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Plant Diversity of Forests

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1. Introduction

Changes in biological diversity of natural ecosystems have in the second half of 20th century become a global problem due to intensive human activities. Therefore, higher attention has been paid to these problems. The year 1992 can be considered as the pivotal year in this field since in this year the Convention on Biological Diversity was approved on the United Nations Conference on Environment and Development in Rio de Janeiro. This document defines biological diversity - biodiversity as „the variety and 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 definition covers three fundamental components of diversity: genetic, species, and ecosystem diversity (Duelli, 1997, as cited in Larsson, 2001; Merganič & Šmelko, 2004). However, also this widely accepted definition like many others fails to mention ecological processes, such as natural disturbances, and nutrient cycles, etc., that are crucial to maintaining biodiversity (Noss, 1990). The complexity of the understanding of the term biodiversity was well documented by Kaennel (1998). Therefore, Noss (1990) suggested that for the assessment of the overall status of biodiversity more useful than a definition would be its characterisation that identifies its major components at several levels of organisation. Franklin et al. (1981 as cited in Noss, 1990) recognised three primary attributes of ecosystems: composition, structure, and function.

1.1 Species diversity

Strictly speaking, species diversity is the number of different species in a particular area (species richness) weighted by some measure of abundance such as number of individuals or biomass. However, conservation biologists often use the term species diversity even when they are actually referring to species richness, i.e. to number of present species (Harrison et al., 2004). Noss (1990) defines species diversity as a composition that refers to the identity and variety of elements in a population, includes species lists and measures of species diversity and genetic diversity.

1.2 Structural diversity

“Structural diversity refers to the physical organisation or pattern of a system, including the spatial patchwork of different physical conditions in a landscape, habitat mosaics, species assemblages of different plant and animal communities, and genetic composition of subpopulations” (Stokland et al., 2003). The main structural indicators that are used to describe the conditions for forest biodiversity include stand vertical structure, age class distribution and the amount of dead wood (Christensen et al., 2004). They represent an indirect approach „as they show, typically on a rather gross scale, how the house is built, but give no information on whether the inhabitants have moved in” (Christensen et al., 2004).

1.3 Functional diversity

According to Noss (1990), function involves all ecological and evolutionary processes, including gene flow, disturbances, and nutrient cycling. “Functional diversity involves processes of temporal change, including disturbance events and subsequent succession, nutrient recycling, population dynamics within species, various forms of species interactions, and gene flow” (Stokland et al., 2003).

2. Factors influencing plant diversity in forest ecosystems

Within certain time and space, diversity is determined by the combination of abiotic constraints, biotic interactions, and disturbances (Frelich et al., 1998; Misir et al., 2007; Nagaraja et al., 2005; Spies & Turner, 1999; Ucler et al., 2007). Abiotic factors, such as elevation, slope, aspect, soil texture, climate etc., specify the conditions of physical environment and thus the primary species distribution. The relations were already regarded and studied in 19th century (Hansen & Rotella, 1999). The parameters affecting the plant growth and nutrient availability, e.g. climate, are considered as primary factors (Terradas et al., 2004), while terrain characteristics, e.g. elevation, are regarded as indirect factors, because they do not influence the plant growth directly, but are correlated to primary factors (Pausas et al., 2003; Bhattarai et al., 2004).

Primary climate and site conditions have influenced and determined biodiversity on a specific site in the long-term development of forest ecosystems (Stolina, 1996). Hence, the actual biodiversity is the result of the adaptation process of species. In the current conditions of climate change the species will have to respond to faster changes. Although the effect of climate change will vary from site to site, it is likely that its impacts on ecosystems will be adverse, as species will have to deal with a variety of new competitors, and biotic factors (diseases, predators), to which they have no natural defense so far (IUCN, 2001).

Indirect factors are often used in the analyses, when the information about the primary factors is not available (Pausas & Saez, 2000). Most often, the relationship between the diversity and elevation is examined (Bachman et al., 2004; Bhattarai & Vetaas, 2003; Grytnes & Vetaas, 2002), while the influence of other topography characteristics is tested only seldom (Johnson, 1986; Palmer et al., 2000). Although modern ecologists focus mainly on other influencing factors, e.g. natural disturbances, the influence of abiotic conditions on species diversity has recently begun to gain attention of researchers (Austin et al., 1996; Burns, 1995; Hansen & Rotella, 1999; Ohmann & Spies, 1998; Rosenzweig, 1995). However,

most of these works analyse the environmental factors only with regard to the number of tree species representing just one part of species diversity.

Abiotic factors, such as elevation, slope, aspect, terrain type etc., create together a unique complex of environmental conditions specifying forest communities (Spies & Turner, 1999). The relation between elevation and species diversity is generally accepted and was documented by several authors, not only for tree species but also regarding the diversity of plants and animals (Rosenzweig, 1995). Very often hump-shaped curves with maximum species diversity at mid-elevations were reported (Bhattarai & Vetaas, 2003; Bachman et al., 2004; Ozcelik et al., 2008). In Merganič et al. (2004), elevation was also found to have a significant influence on tree species diversity, but at mid-elevations the lowest values of tree species diversity were observed. This performance can most probably be explained by the fact that in the Slovak Republic at about 600 m above sea level, beech has its optimum growing conditions, which causes that at these altitudes beech is so vital and competitive that other species become rare. Johnson (1986) and Ozcelik et al. (2008) detected the significant correlation between tree species diversity and aspect.

2.1 Forest management

In Europe forests have played an important role since their establishment after the last ice age that ended 12,000 years ago. In the human thoughts, the forest was an unknown and untouched place with secrets and dangers. It provided a man with a shelter, fuel wood, and construction material (Reinhold, 1999). A man started to have a stronger influence on a forest ecosystem around the year 4,000 B.C. The impact was first low; he cut trees to obtain space for settlements and for grazing of his animals. With the increasing demands on space, forest ecosystems were more and more utilised, which led to the significant decrease of forest area in the whole Europe. In 16th century, the first attempts to grow introduced tree species, namely *Castanea sativa*, occurred. However, the most significant changes of forest ecosystems started in 19th century with the beginning of a so-called “spruce and pine mania”. In this period, the majority of forestland was afforested with spruce, even in completely unsuitable conditions. The main reason of this boom was to maximise wood production. Nowadays, it is known that such an approach has had a negative impact on stand stability, as well as on forest biodiversity. The look of the forests today particularly in the densely inhabited areas is related to management intensity and methods (Hédl & Kopecký, 2006). The absence of suitable management is another cause of decreasing forest biodiversity (Hédl, 2006).

