Forest Ecology and Management 330 (2014) 82–93

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The role of forest stand structure as biodiversity indicator

Tian Gao [a,b,*], Marcus Hedblom [b,1], Tobias Emilsson [b,2], Anders Busse Nielsen [b,c,2,3]

[a] Northwest A & F University, College of Forestry, 712100 Yangling, China
[b] Swedish University of Agricultural Sciences, Alnarp, Sweden
[c] University of Copenhagen, Copenhagen, Danmark

ARTICLE INFO

Article history:
Received 23 February 2014
Received in revised form 30 June 2014
Accepted 2 July 2014

Keywords:
Biodiversity indicator
Biotope mapping model
Soil conditions
Nature conservation
Sustainable forest management

ABSTRACT

Biodiversity conservation is a key objective for sustainable forest management, but the multi-dimensional and multi-scale character of biodiversity renders full assessment difficult at large scale. Therefore, indicators are often used to monitor biodiversity. Important cost-benefit synergies can be achieved if indicators are derived from existing data. In this study, a model for classifying forest stand structures was developed and tested as an indicator of overall plant species diversity at stand level. The model combines four stand structure parameters: canopy coverage, age of canopy trees, tree species composition and canopy stratification. Using data from the National Inventory of Landscapes in Sweden and General Linear Mixed Model, plant species diversity (Shannon diversity index, SHDI) and composition (Sørensen-Dice index, SDI) were tested between 26 different stand structure types and nine soil classes. The results showed that mature stands with a stratified canopy had the highest plant species diversity across the soil classes, particularly if they comprised mixed coniferous and broadleaved species with a semi-open canopy. In contrast, young (<30 years) single-layered stands had consistently low species diversity. Of the four stand structure parameters in the model, age of canopy trees was most influential for SHDI value, followed by canopy stratification, tree species composition and canopy coverage. According to the SDI values, different stand structure types represented different species composition regardless of soil class and species diversity (SHDI value). However, most SDI values were higher than 0.5, indicating that fewer than 50% of the species changed between stand structure types. The stand parameters included in the model can probably be extracted from national forest inventories in many countries and understood without specialist taxonomic knowledge, making the model applicable in practice to support forest management decision-making on enhancing forest biodiversity at stand level.

1. Introduction

Biodiversity has been shown to play a key role at all levels of the ecosystem service hierarchy (Mace et al., 2012). The diverse habitats and microhabitats contained in forest ecosystems hold the majority of the world's terrestrial species (Ozanne et al., 2003). However, these biologically diverse systems are increasingly being threatened by deforestation and forest degradation via varied direct or indirect mechanisms (Singh et al., 2001; Dirzo and Raven, 2003). Therefore, conserving forest biodiversity has become a critical task at local, national and global level.

One prerequisite for sound integration of biodiversity conservation in forest management planning is monitoring of its spatial and temporal changes. However, the broad, multi-dimensional and multi-scale characteristics of biodiversity render full assessment difficult and extremely costly at large scale (Gaston, 1996; Green et al., 2005). Therefore indicators, i.e. surrogate measures of other components of forest biodiversity, are increasingly being used to monitor temporal and spatial changes in biodiversity (Boutin et al., 2009). From a cost-benefit and time-efficiency perspective, indicators that can be derived from existing datasets, e.g. data parameters collected as part of National Forest Inventories (NFIs), would be a viable option (Chirici et al., 2012).

* Corresponding author. Address: Swedish University of Agricultural Sciences, Faculty of Landscape Planning, Horticulture and Agricultural Science, Department of Landscape Architecture, Planning and Management, 230 53 Alnarp, Sweden. Tel.: +46 729455641.

E-mail addresses: dracogao.2121@aliyun.com, tian.gao@slu.se (T. Gao), marcus.hedblom@slu.se (M. Hedblom), tobias.emilsson@slu.se (T. Emilsson), anders.busse.nielsen@slu.se (A.B. Nielsen).

[1] Address: Swedish University of Agricultural Sciences, Faculty of Forest Sciences, Department of Forest Resource Management, 901 83 Umeå, Sweden.

[2] Address: Swedish University of Agricultural Sciences, Faculty of Landscape Planning, Horticulture and Agricultural Science, Department of Landscape Architecture, Planning and Management, 230 53 Alnarp, Sweden.

[3] Address: University of Copenhagen, Department of Geosciences and Natural Resource Management, DK-1958, Copenhagen, Danmark.

http://dx.doi.org/10.1016/j.foreco.2014.07.007
0378-1127/

While many indicators have been presented to date for assessing different aspect of biodiversity in forest ecosystems (e.g. Berglund and Jonsson, 2001; Smith et al., 2008; Chirici et al., 2012; Coote et al., 2013), studies of ecosystems such as urban, agricultural and mountain landscapes have shown that plant species diversity is the best predictor of overall biodiversity (e.g. Simonson et al., 2001; Sauberer et al., 2004; Bräuniger et al., 2010). However, in a review of NFIs from 25 European countries and the United States, Chirici et al. (2012) found that data on plant species diversity are limited in many countries because ground layer vegetation is not included or is collected in different ways, making generalisation very difficult. Development of an indicator for overall plant species diversity at forest stand level would therefore be of great value.

