values for unlogged area. This difference is most probably related to management differences between both regions and selective logging. These findings are in accordance with Brown and Gurevitch (2004) who reported that logging operation decreases species diversity; independent of how many years ago clear cutting or selective cutting were done. Forest utilization by logging may result in better conditions for invasive species (Drake et al. 1989) and poses a threat to biodiversity by possibly displacing native plants or reducing their diversity. Even though logging might reduce competition, it increases light by creating gaps in canopy and increases the chance of soil contact for incoming propagates (Robert and Dong 1993), in long term managed forests do not retrieve their primary tree species diversity. Other studies showed a positive effect of management on the total species richness of vascular plants (Schmidt 2005), which could be a specific response to the disturbance that causes an increment in species diversity. In fact, the increase in diversity in some harvested forests has been related to a short-term response of the system to disturbance (Pitkanen 2000; Peltzer et al. 2000; Roberts and Zhu 2002). Some studies showed that in the first 20 years of management practices, species richness was higher in managed than to unmanaged forests; after the 20-year cutoff, higher species richness is observed in unmanaged forests (Paillet et al. 2010).

Regarding to tree structural diversity, the results also indicated that all diversity indices in the overstorey were greater in unlogged area, whereas in the middle- and understorey only species richness and heterogeneity were higher in the unlogged area, but evenness values were greater in the logged area. In most sample plots in unlogged area the middle storey consisted of semi shade tolerant species such as *Carpinus betulus* and *Parrotia persica*, which hindered presence of other species and resulted in uneven distribution of species in these layers. In analyzing tree structural diversity it was observed that species richness decreased from understorey to overstorey in the unlogged area. It seems in parallel with tree individual's diameter and height increment and transition to higher layers, some species were outcompeted because of competition for ecological conditions like light, moisture, nutrients, etc. In contrary, the trend of species richness changes was different in the managed area; it decreased from understorey to middle storey and then increased to overstorey, in other words this index had its highest value in the top layer. Heterogeneity indices had their highest values in the middle storey layer, in this study three factors played important roles in calculating heterogeneity indices: i) number of species in each layer, ii) summation of basal area of tree individuals iii) distribution of basal area among species. Greater value of heterogeneity indices in the middle storey compared to understorey was related to higher value of basal area of trees in this layer not to the more number of tree species; because species richness values were greater in the understorey. These findings may explain the essence of using the variable related to size of trees (e.g. diameter, basal area or volume) rather than number of individuals for calculating species diversity in forest stands. Diversity indices calculated for shrubs showed significant differences between two regions with higher value for the managed area. It seems that gaps created by logging allowed the understorey to outspread more because canopy closure restricts spread of most herbs and shrubs. Frequent disturbances in managed forests such as canopy openings, litter removal, and soil disturbance, all strongly favor understorey plants, especially shade intolerant and competitive species. Structural diversity which is proved to be a good indicator of forest structure has also significantly affected by disturbance in this study. Hence, development of indicators based on only one dimension of diversity may not be sufficient to assess the effect of management on biodiversity (Roberts and Gilliam 1995).

Biodiversity conservation is increasingly considered a key to sustainable forest management and understanding of biodiversity in forest ecosystems is essential to reveal forest dynamics and providing methods and approaches to manage forest stands. Growing empirical evidence demonstrates that biodiversity loss can affect major ecosystem properties such as primary productivity and nutrient cycling (Cardinale et al. 2012; Isbell et al. 2011; Ratcliffe 2015).

Trees are the most important components in forest ecosystems and provide resources and habitats for many other forest species which depend on tree species. Tree species diversity has the potential to increase productivity in a temperate forest through facilitation and/or complementary resource use if the resource considered limits productivity (Schmidt et al. 2015).

So in forests in which a selection cutting system is applied for timber production, these species and consequently forest species diversity may be endangered in long term, especially if only some specific species and diameters are selected. In the most cases some improvement in design and management of forests can conserve biodiversity better, often with little or no reduction in timber production (Hartley 2002). Finally, as forestry operations result in changes in various forest characteristics including plant composition, forest structure, soils and species diversity, in management plans for Hyrcanian forests of Iran, assessing and monitoring the effect of management programs like logging operations on forest diversity is essential.

REFERENCES

Aerts R, Honnay O. 2011. Forest restoration, biodiversity and ecosystem functioning. BMC Ecol 11: 29. DOI: 10.1186/1472-6785-11-29.

Balvanera P, Pfisterer AB, Buchmann N, He JS, Nakashizuka T, Raffaelli D, Schmid B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9: 1146-1156.

Baskent EZ. 2000. Exploring the concept of a forest landscape management paradigm. Turk J Agric For 24: 443-451.

Bengtsson J, Nilsson SG, Franc A, Menozzi P. 2000. Biodiversity, disturbances, ecosystem functions and management of European forests. For Ecol Manag 132: 39-50.

Bernasconi A. 1996. Von der Nachhaltigkeit Zu Hachhaltigea, Systemen: Florstliche Planungals Grundlagenachhaltiger Waldbewirtschaftung. Beiheftzur Schweizerischen Zeitschrift fur Forstuesen, 76: 176.

Bertomeu M, Romero C. 2001. Managing forest biodiversity: A zero-one goalprogramming approach. Agric Syst 68: 197-213.