Although currently biodiversity has become a key component of Central European forests, there is only a limited number of studies, which examine the influence of forest management on biodiversity of e.g. plants (Prevosto, 2011). In addition, the results are often contradictory. On one side, some works present that forest management has a negative effect on biodiversity (Gilliam & Roberts, 1995; Sepp & Liira, 2009). Other works (e.g. Battles, 2001; Newmaster, 2007; Ramovs & Roberts, 2005; Ravindranath, 2006; Wang & Chen, 2010) show that a well-chosen management can influence biodiversity positively. The compatibility of suitable management activities with biodiversity conservation is critical to ensure wood harvesting and other ecologically valuable aspects in forested land (Eriksson & Hammer, 2006). Sustainable forest management represents how high biodiversity can be

achieved together with high wood production. This type of management maintains forests and forest soil in order to secure biodiversity, productivity, regeneration capacity, vitality, and abilities to fulfil all ecological, economic, and social functions today and in future on any spatial scale (local, regional, national) without the drawback on other ecosystems (Poleno, 1997). Sustainability means the ability to provide current and future generations with permanent and optimal wood yield and other forest ecosystem products (Smola, 2008).

3. Diversity assessment

Due to the complexity of biodiversity and of forest ecosystems, complete assessments of biodiversity are not practically achievable (Humphrey & Watts, 2004) because of the impossibility to monitor all taxa or features (Lindenmayer, 1999). Therefore, means to reduce complexity are necessary (Christensen et al., 2004). In this context, reliable indicators or short-cut measures of biodiversity are searched for (Ferris & Humphrey, 1999; Jonsson & Jonsell, 1999; Noss, 1999; Simberloff, 1998 as cited in Humphrey & Watts, 2004). From the long-term perspective, the basic criterion for any biodiversity assessment system is that it is based on an enduring set of compositional, structural and functional characteristics (Allen et al., 2003). In addition, a complete long-term biodiversity strategy must take into account both interactions between the different geographical levels and the fact that different elements of biodiversity are dependent on different geographical scales, in different time perspectives (Larsson, 2001).

3.1 Species diversity

Species diversity can be evaluated by a great number of different methods (e.g. see Krebs, 1989; Ludwig & Reynolds, 1988). All of the proposed methods are usually based on at least one of the following three characteristics (Bruciamacchie, 1996):

- species richness – the oldest and the simplest understanding of species diversity expressed as a number of species in the community (Krebs, 1989);
- species evenness – a measure of the equality in species composition in a community;
- species heterogeneity – a characteristic encompassing both species abundance and evenness.

The most popular methods for measurement and quantification of species diversity are species diversity indices. During the historical development, the indices have been split into three categories: indices of species richness, species evenness and species diversity (Krebs, 1989; Ludwig & Reynolds, 1988). The indices of each group explain only one of the above-mentioned components of species diversity (Merganič & Šmelko, 2004).

3.1.1 Species richness

The term species richness was introduced by McIntosh (1967) to describe the number of species in the community (Krebs, 1989). Surely, the number of species S in the community is the basic measure of species richness, defined by Hill (1973) as diversity number of 0th order, i.e. N_0 . The basic measurement problem of N_0 is that it is often not possible to enumerate all species in a population (Krebs, 1989). In addition, S depends on the sample size and the time spent searching, due to which its use as a comparative index is limited

(Yapp, 1979). Hence, a number of other indices independent of the sample size have been proposed to measure species richness. These indices are usually based on the relationship between S and the total number of individuals observed (Ludwig & Reynolds, 1988). Two such well-known indices are $R1$ and $R2$ proposed by Margalef (1958) and Menhinick (1964), respectively. Hubálek (2000), who examined the behaviour of 24 measures of species diversity in a data from bird censuses, assigned to the category of species richness-like indices also the index α (Fischer et al., 1943; Pielou, 1969), Q (Kempton & Taylor, 1976, 1978), and $R500$ (Sanders, 1968; Hurlbert, 1971).

3.1.2 Species evenness

Lloyd & Ghelardi (1964) were the first who came with idea to measure the evenness component of diversity separately (Krebs, 1989). The principle of the evenness measures is to quantify the unequal representation of species against a hypothetical community in which all species are equally common. Ludwig & Reynolds (1988) present five evenness indices $E1$ (Pielou, 1975, 1977), $E2$ (Sheldon, 1969), $E3$ (Heip, 1974), $E4$ (Hill, 1973), and $E5$ (Alatalo, 1981), each of which may be expressed as a ratio of Hill's numbers. The most common index $E1$, also known as J' suggested by Pielou (1975, 1977) expresses H' relative to maximum value of H' ($= \log S$). Index $E2$ is an exponentiated form of $E1$. Based on the analysis of Hubálek (2000), McIntosh's diversity D (McIntosh, 1967; Pielou, 1969), McIntosh's evenness DE (Pielou, 1969), index J of Pielou (1969) and G of Molinari (1989), are also evenness measures.

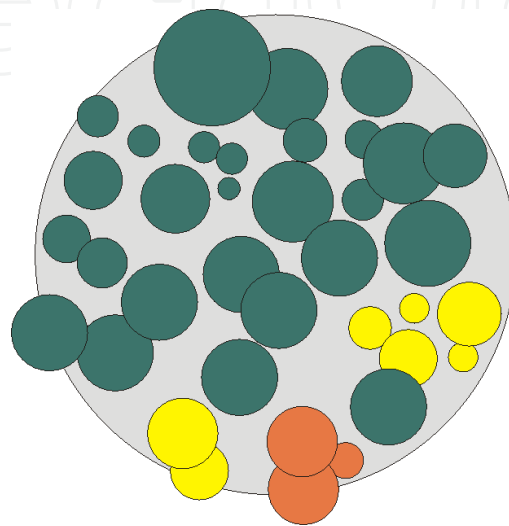
3.1.3 Species heterogeneity

This concept of diversity was introduced by Simpson (1949) and combines species richness and evenness. The term heterogeneity was first applied to this concept by Good (1953). Many ecologists consider this concept to be synonymous with diversity (Hurlbert, 1971, as cited in Krebs, 1989). According to Peet (1974, as cited in Ludwig & Reynolds, 1988), an infinite number of diversity indices exist. Simpson proposed the first heterogeneity index λ , which gives the probability that two individuals picked at random from the community belong to the same species. This means that if the calculated probability is high, the diversity of the community is low (Ludwig & Reynolds, 1988). To convert this probability to a diversity measure, the complement of Simpson's original measure, i.e. $1-\lambda$, is used (Krebs, 1989).