The structural parameters and tree species records collected at stand level in most NFIs to enable growing stock estimations and other variables important for commercial forest management are also important components for biodiversity because both horizontal (spatial) and vertical (stratification) heterogeneity and the array of tree species provide habitats for a range of plants and animal species (e.g. Lindenmayer et al., 2000). Some studies have related overstory coverage to species richness of vascular plant (Zerbe et al., 2007; Smith et al., 2008), bryophyte (Zerbe et al., 2007; Coote et al., 2013), lichen (Berglund and Jonsson, 2001), bird (Smith et al., 2008; Patthey et al., 2012) etc. Some studies have focused on vertical stratification (number of canopy layers) with bird species diversity (Kati et al., 2009; Titchenell et al., 2011; Patthey et al., 2012). Tree age has also been used as an indicator for species richness of bird (Jansson and Andrén, 2003; Gil-tena et al., 2009), insect (Jukes et al., 2001; Arnan et al., 2009), vascular plant (Dumortier et al., 2002; Smith et al., 2008), bryophyte (Fritz et al., 2008; Coote et al., 2013), lichen (Uliczka and Angelstam, 1999; Johansson et al., 2007), fungus (Nordén and Paltto, 2001; Heilmann-Clausen and Christensen, 2005) etc. Meanwhile, some other studies have compared species diversity of vascular plant (Máliš et al., 2010), bryophyte (Brunialti et al., 2010), lichen (Uliczka and Angelstam, 2000), fungus (Rudolf et al., 2012), bird (Kati et al., 2009) etc. between different forest types. Lindgren et al. (2006) show that structural diversity induced by pre-commercial thinning enhances the abundance and species diversity of the plant community in even-aged commercial forest stands.

In this study, four stand structure parameters that can be derived from NFI field inventory data in most countries were combined to form a uniform classification of forest stand into structural types. The four structural parameters are; (1) Canopy coverage, (2) age of canopy trees, (3) tree species composition, and (4) canopy stratification. With the overarching aim to evaluate the stand structural types as indicator of plant species diversity at stand level, the objective of this study were to:

- Analyse the relationship between the four stand structure parameters and plant species diversity.
- Identify the most influential structural parameter(s) for plant species diversity at stand level.
- Establish a gradient of forest stand structure types in relation to their plant species diversity and composition.

2. Materials and methods

2.1. National Inventory of Landscapes in Sweden (NILS) programme

Raw data on structural parameters and plant species records collected in permanent sampling plots within the National Inventory of Landscapes in Sweden (NILS) programme were used as data input. NILS is a nation-wide monitoring programme established in 2003 to monitor conditions and changes in the Swedish landscape, with the main focus on following the changes in prerequisites for biodiversity at landscape level. In a similar way to NFIs, NILS collects data enabling growing stock estimations and other variables important for commercial forest management, but it also rigorously records ground and field layers for biodiversity assessments.

2.2. Study area with the background of Swedish forestry

The present study covered the entire temperate forest zone in southern Sweden, approximately below the Limes Norrlandicus and covering Strata 1-6 (out of 10 strata, Fig. 1) including 224 (out of 631) permanent sampling units (Ståhl et al., 2011). Together, these six strata cover an area of approximately 140,000 km^2. In Strata 1, 2 and 3, agriculture is the dominant land use, Stratum 4 represents a mosaic landscape with small-scale farming and forest, and forestry is the dominant land use in Strata 5 and 6. The large area covered by the study makes it difficult to explain standard practices in detail. In general, the forested area in Sweden is about 28 million ha occupying 51% of the Swedish territorial area. 23 million ha is productive forest and 3.6% of which is under protection (Swedish Statistical Yearbook of Forestry, 2012) resulting in a very high proportion of managed forest in the study area. Tree species mainly consists of Spruce (45%), Pine (39%), Birch (10%), Oak (1%), Beech (1 %) and others (4%) (Gustafsson and Ahlén, 1996), and the annual growth is about 2–3 m^3/year in the North and 7–8 m^3/year in the South (Jansson, 2011).

The way of using the forest is of felling the old forest (clear felling) and planting new forest or natural regeneration by seed trees (rarely sowing). The young forest is cleared to suitable spacing of the trees left standing, and middle aged forest is thinned from one to five times. Depending on tree species and location, clear felling takes place at an age of 50–120 years and new forest is established. Nearly half of the total area of productive forest land has been clear-felled and regenerated since the 1950s and most of the remainder has been affected by the thinning or other human interventions. Extensive areas in Sweden have less than 20% of old forest (>80 years is old forest in southern Sweden, >100 years in middle Sweden and >120 years in northern Sweden) (Jansson, 2011).