Bobiec A. 1998. The mosaic diversity of field layer vegetation in the natural and exploited forests of Bialowieza. Plant Ecol 136: 175-187.

Brown AK, Gurevitch J. 2004. Long - term impact of logging on forest diversity in Madagascar. Proc Nat Acad Sci USA 101 (16): 6045-6049.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S. 2012. Biodiversity loss and its impact on humanity. Nature 486: 59-67.

Dale VH, Offerman H, Frohn R, Gardner RH. 1994. Landscape characterization and biodiversity research. In: Boyle TJB, Boontawee B (eds) Proceedings of IUFRO Symposium on Measuring Biology Diversity in Tropical and Temperate Forest. Chiang Mai, Thailand, 28 August - 2 September.

Drake JA, Mooney JA, dicastri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M. 1989. Biological Invasions: A Global Perspective. John Wiley and Sons, Chichester.

Forest and Rangelands Organization. 1997. Some data of forest in Iran. Ministry of Jihad-e-Sazandegi, Iran.

Graae BJ, Heskjaer VS. 1997. A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark. For Ecol Manag 96: 111-123.

Guner S. 2002. Natural forest types and their differential species on Genya Mountain-Artvin. Turk J Agric For 26: 225-232.

Hahn WA, Knoke T. 2010. Sustainable development and sustainable forestry: analogies, differences, and the role of flexibility. Eur J Forest Res 129: 787-801.

Hartley Mj, 2002. Rationale and methods for conserving biodiversity in plantation forests. For Ecol Manag 155: 81-95.

Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75: 3-35.

Huston MA. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, New York.

Isbell F, Calcagno VA, Hector J, Connolly WS, Harpole PB, Reich M, Scherer-Lorenzen B, Schmid, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M. 2011. High plant diversity is needed to maintain ecosystem services, Nature 477: 199–202.

Ishii TH, Tanabe Sh, Hiura T. 2004. Exploring the relationship among canopy structure, stand productivity and biodiversity of temperate forest ecosystem. For Sci 50 (3): 342-354.

Kint V, Lust N, Ferris R, Olsthoorn AFM. 2000. Quantification of forest stand structure applied to Scots pine (Pinus sylvestris L.) forests. For Syst 1: 147-163.

Krebs CJ. 1989. Ecological Methodology. Harper Collins, New York.

Larsson S, Danell K. 2001. Science and management of boreal forest biodiversity. Scand J For Res 3: 5-9.

Lindgren PMF, Sullivan TP. 2001. Influence of alternative vegetation management treatments on conifer plantation attributes: abundance, species diversity and structural diversity. For Ecol Manag 142: 163-182.

Ludwig JA, Reynolds JF. 1988. Statistical ecology: A Primer on Methods and Computing. John Wiley & Sons, New York.

Magurran AE. 1988. Ecological Diversity and its Measurement. Princeton University Press, New Jersey.

Merganic J, Smelko S. 2004. Quantification of tree species diversity in forest stands - model BIODIVERSS. Eur J For Res 123: 157-165.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. World Resources Institute, Washington, DC.

Mönkkönen M, Juutinen A, Mazziotta A, Miettinen K, Podkopaev D, Reunanen P, Salminen H, Tikkanen O. 2014. Spatially dynamic forest management to sustain biodiversity and economic returns, J Environ Manag 134: 80-89.

Noss RF. 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. For Ecol Manag 115: 135-146.

Okland T, Rydgren K, Okland R, Storaunet HKO, Rolstad J. 2003. Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea-Abies* forest stands. For Ecol Manag 177: 17-37.

Paillet Y, Bergès L, Hjältén J, Ódor P, Avon C, Bernhardt-Römermann M, Bijlsma RJ, De Bruyn L, Fuhr M, Grandin U, Kanka R, Lundin L, Luque S, Magura T, Matesanz S, Mészáros I, Sebastià MT, Schmidt W, Standovár T, Tóthmérész B, Uotila A, Valladares F, Vellak K, Virtanen R. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol 24 (1): 101-112.

Peltzer DA, Bast ML, Wilson SD, Gerry AK. 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. For Ecol Manag 127: 191-203.

Pitkanen S. 2000. Classification of vegetation diversity in managed boreal forests in eastern Finland. Plant Ecol 146: 11-28.

Ratcliffe S, Holzwarth F, Nadrowski K, Levick S, Wirth C. 2015. Tree neighborhood matters - Tree species composition drives diversity-productivity patterns in a near-natural beech forest, For Ecol Manag 335: 225-234.

Roberts MR, Gilliam FS. 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol Appl 5: 969-977.

Roberts MR, Zhu L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. For Ecol Manag 155: 17-31.

Schmidt M, Veldkamp E, Corre MD. 2015. Tree species diversity effects on productivity, soil nutrient availability and nutrient response efficiency in a temperate deciduous forest. For Ecol Manag 338: 114-123.

Schmidt W. 2005. Herb layer species as indicators of biodiversity of Managed and unmanaged beech forests. For Snow Landsc Res 79: 111-125.

Shannon CE. 1949. The mathematical theory of communication. In: Shannon CE, Weaver W (eds). The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL.

Siitonen J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. Ecol Bull 49: 11-41.

Simpson EH. 1949. Measurement of diversity. Nature 163: 688-688.