Probably the most widely used heterogeneity index is the Shannon index H' (or Shannon-Wiener function), which is based on information theory (Shannon & Weaver, 1949). It is a measure of the average degree of "uncertainty" in predicting to what species an individual chosen at random from a community will belong (Ludwig & Reynolds, 1988). Hence, if $H' = 0$, the community consists of only one species, whereas H' is maximum ($= \log(S)$) if all species present in the community are represented by the same number of individuals. Shannon index places most weight on the rare species in the sample, while Simpson index on the common species (Krebs, 1989).

From other heterogeneity measures we mention Brillouin Index H (Brillouin, 1956), which was first proposed by Margalef (1958) as a measure of diversity. This index is preferred being applied to data in a finite collection rather than H' . However, if the number of individuals is large, H and H' are nearly identical (Krebs, 1989). The indices $N1$ and $N2$

from Hill's family of diversity numbers (Hill, 1973), which characterise the number of "abundant", and "very abundant" species, respectively, also belong to diversity measures. The McIntosh index is based on the representation of a sample in an S-dimensional hyperspace, where each dimension refers to the abundance of a particular species (Bruciamacchie, 1996). According to the evaluation performed by Hubálek (2000), NMS "number of moves per specimen" proposed by (Fager, 1972), H'_{adj} , which is an adjusted H' by the $d(H)$ correction (Hutcheson, 1970), and R100 (Sanders, 1968; Hurlbert, 1971) can also be regarded as heterogeneity indices.



Legend:

● *Fagus sylvatica*, ● *Picea abies*, ● *Abies alba*

Species richness: 3, Species evenness: Low, Species heterogeneity: Low.

Fig. 1. Assessment of tree species diversity.

3.2 Structural diversity

Structural diversity is defined as the composition of biotic and abiotic components in forest ecosystems (Lexer et al., 2000), specific arrangement of the components in the system (Gadow, 1999) or as their positioning and mixture (Heupler, 1982 as cited in Lübbes, 1999). According to Zenner (1999) the structure can be characterised horizontally, i.e. the spatial distribution of the individuals, and vertically in their height differentiation. Gadow & Hui (1999) define the structure as spatial distribution, mixture and differentiation of the trees in a forest ecosystem.

There exist a number of different methods to describe the structure and its components. The classical stand description is based on qualitative description of stand closure, mixture, density, etc. Graphical methods presenting diameter distribution, stand height distribution curves, tree maps, etc. are also useful. However, both verbal and graphical methods may not be sufficient to reveal subtle differences (Kint et al., 2000). Therefore, a number of quantitative methods have been proposed that should overcome these shortages. Partial reviews can be found in Pielou (1977), Gleichmar & Gerold (1998), Kint et al. (2000), Földner (1995), Lübbes (1999), Gadow & Hui (1999), Neumann & Starlinger (2001), Pommerening (2002) etc.

3.2.1 Horizontal diversity

The indices characterising forest horizontal structure usually compare a hypothetical spatial distribution with the real situation (Neumann & Starlinger, 2001). Probably the most well-known index is the aggregation index R proposed by Clark & Evans (1954) that describes the horizontal tree distribution pattern (or spacing as named by Clark & Evans (1954), or positioning as defined by Gadow & Hui (1999)). It is a measure of the degree to which a forest stand deviates from the Poisson forest, where all individuals are distributed randomly (Tomppo, 1986). It is the ratio of the observed mean distance to the expected mean distance if individuals were randomly distributed.

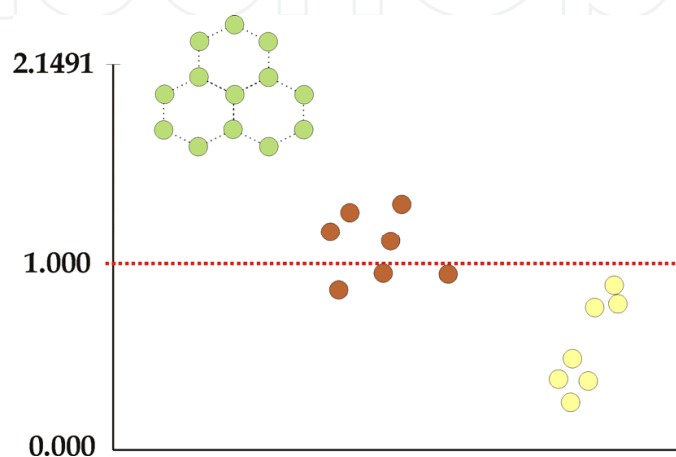


Fig. 2. Schematic visualisation of the assessment of forest horizontal structure using R index by Clark & Evans (1954).

A similar measure is the Pielou index of nonrandomness (Pielou, 1959), which quantifies the spatial distribution of trees by the average minimum distance from random points to the nearest tree (Neumann & Starlinger, 2001). The Cox index of clumping (Strand, 1953; Cox, 1971) is the ratio of variance to mean stem number on sub-plots. Gadow et al. (1998) proposed an index of neighbourhood pattern based on the heading angle to four next trees. Another commonly used measures of horizontal structure are methods proposed by Hopkins (1954), Prodan (1961), Köhler (1951) and Kotar (1993 as cited in Lübberts, 1999).

According to Gadow & Hui (1999), mixture is another component of structure. For the quantification of mixing of two tree species, Pielou (1977) proposed the segregation index based on the nearest neighbour method like the index A of Clark & Evans, while the calculated ratio is between the observed and expected number of mixed pairs under random conditions. Another commonly used index is the index DM (from German *Durchmischung*) of Gadow (1993) adjusted by Földner (1995). On the contrary to the segregation index, DM accounts for multiple neighbours (Gadow, 1993 used 3 neighbours) and is not restricted to the mixture of two species (Kint et al., 2000).