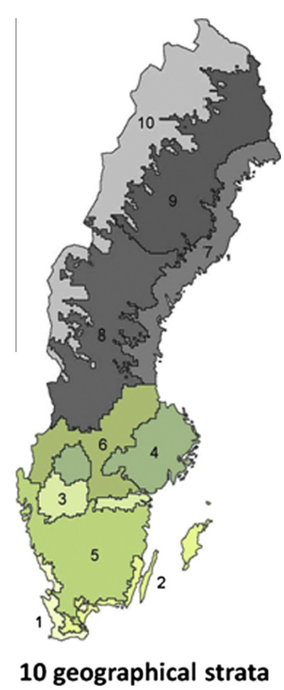

Fig. 1. Study area and method design in Sweden. Green shades indicate Strata 1-6 for which data were used in this study. Grey shades indicate Strata 7-10, data on which were not used in the study. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. NILS data

The 224 permanent sampling units (5 km × 5 km) used here are randomly distributed within the six strata, with 7, 28, 26, 47, 76 and 40 sampling units in Stratum 1-6, respectively. Landscape composition and land cover types are determined based on manual interpretation of colour infrared (CIR) aerial photos (scale approx. 1:30,000) of a 1 km × 1 km square located at the centre of each sampling unit. Within the 1-km^2 square, 12 circular sampling plots of 20 m radius and 250 m apart are inventoried in the field. For the present study, only data obtained from plots located within semi-open and closed forest throughout Strata 1-6 were included (n = 1290) (Fig. 2).

Each circular NILS sampling plot consists of the following set of concentric circular plots: (a) A 20 m radius plot in which the basic conditions in the plot, e.g. canopy tree species, coverage, forest stand variables, are assessed; (b) a 10 m radius plot in which understory and shrub layer species (if present) and their coverage are measured and basic assessments of field layer vegetation are made based on broad taxonomy of plants, i.e. herb, fern, dwarf shrub and graminoid; and (c) three 0.28 m radius plots in which field/ground layer species/genera, including mosses and lichens, are documented in detail by measuring their frequency of occurrence (Fig. 2). The NILS species monitoring scheme does not include total species richness, but instead a frequency record based on a preselected list of species that indicate habitat characteristics or turnover. In the dataset used in this study, field inventories distinguished 286 plant species comprising 35 tree species, 42 shrub species and 209 field layer species. According to taxonomic classification, the 1290 plots located within semi-open and closed forest throughout Strata 1-6 included 237 vascular plant species, 33 bryophyte species and 16 lichen species. However, 6 tree species were only identified to genus level, namely *Abies* spp., *Betula* spp., *Quercus* spp., *Ulmus* spp., *Tilia* spp. and *Malus* spp., plus 13 other species that mostly occurred sporadically in the sampling plots (Table 1).

2.4. Classification of forest stand structures

Based on the biotope classification model designed by Gao et al. (2012), a model for classifying the NILS sampling plots into different forest stand structure types was developed (Table 2). The first dimension in this model was canopy coverage (i.e. horizontal structure), where sampling plots with 30–80% canopy cover were classified as stands with a semi-open canopy and sampling plots with >80% canopy cover as stands with a closed canopy. The second dimension was the age of canopy trees, with a distinction made between young (<30 years), middle-aged (30–80 years) and old (>80 years) trees. In accordance with Hägglund and Lundmark (1982), tree age was estimated here by relating data on tree height from the NILS dataset to soil conditions (see Section 2.4). The third dimension in the model was tree species composition, where areas with broadleaved trees or coniferous trees occupying more than 70% of the canopy cover were defined as

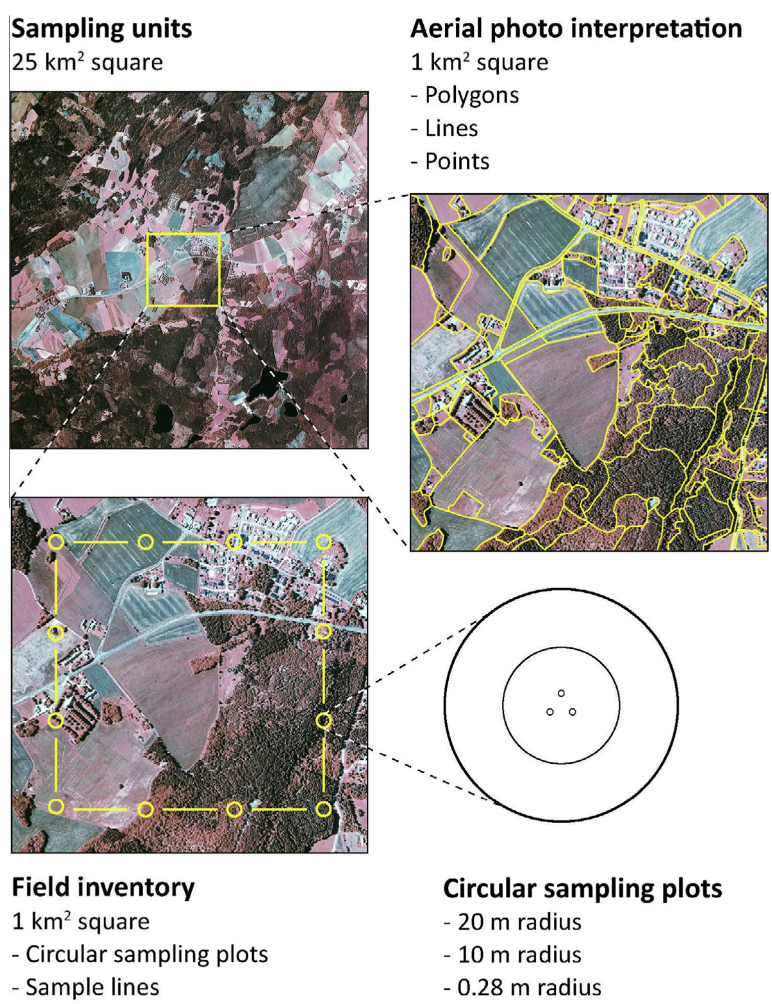

Fig. 2. The scheme of sampling structure by NILS programme combining aerial photo interpretation and field inventory.

Table 1
The species presented in NILS dataset on the genus level and its frequency of occurrence (%) based on the sum of sampling plot ($N = 1290$).

Genus	No. of plot found (with %)	Genus	No. of plot found (with %)	Genus	No. of plot found (with %)
Amelanchier spp.	16 (1.2%)	*Drosera* spp.	5 (0.4%)	*Hieracium* spp.	13 (1.0%)
Cotoneaster spp.	4 (0.3%)	*Melampyrum* spp.	>20 (11%)	*Umbilicaria* spp.	7 (0.5%)
Crataegus spp.	>20 (2.1%)	*Rhinanthus* spp.	2 (0.1%)	*Stereocaulon* spp.	5 (0.4%)
Lupinus spp.	7 (0.5%)	*Valeriana* spp.	6 (0.5%)		
Typha spp.	2 (0.1%)	*Taraxacum* spp.	>20 (3.7%)		

Table 2
Model for classification of forest stand structures into 36 different types, e.g. C2D1: a closed canopy forest with mainly 30–80-year-old broadleaved trees with 1 vertical layer.

Dimension 1 – Canopy coverage	Dimension 2 – Age of canopy trees	Dimension 3 – Tree species composition	Dimension 4 – Canopy stratification
Semi-open canopy (S)	<30 years (1)	Broadleaved (D)	1-layered (1)
Closed canopy (C)	30–80 years (2)	Coniferous (C)	>1-layered (2)
	>80 years (3)	Mixed (M)	

broadleaved stands or coniferous stands, respectively, while plots where both species groups contributed 30–70% to the canopy cover were defined as mixed stands. The fourth dimension was canopy stratification, i.e. vertical stand structure including canopy layer, understory and shrub layer, with a distinction made between 1-layered and >1-layered stand structures. The field/ground layer was not considered in the vertical structure in the model.

2.5. Soil condition matrix

As a supplement to the model for stand structures, the NILS sampling plots were classified into different soil classes. Using a revised version of the Ellenberg's indicator values (Hill et al., 1999), data on field layer vascular plant species ($n = 132$) were used to divide sampling plots into a uniform matrix reflecting nine soil classes in terms of soil water condition (SWC) and soil pH value (see Appendix A). Each sampling plot was assigned to a soil class according to the Ellenberg's indicator values of majority ($\geqslant$80%) of vascular plant species.

2.6. Statistical analysis

The Shannon diversity index (SHDI) was used for calculating the plant species diversity of each forest sampling plot. The Sørensen-Dice index (SDI) was used for comparing similarities in plant species composition between stand structure types (Eq. (1)):

$$\mathrm{SDI} = \frac{2c_{ij}}{a_i + b_j} \tag{1}$$

where a and b are the pooled number of species of stand structure types i and j in a certain soil class, respectively, and c is the pooled number of species shared by the two stand structure types. SDI is the similarity ratio for two stand structure types and ranges from 0 to 1.

The impacts of soil class, the four stand structure parameters, their interactions and sub-categories, as well as the impacts of stand structure types on plant species diversity (SHDI value), were tested using General Linear Mixed Model (GLMM). In this analysis, the random factor defined spatial autocorrelation between clustered 20 m plots, and the identity number of each 1 km × 1 km square was treated as the random variable in the model in order to remove the influence of spatial autocorrelation. More specifically, the following steps were carried out: (1) Soil class effect on SHDI value; (2) individual stand structure parameters and their interactive effect on SHDI value within soil classes; (3) differences in SHDI value between sub-categories of each stand structure parameter based on post-hoc analysis (Tukey Method), i.e. semi-open vs. closed canopy, young/mature/old, mixed/coniferous/broadleaved, and one-layer vs. >one-layer; and (4) comparisons of SHDI value between forest stand structure types within and across soil classes. The simplified data was used in the latter, i.e. forest stand structures with less than 10 sampling plots were excluded from the comparisons (except old stand structures) to improve the accuracy of the correlation. The Minitab 16 programme was used for these statistical analyses. In addition, the impact of stand structure type on plant species composition was calculated based on the simplified data. Species composition change (SDI value), i.e. species turnover, was tested between stand structure types within each soil class using pooled species number of each stand structure type. Microsoft Office Excel 2007 was used for the calculation and analysis of SDI value in terms of Eq. (1).