Differentiation is the third component of structure (Gadow & Hui, 1999), which describes the relative changes of dimensions between the neighbouring individuals (Kint et al., 2000). Gadow (1993) and Földner (1995) proposed the differentiation index T , which is an average of the ratios of the smallest over the largest circumference calculated for each tree and its n nearest neighbours. Instead of the circumference, diameter at breast height can be used in

this index to describe the horizontal differentiation as presented by Pommerening (2002). Values of the index T close to 0 indicate stands with low differentiation, since neighbouring trees are of similar size. Aguirre et al. (1998) and Pommerening (2002) suggested the scales of five or four categories of differentiation, respectively.

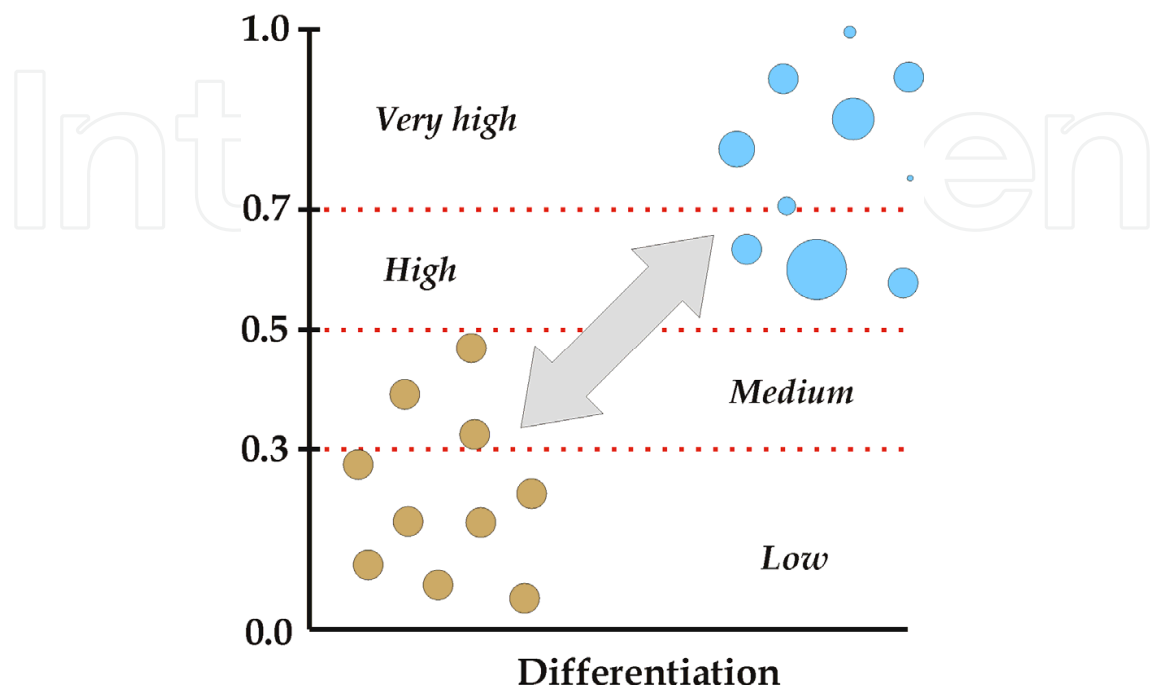


Fig. 3. Schematic visualisation of the assessment of stand differentiation according to Földner (1995) with categories proposed by Aguirre et al. (1998).

3.2.2 Vertical diversity

While there are many indices that measure horizontal structure, there are only few for vertical structure (Neumann & Starlinger, 2001). Simple measures such as the number of vegetation layers within a plot can be used as an index of vertical differentiation (Ferris-Kaan & Patterson, 1992 as cited in Kint et al., 2000). The index A developed by Pretzsch (1996, 1998) for the vertical species profile is based on the Shannon index H' . In comparison with H' the index A considers species portions separately for a predefined number of height layers (Pretzsch distinguished 3 layers). The index proposed by Ferris-Kaan et al. (1998) takes the cover per layer into account, but needs special field assessments (Neumann & Starlinger, 2001). Therefore, using the same principles as Pretzsch (1996), i.e. Shannon index and stratification into height layers, Neumann & Starlinger (2001) suggested an index of vertical evenness VE that characterises the vertical distribution of coverage within a stand. The differentiation index T of Gadow (1993) is also applicable for the description of vertical differentiation, if the index is calculated from tree heights.

3.2.3 Complex diversity

Complex indices combine several biodiversity components in one measure. These indices are usually based on an additive approach, i.e. the final value is obtained as a sum of the values of individual biodiversity components. Usually, two ways of quantification

individual biodiversity components are applied: (1) by assigning the value on the base of a pre-defined scale, or (2) to use the real measurement units. In addition, if required individual biodiversity components can be assigned different weights according to their importance for the whole biodiversity.

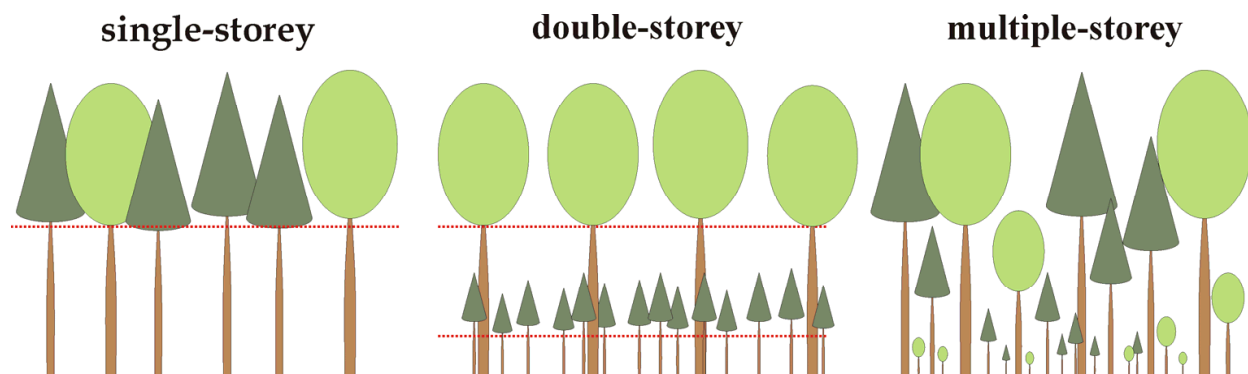


Fig. 4. Quantification of vertical diversity.