3. Results

The 1290 sampling plots were allocated to 26 different stand structure types (Table 3). Young (<30 years) and mature (30–80 years) stands were well represented, with single-layered (S), young (1), coniferous (C), closed canopy (1) stands (overall code S1C1) occupying the highest number of sampling plots, mostly allocated to soil classes IV, V, VII and VIII. However, only 12 plots were classified as old (>80 years) and these were all 1-layered coniferous stands with a closed ($n = 7$) or semi-open canopy ($n = 5$) allocated to soil class V. The low number of old stands reflects the high proportion of commercially managed forest in the study area.

The sampling plots represented all soil classes except class IX, i.e. water-logged areas with high pH levels (Table 3). The highest number of sampling plots occurred on mesic soils with low pH (class IV) followed by mesic soils with medium pH (class V) and mesic soils with high pH (class VII). In comparison, few sampling plots were located on dry sites (class I–III).

3.1. Impact of soil conditions on plant species diversity

The SHDI value for sampling plots located in different soil classes differed significantly ($\mathrm{DF} = 7$, $F = 42.54$, $P < 0.001$) in terms of plant species diversity once the influence of spatial autocorrelation (SA) was removed ($\mathrm{DF} = 223$, $F = 1.38$, $P = 0.001$, hereafter $\mathrm{DF_{SA}}$, F_{SA} and P_{SA}) (Table 4). Plots on mesic soils with high pH (class VI) and plots on wet soils with medium pH (class VIII) had the highest SHDI values, while the few sampling plots located on dry soils (classes I–III) had the lowest SHDI values (Table 4). There was no interactive effect of soil class and stand structure type on the SHDI value ($\mathrm{DF} = 64$, $F = 1.33$, $P = 0.064$).

Table 3
Number of sampling plots for 26 stand structures in relation to soil classes to which samples were allocated. See Table 2 for explanation of stand structure abbreviations.

Stand structure abbreviation	Number of sampling plots in each soil class								Number of sampling plots for each stand structure
	I	II	III	IV	V	VI	VII	VIII	
C1C1	4	3	6	60	27	5	30	14	149
C1C2				2	4	4	2	2	14
C1D1		1		6	10	11	11	1	40
C1D2					6	3		7	16
C1M1	1			6	6	3	7	3	26
C1M2				3	3	1	3	3	13
C2C1	1	1	1	49	40	4	30	5	131
C2C2					7	4	6	3	20
C2D1			1	2	9	1	2	5	20
C2D2					9	7	11	4	31
C2M1				8	7	4	6	4	29
C2M2					10	2	11	10	33
C3C1					7				7
S1C1	6	3	2	78	61	6	27	23	206
S1C2				12	7	2	4	3	28
S1D1	1			7	9	11	4	15	47
S1D2					8	6		2	16
S1M1			1	13	21	3	13	5	56
S1M2					8	3	6	5	22
S2C1	3	1	1	87	28	7	40	10	177
S2C2				10	7	7	5	4	33
S2D1				7	9	7		8	31
S2D2				12	10	13	3	3	41
S2M1				19	16	1	10	7	53
S2M2				12	11	12	10	1	46
S3C1					5				5
Number of sampling plots for each soil class	16	9	12	393	345	127	241	147	

Table 4
Number of sampling plots and Shannon diversity index (SHDI) value for each of the eight soil classes to which samples were allocated.

Soil class	Number of plots	SHDI (±S.E.)
VI	127	2.87 ± 0.07 a
VIII	147	2.80 ± 0.06 a
V	345	2.57 ± 0.04 ab
VII	241	2.46 ± 0.05 b
IV	393	2.22 ± 0.04 c
I	16	0.88 ± 0.19 d
II	9	0.68 ± 0.25 d
III	12	0.68 ± 0.21 d

Note: LS-Mean SHDI values followed by different letters are significantly different at $P < 0.001$. Random influence by each 1 km × 1 km square is at $P_{SA} = 0.001$.

3.2. Impact of stand structure parameters on plant species diversity within and between soil classes

As a consequence of the limited number of sampling plots, soil classes I, II, III and IX were excluded from the GLMM. Furthermore, as soil classes VI and VIII had comparable SHDI values, they were combined in the tests as one soil class.