The first system of biodiversity assessment using scores is simple and easy to use (Meersschaut & Vandekerckhove, 1998). Such quantification was already used in 1969 by Randwell to assess the need for the protection of seashore sites on the base of Comparative Biological Value Index (Nunes et al., 2000). Meersschaut & Vandekerckhove (1998) developed a stand-scale forest biodiversity index based on available data from forest inventory. The index combines four major aspects of a forest ecosystem biodiversity: forest structure, woody and herbaceous layer composition, and deadwood. Each aspect consists of a set of indicators, e.g. forest structure is defined by canopy closure, stand age, number of stories, and spatial tree species mixture. The indicators are given a score determined on the basis of a common agreement. The biodiversity index is calculated as the sum of all scores, while its maximum value is set to 100. Another complex index named Habitat Index HI was developed by Rautjärvi et al. (2005). The authors also use the name habitat index model as it was produced as a spatial oriented model. The inputs in the model come from thematic maps from Finnish Multi-source national forest inventory (predicted volume of growing stock, predicted stand age, and predicted potential productivity) and kriging interpolation maps from national forest inventory plot data (volume of dead wood, and a measure for naturalness of a stand). The input variables were selected based on the forest biodiversity studies in Scandinavia. The index is of additive form where all input layers contribute to the result layer. All input variables (layers) are reclassified and enter the model as discrete variables, while each input layer is assigned a different weight according to its importance to biodiversity.

The second quantification method was used in the model BIODIVERSS proposed by Merganič & Šmelko (2004) that estimates tree species diversity degree of a forest stand by summing up the values of 5 diversity indices ($R1$, $R2$, λ , H' and $E1$). The fundamental method of the model BIODIVERSS is a predictive discriminant analysis (StatSoft Inc., 2004; Huberty, 1994; Cooley & Lohnes, 1971), which means that each species diversity degree is represented by one discriminant equation. For each examined forest stand, four discriminant scores are calculated, and the stand is assigned a species diversity degree with maximum discriminant score.

LLNS index proposed by Lähde et al. (1999) is a complex index for calculating within-stand diversity using the following indicator variables: stem distribution of live trees by tree species, basal area of growing stock, volume of standing and fallen dead trees by tree species, occurrence of special trees (number and significance), relative density of undergrowth, and volume of charred wood. The LLNS index is calculated as the sum of diversity indices describing particular components (i.e. living trees, dead standing trees etc.). However, the authors also developed a scoring table for the indicator variables. The final value of LLNS is then obtained by adding all the scores together. The evaluation of this index using Finnish NFI data revealed, that the LLNS index differentiates even-sized and uneven-sized stand structures, the development classes of forest stands and site-types fairly well (Lähde et al., 1999).

A special category of complex indices covers complex structural indices that encompass several components of structural diversity. For example, Jaehne & Dohrenbusch (1997) proposed the Stand Diversity Index that combines the variation of species composition, vertical structure, spatial distribution of individuals and crown differentiations. The Complexity Index by Holdridge (1967) is calculated by multiplying four traditional measures of stand description: dominant height, basal area, number of trees and number of species. Hence, this index contains no information on spatial distribution nor accounts for within stand variation (Neumann & Starlinger, 2000). Zenner (1999), and Zenner & Hibbs (2000) developed the Structural Complexity Index (SCI) based on the vertical gradient differences between the tree attributes and the distances between the neighbouring trees. When all trees in a stand have the same height, the value for SCI is equal to one, which is the lower limit of SCI (Zenner & Hibbs, 2000).

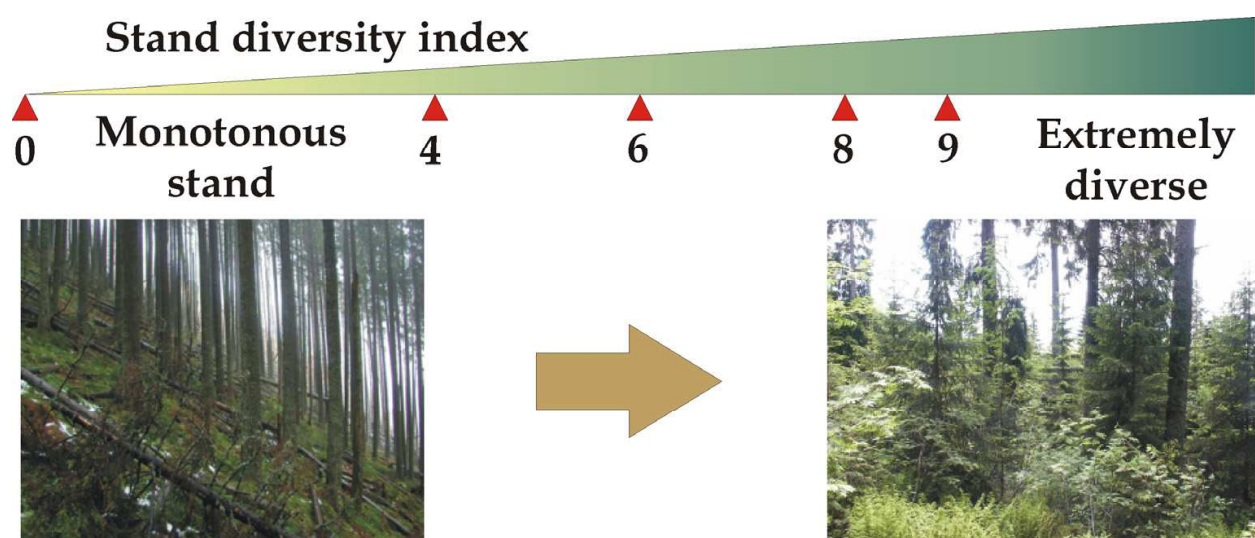


Fig. 5. Complex assessment of stand diversity according to Jaehne & Dohrenbusch (1997).

3.3 Functional diversity

From a functional point of view, species can be subdivided into categories like primary producers, herbivores, predators, and decomposers (Stokland et al., 2003). Belaoussoff et al. (2003) defined a functional group as a group of species, which do not necessarily have to be related, but which exploit a common resource base in a similar fashion. Hence, there

is an overlap in resource requirements between species in a functional group (Belaoussoff et al., 2003).