In the remaining four soil classes, i.e. classes IV ($DF_{SA} = 178$, $F_{SA} = 2.18$, $P_{SA} < 0.001$), V ($DF_{SA} = 181$, $F_{SA} = 1.33$, $P_{SA} = 0.033$), VII ($DF_{SA} = 139$, $F_{SA} = 1.21$, $P_{SA} = 0.161$) and VI + VIII ($DF_{SA} = 160$, $F_{SA} = 0.91$, $P_{SA} = 0.704$), age of canopy trees had a highly significant impact on SHDI (DF = 1, $F = 12.76$, $P < 0.001$ for class IV; DF = 2, $F = 8.08$, $P < 0.001$ for class V; DF = 1, $F = 17.92$, $P < 0.001$ for class VII; and DF = 1, $F = 11.32$, $P = 0.001$ for class VI + VIII). Canopy stratification had a similarly significant impact (DF = 1, $F = 17.35$, $P < 0.001$ for classes V; DF = 1, $F = 17.79$ for class VI + VIII; DF = 1, $F = 10.69$, $P = 0.001$ for class IV; and DF = 1, $F = 7.10$, $P = 0.009$ for class VII). Canopy coverage had a highly significant impact on SHDI for soil class IV (DF = 1, $F = 17.49$, $P < 0.001$) and VI + VIII (DF = 1, $F = 3.23$, $P = 0.007$), a less pronounced impact for class V (DF = 1, $F = 6.36$, $P = 0.013$), but no impact for class VII (DF = 1, $F = 0.97$, $P = 0.327$). Tree species composition had a highly significant impact on SHDI for soil class IV (DF = 2, $F = 5.45$, $P = 0.005$), a less pronounced, but still significant impact, for class VII (DF = 2, $F = 3.01$, $P = 0.013$) and VI + VIII (DF = 2, $F = 2.03$, $P = 0.042$), and no impact for class V (DF = 2, $F = 1.21$, $P = 0.301$) (Table 5). There was almost no interactive effect between the four stand structure parameters within each soil class (Fig. 3), with only tree species composition and canopy stratification showing a weak interaction (DF = 2, $F = 3.27$, $P = 0.043$) in soil class VII (Fig. 3c).

Post-hoc analysis on plant species diversity within sub-categories of each structure parameter showed four relatively clear and similar patterns across the soil classes (Table 5): (1) Stands with a semi-open canopy had higher SHDI values than stands with a closed canopy, although there was no significant difference in soil class VII ($P = 0.327$); (2) stands dominated by mature and old trees had higher SHDI values than young stands; (3) mixed stands consistently had higher SHDI values than coniferous or broadleaved stands, although there was no significant difference in soil class V ($P = 0.301$); and (4) stands with more than one layer always had higher SHDI values than single-layered stands (Table 5).

Comparison of plant species diversity between forest stand structures represented by 10 or more sampling plots per soil class was possible for 10 stand structure types in soil classes IV and VII and 12 stand structure types in classes V and VI + VIII (Table 3). Despite the low numbers of sampling plots, old stand structures were also included in the comparison in order to obtain an indication of how they ranked overall in supporting plant species diversity (Table 3). Within this limitation, there was a highly significant difference ($P \leqslant 0.005$) in plant species diversity between forest stand structure types, which followed a similar pattern for all soil classes (Fig. 4). Stand structure types with more than one layer and dominated by mature trees always had high SHDI values, particularly if the stand structure was mixed forest with a semi-open canopy (S2M2, see Table 2 for explanation of stand structure codes). Conversely, single-layered structure types dominated by young trees always had low SHDI values, particularly if the stand was coniferous forest with a closed canopy (C1C1).

Table 5
Shannon diversity index (SHDI) values for sub-categories of each parameter in soil classes IV, V, VII and VI + VIII.

Soil class	Parameter	Sub-category	SHDI (±S.E.)	Parameter	Sub-category	SHDI (±S.E.)
IV (P_{SA} < 0.001)	Canopy coverage	Semi-open (S)	2.55 ± 0.06 a***	Tree species composition	Coniferous (C)	2.32 ± 0.06 b**
		Closed (C)	2.28 ± 0.08 b***		Broadleaved (D)	2.30 ± 0.12 b**
	Age of canopy trees	<30 years old (1)	2.30 ± 0.07 b***		Mixed (M)	2.62 ± 0.09 a**
		30-80 years old (2)	2.53 ± 0.07 a***	Canopy stratification	1-layered (1)	2.23 ± 0.05 b***
					>1-layered (2)	2.60 ± 0.11 a***
V (P_{SA} = 0.033)	Canopy coverage	Semi-open (S)	3.00 ± 0.12 a*	Tree species composition	Coniferous (C)	2.77 ± 0.12 a
		Closed (C)	2.73 ± 0.12 b*		Broadleaved(D)	2.85 ± 0.15 a
	Age of canopy trees	<30 years old (1)	2.51 ± 0.09 b***		Mixed (M)	2.98 ± 0.15 a
		30-80 years old (2)	2.93 ± 0.07 a***	Canopy stratification	1-layered (1)	2.59 ± 0.11 b***
		>80 years old (3)	3.15 ± 0.30 a***		>1-layered (2)	3.13 ± 0.14 a***
VII (P_{SA} = 0.161)	Canopy coverage	Semi-open (S)	2.56 ± 0.08 a	Tree species composition	Coniferous (C)	2.60 ± 0.08 b*
		Closed (C)	2.66 ± 0.10 a		Broadleaved (D)	2.48 ± 0.20 ab*
	Age of canopy trees	<30 years old (1)	2.39 ± 0.09 b***		Mixed (M)	2.75 ± 0.10 a*
		30-80 years old (2)	2.83 ± 0.09 a***	Canopy stratification	1-layered (1)	2.42 ± 0.09 b**
					>1-layered (2)	2.80 ± 0.12 a**
VI + VIII (P_{SA} = 0.704)	Canopy coverage	Semi-open (S)	3.00 ± 0.09 a**	Tree species composition	Coniferous (C)	2.68 ± 0.12 b*
		Closed (C)	2.72 ± 0.11 b**		Broadleaved (D)	2.84 ± 0.12 ab*
	Age of canopy trees	<30 years old (1)	2.60 ± 0.10 b***		Mixed (M)	3.07 ± 0.14 a*
		30-80 years old (2)	3.12 ± 0.10 a***	Canopy stratification	1-layered (1)	2.52 ± 0.09 b***
					>1-layered (2)	3.20 ± 0.12 a***

Note: LS-Mean SHDI values followed by different letters are significantly different. No asterisk means no significant difference between sub-categories. Random influence by each 1 km × 1 km square was considered.
*** $P \leqslant 0.001$.
** $P \leqslant 0.01$.
* $P \leqslant 0.05$.

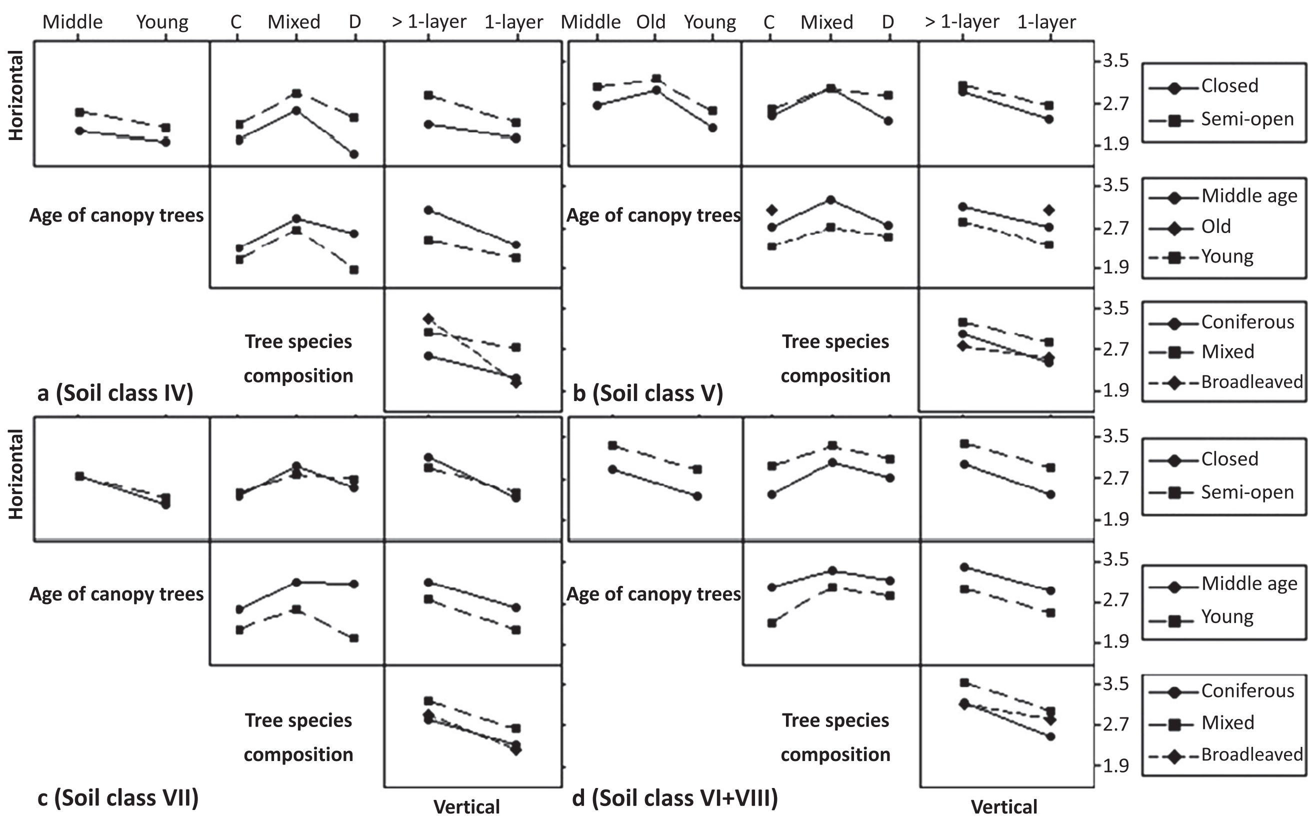

Fig. 3. Interactions between the parameters as regards Shannon diversity index (*y*-axis) in soil classes IV, V, VII and VI + VIII.