The BEAR-project strongly recommends including functional indicators in any Biodiversity Evaluation Tool. Within the framework of the BEAR project, fire, wind and snow, and biological disturbance have been identified as the most important functional key factors in the group of “natural influences”, while the area affected by a particular factor are suggested as possible indicators with high ecological significance (BEAR Newsletter 3). Although in reality the ecosystem function might be more important than species diversity (Sobek & Zak, 2003), structural and compositional indicators are considered to be more tractable for end-users (Angelstam et al., 2001 as cited in Humphrey & Watts, 2004).

3.4 Diversity inventory in forest ecosystems

To get an overview, forest inventory data can be a cost effective source of information for large areas (Söderberg & Fridman, 1998), because forest inventories represent a major source of data concerning forests (Estreguil et al., 2004). The original aim of forest inventories was to describe the main features of forests in terms of size, condition, and change, particularly from the production perspective (Rego et al., 2004). An increasing demand for information on non-productive functions of forests caused that recently variables more related to biodiversity have been introduced to forest inventories (Söderberg & Fridman, 1998). For example, the recognition of the ecological importance of decaying wood has led to the incorporation of quantitative measures of deadwood in forest inventories (Humphrey et al., 2004). Hence, national forest inventories are becoming more comprehensive natural resources surveys (Corona & Marchetti, 2007).

Basically, forest inventories provide us with the information about: 1) forest area and land cover, 2) resource management (growing stock), 3) forestry methods and land use (felling systems, regeneration methods, road network density), 4) forest dynamics with regard to different disturbance factors (fire, storm, insect, browsing), 5) forest state (tree species composition, age distribution, dimension of living trees, tree mortality and deadwood), and partly also about 6) conservation measures, i.e. protected forest areas (Stokland et al., 2003). Hence, data from forest inventories are also useful for biodiversity assessment. For example, these data can be used for the quantification of several biodiversity indicators related to species composition, mainly in terms of species richness and the presence of species of high conservation value (threatened or endemic species, Corona & Marchetti, 2007).

However, data from forest inventories may not be suitable for every analysis. For example, national forest inventory field plots are inadequate for measuring landscape patterns of structural ecosystem diversity because of the small plot size (Stokland et al. 2003). In addition, in many cases precision guidelines for the estimates of many variables cannot be satisfied due to budgetary constraints and natural variability among plots (McRoberts et al. 2005). In neither of the cases, it is efficient to increase the plot size or their number. Instead, other data sources that enable rapid data generation, e.g. digital photogrammetry; geographical information systems (GIS), digital elevation model (DEM), global positioning system (GPS) or remote sensing (Gallaun et al., 2004; Kias et al., 2004 as cited in Wezyk et al., 2005) can be used more efficiently. Fieldwork itself has been enhanced by satellite positioning systems (GPS), automatic measuring devices, field computers and wireless data transfer (Holopainen et al., 2005).

For special purposes, specific monitoring programmes are needed. These programmes attempt to investigate particular features of a forest ecosystem that are of specific interest and their monitoring is not included within national forest inventories. Many of such surveys have been performed by non-governmental organisations and within the frame of specific forest monitoring programmes (Heer et al., 2004). Although this kind of information can be of high value at a local or national scale, its applicability at a higher level (region, Europe) is restricted and requires pre-processing of data with regard to their quality, and biases and gaps in time and space (Heer et al., 2004). Therefore, many international projects dealing with biodiversity have been solved in the last decade (e.g. BioAssess, BEAR, ForestBIOTA, ALTER-Net, SEBI, DIVERSITAS).

The quantification of biodiversity indicators can be performed in two ways, which affect the calculation of their confidence intervals. One method is that the indicator is calculated from the summary data about the whole population. In this case, there are several possibilities how to obtain the summary data:

- by accurate measurement of all individuals in population, i.e. complete survey;
- by visual estimation during the inspection of the examined population;
- by sampling methods in such a way, that the summary information is obtained by summing up the data collected on several places in a forest stand.

We call this approach the “method of sum”. Biodiversity indicator determined with this method refers to the area that is larger than the minimum area. Hence, the comparison of the results of different populations is usually correct. In other cases, it is possible to use various standardisation methods given in e.g. Ludwig & Reynolds (1988) or Krebs (1989).

The second approach is called the “method of mean”, because in this case biodiversity indicators are determined on several locations distributed over the whole community, and from them the average value typical for the whole population is derived. An important condition of this method is to assess biodiversity indicators on the samples of equal size, because in this case area has a significant effect on the value of biodiversity indicator. The final value of the biodiversity indicator refers to the area of the samples. Another alternative of this method is to determine indicator on the same number of individuals, e.g. 20 trees (Merganič & Šmelko, 2004).

At the ecosystem and landscape level, remote sensing represents a powerful and useful tool for biodiversity assessment (Ghayyas-Ahmad, 2001; Innes & Koch, 1998; Foody & Cutler, 2003). This method can provide cost efficient spatial digital data which is both spatially and spectrally more accurate than before (Holopainen et al., 2005). Moreover, remote sensing technology can provide the kind of information that was previously not available to forestry at all or was not available on an appropriate scale (Schardt et al., 2005). According to Innes & Koch (1998), “remote sensing provides the most efficient tool available for determining landscape-scale elements of forest biodiversity, such as the relative proportion of matrix and patches and their physical arrangement. At intermediate scales, remote sensing provides an ideal tool for evaluating the presence of corridors and the nature of edges. At the stand scale, remote sensing technologies are likely to deliver an increasing amount of information about the structural attributes of forest stands, such as the nature of the canopy surface, the presence of layering within the canopy and presence of coarse woody debris on the forest floor.”

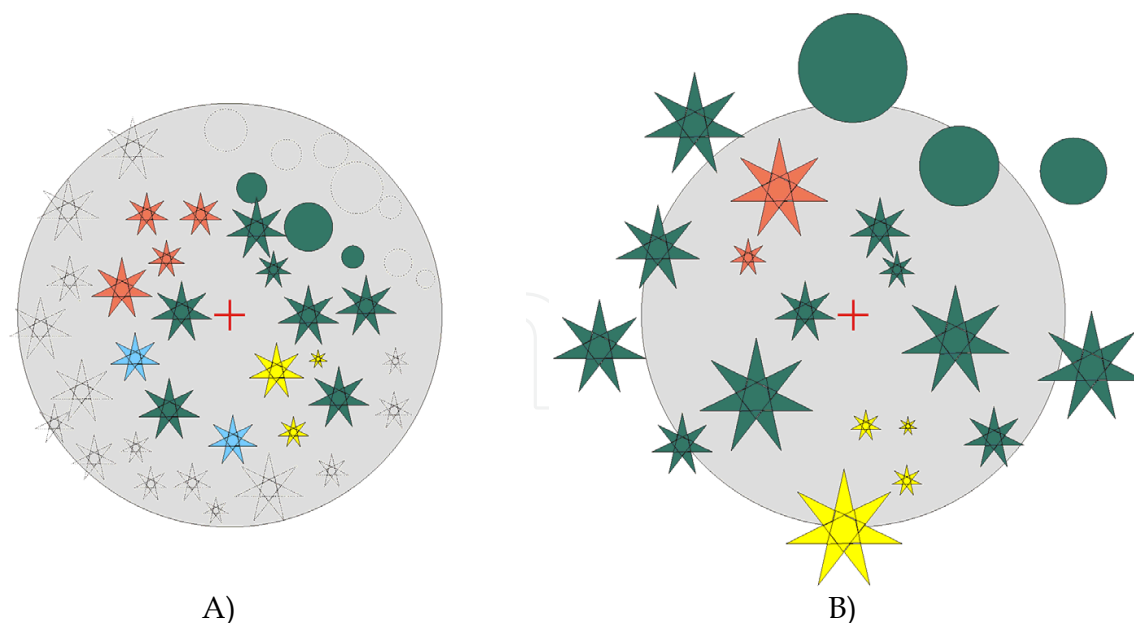


Fig. 6. Assessment and quantification of tree species diversity on a set of 20 trees in case of a dense (A) and released (B) stand. In contrast to sampling on the plots with constant area, the sampled area varies.

Literature survey revealed that remote sensing data have been successfully used for:

1. habitat categorisation and estimation of their changes over large areas (Brotherton, 1983; Cushman & Wallin, 2000 as cited in Humphrey & Watts, 2004)
2. estimation of forest characteristics, e.g. basal area, stand volume, stem density, (Ingram et al., 2005; Maltamo et al., 2006 ; Reese et al., 2003; Tuominen & Haakana, 2005)
3. measuring vegetation (forest) structure (Ingram et al., 2005; Maltamo et al., 2005; Prasad et al., 1998; Wack & Oliveira, 2005)
4. analysis of canopy surface and canopy gaps (Nuske & Nieschulze, 2005)
5. identification of dead standing trees (Butler & Schlaepfer, 2004) and estimation of their amount (Uuttera & Hyppanen, 1998)
6. stratification for ground inventory (Roy & Sanjay-Tomar, 2000; Ghayyas-Ahmad, 2001; Jha et al., 1997) or to increase the precision of estimates (McRoberts et al., 2003, 2005; Olsson et al., 2005)

Nagendra (2001) who evaluated the potential of remote sensing for assessing species diversity distinguished three types of studies:

1. direct mapping of individuals and associations of single species,
2. habitat mapping using remotely sensed data, and prediction of species distribution based on habitat requirements,
3. establishment of direct relationships between spectral radiance values recorded from remote sensors and species distribution patterns recorded from field observations.

Direct mapping is applicable over smaller areas to obtain detailed information on the distribution of certain canopy tree species or associations. Habitat maps appear most capable of providing information on the distributions of large numbers of species in a wider variety of habitat types (Nagendra, 2001).

Turner et al. (2003) recognise two general approaches to the remote sensing of biodiversity. „One is the direct remote sensing of individual organisms, species assemblages, or ecological communities from airborne or satellite sensors. The other approach is the indirect remote sensing of biodiversity through reliance on environmental parameters as proxies“ (Turner et al., 2003), that can be clearly identified remotely.

4. Importance of diversity

4.1 Productivity

Experimental relationship between site productivity and biodiversity of community is a widely discussed question in scientific literature. This problem was studied in detail at the end of 1980s (Rozenzweig & Abramsky, 1993). In many cases, this relationship has a humped shape with maximum species diversity at average productivity and minimum at both extremes, i.e. at low and high productivity. This shape was observed both in plant and animal communities. However, no general model that would explain this relationship has been derived yet. The humped shape can be linked with the theory of the limiting factor. On every site each species has a specific productivity threshold. Site factors are limiting for the survival of the species. As the site productivity increases, more and more species exceed their threshold value and hence, can survive in the environment. The decline of diversity with increasing productivity after the peak of the curve is a mystery that has been in the centre of interests of many scientists, who presented several explanations and hypotheses. However, none of them was sufficiently satisfactory. As an example we present two of them.

In the first hypothesis, species diversity is related to micro-site diversity (Rozenzweig & Abramsky, 1993). In theoretical ecology it is a well-known fact that one ecological niche can carry only one species. This theory, also called as “niche theory” says that average sites have more niches than very poor or very rich sites. Hence, we can conclude that they also have higher species diversity. This can be illustrated using three basic site factors: temperature, moisture, nutrients. On poor sites (cold, dry, and nutrient poor), all factors have low values, which results in a unique combination of factors that represent a specific site with very low productivity. Similarly, rich sites (warm, moist, and nutrient rich) are also the result of a unique combination of factors leading to one specific site. However, on average sites, a great number of combinations of site factors exist, while each combination represents a specific niche, which can carry a specific community. According to this theory, site diversity is maximum on average sites, and therefore, species diversity is maximum on average sites.

The second hypothesis is based on the theory of the „right of the limiting factor“ (Rozenzweig & Abramsky, 1993). When the site productivity is high, all species have the potential to survive. However, a large number of species on the site leads to a strong competition resulting in the reductions in species number. Hence, low diversity can be caused by the strong competition of the most vital species, which suppress other species.

In forestry applications, this issue is closely related to the production in mixed forest stands, which is becoming an up-to-date theme due to accepting the principles of sustainable and close-to-nature forestry and consequently the transformation of forest management. This management results in greater area of uneven-aged and heterogenous forest stands, which complicates the use of traditional dendrometric models. Some efforts have been made to

create models that would enable to determine the volume of several mixture types and forms. From this point of view, tree growth simulators are promising tools that are able to predict the development of mixed forests (Fabrika, 2005; Hasenauer, 1994; Kahn & Pretzsch, 1997; Nagel, 1995; Sterba et al., 1995).

4.2 Stability

Most ecologists agree that species diversity is a good basis for long-term existence of communities, i.e. communities that are composed of only a small number of species are more susceptible to extinction than species-rich communities. Due to this fact, diversity is implicitly linked to stability. However, this theory was disapproved, when May (1973) using Lotka - Volter systems presented that stability decreases with increasing complexity of iterations, i.e. with the increasing value of Simpson diversity index. May's argument was based on the analysis of system stability through the linearisation of the surrounding balance. In other words, random Lotka-Volter system is stable if it consists of several interconnected species, or if the intensity of connections is low. A lot of important connections lead to system instability. It is still questionable if this is generally valid for all systems. This statement caused wide discussions. Anti-arguments say that in the ecosystem the interconnections are not randomly distributed, but consistently structured, which should cause the increase of stability. A short review of the progress in this field since the work of May (1973) can be found in Sigmund (1995).

In forestry field, stand stability is one of the main principles of sustainable forest management, which was approved in Helsinki Ministerial Conference on the Protection of Forests in Europe. Its importance increases particularly in the last time, which is characterised by more frequent occurrence of large-scale disturbances. Concerning the relationship of stability to biodiversity, Stolina (1996) stated that:

- natural forest ecosystems that are not influenced by anthropogenic activities are characterised by specific species diversity which is adequate to conditions of abiotic environment, because it has resulted from the long-term adaptation process.
- species diversity can be taken as an indicator of forest ecosystem stability;
- not every increase of species diversity measures indicate the increase of stability.

4.3 Naturalness – Diversity indicators of forest naturalness

Both biodiversity and naturalness are frequently used in conservation (Schnitzler et al., 2008), as the criteria for assessing the conservation status of forest ecosystems. Their significance was approved in many international schemes, e.g. both concepts were included in the list of pan-European indicators of sustainable forest management (MCPFE, 2002). The concepts are closely interlinked. For example, the degrees of forest naturalness distinguished within the scope of MCPFE are characterised with regard to biodiversity and its components. In forests undisturbed by man, processes and species composition remain natural to a considerable extent or have been restored. Semi-natural forests can keep certain natural characteristics allowing natural dynamics and biodiversity closer to the original ecosystem. Plantations represent man-made (artificial) forest communities, which are completely distinct from the original ecosystem (MCPFE, 2002).

The objective assessment of forest naturalness presented by several authors (e.g. Bartha et al., 2006; Machado, 2004; Moravčík et al., 2010; Winter et al., 2010) is based on a number of compositional, structural, and functional attributes of biodiversity, such as species composition and structure of different forest layers, occurrence of deadwood, etc. Tree species composition is the most common attribute used for the assessment of forest naturalness (Glončák, 2007; Guarino et al., 2008; Šmídt, 2002; Vladovič, 2003), but recently the amount of deadwood has also gained attention due to the large differences between managed and unmanaged stands. From other structural characteristics, horizontal structure characterised by diameter distribution (Pasierbek et al., 2007), differentiation of vertical and age structure are biodiversity indicators used in the assessment of forest naturalness (Moravčík et al., 2010).

5. Conclusion

Biodiversity is a keystone of ecosystem functioning. Its actual state determines if the ecosystem is sustainable, and hence, if it can fulfil particular functions, or ecosystem services. Since nowadays biodiversity has been receiving much attention worldwide, it is of great importance to understand this term thoroughly and to be able to quantify it mathematically. Various assessment methods and evaluation procedures have been used for the quantification of partial components of biodiversity, which allow users to evaluate and compare ecosystems objectively. In the presented chapter, we reviewed the current state-of-art of plant diversity assessment and examined the relationship of plant diversity to main forestry issues, namely forest management, productivity, stability and naturalness. The review of the available knowledge indicates that for the proper utilisation of biodiversity measures, their values should always refer to the area they represent. The questions about the relationships between biodiversity and forest productivity, stability and consequently management remain open for future research.

6. Acknowledgments

This work was supported by the National Agency for Agriculture Research in Czech Republic under the contract No. QH91077 and the Slovak Research and Development Agency under the contracts No. APVT-27-009304, and APVV-0632-07.

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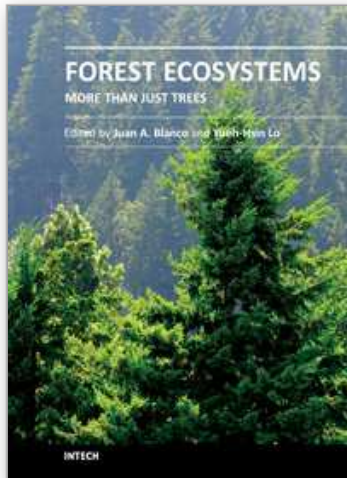
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Forest Ecosystems - More than Just Trees

Edited by Dr Juan A. Blanco

ISBN 978-953-51-0202-1

Hard cover, 464 pages

Publisher InTech

Published online 07, March, 2012

Published in print edition March, 2012

The common idea for many people is that forests are just a collection of trees. However, they are much more than that. They are a complex, functional system of interacting and often interdependent biological, physical, and chemical components, the biological part of which has evolved to perpetuate itself. This complexity produces combinations of climate, soils, trees and plant species unique to each site, resulting in hundreds of different forest types around the world. Logically, trees are an important component for the research in forest ecosystems, but the wide variety of other life forms and abiotic components in most forests means that other elements, such as wildlife or soil nutrients, should also be the focal point in ecological studies and management plans to be carried out in forest ecosystems. In this book, the readers can find the latest research related to forest ecosystems but with a different twist. The research described here is not just on trees and is focused on the other components, structures and functions that are usually overshadowed by the focus on trees, but are equally important to maintain the diversity, function and services provided by forests. The first section of this book explores the structure and biodiversity of forest ecosystems, whereas the second section reviews the research done on ecosystem structure and functioning. The third and last section explores the issues related to forest management as an ecosystem-level activity, all of them from the perspective of the other parts of a forest.

How to reference

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Ján Merganič, Katarína Merganičová, Róbert Marušák and Vendula Audolenská (2012). Plant Diversity of Forests, *Forest Ecosystems - More than Just Trees*, Dr Juan A. Blanco (Ed.), ISBN: 978-953-51-0202-1, InTech, Available from: <http://www.intechopen.com/books/forest-ecosystems-more-than-just-trees/plant-diversity-of-forests>

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