3.3. Species turnover along the stand structure gradient of increasing SHDI value

Plots in soil class IV had a lower variation in species composition than plots in other soil classes. The mean value for the measure of SDI was 0.72 in soil class IV, and 0.61 in classes V, VII and VI + VIII. This indicated that, although species composition did not change markedly (increase or decrease) between stand structure types, different stand structure types represented different plant species composition, regardless of soil classes and their species richness/diversity. Among all soil classes, the highest similarity of species composition found was between C1C1 and C1C2

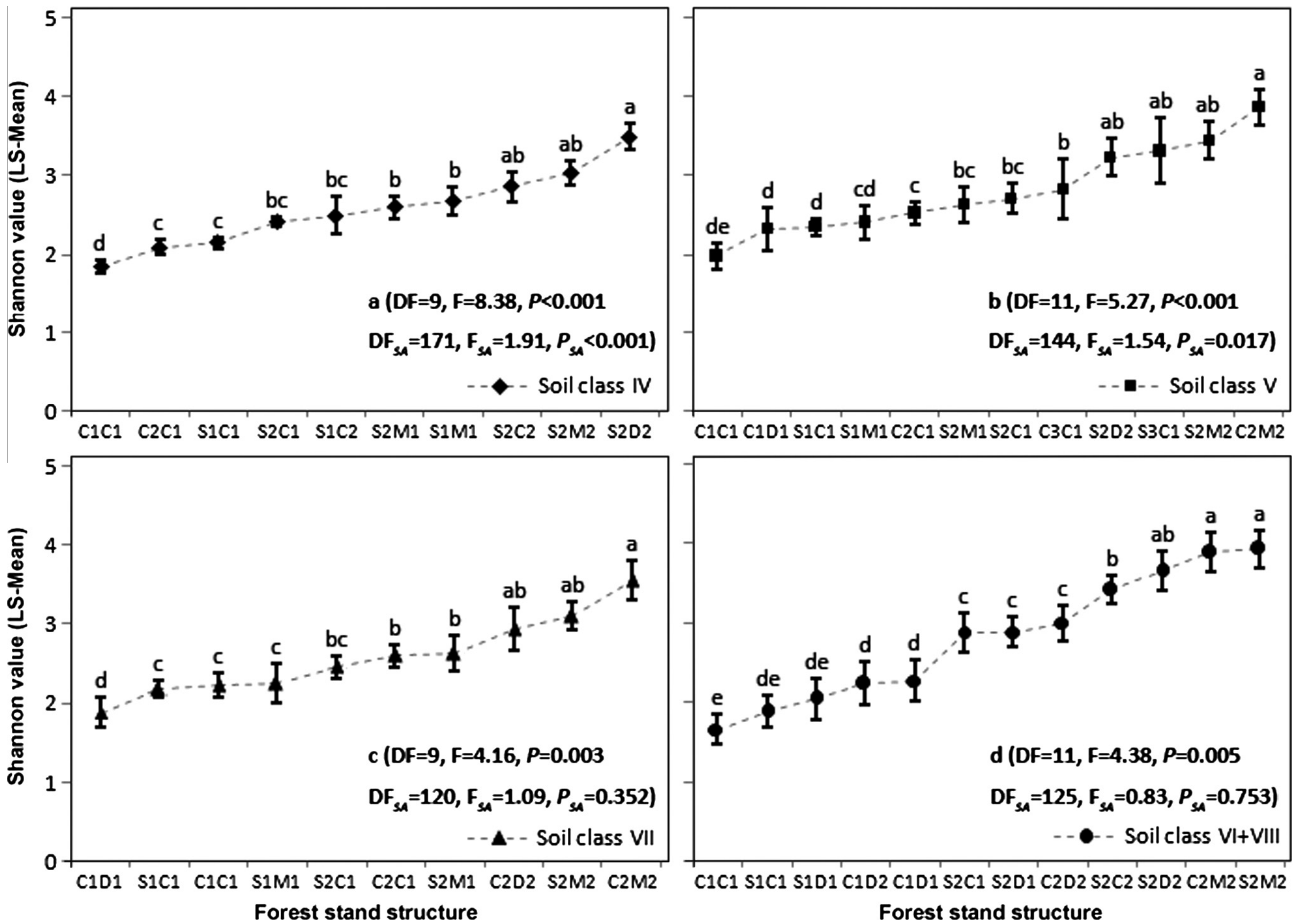

Fig. 4. Line chart of Shannon diversity index value (*y*-axis) for each forest stand structure (*x*-axis) in soil class IV, V, VII and VI + VIII, e.g. (a) S2D2 (3.49 ± 0.16), S2M2 (3.04 ± 0.14), C1C1 (1.85 ± 0.08); (b) C2M2 (3.87 ± 0.22), S2M2 (3.45 ± 0.24), C1C1 (1.98 ± 0.17), C1D1 (2.33 ± 0.27), S3C1 (3.32 ± 0.42) and C3C1 (2.83 ± 0.37); (c) C2M2 (3.56 ± 0.25), S2M2 (3.11 ± 0.18), C1D1 (1.88 ± 0.20), S1C1 (2.18 ± 0.11); (d) S2M2 (3.94 ± 0.23), C2M2 (3.89 ± 0.25), C1C1 (1.66 ± 0.19), S1C1 (1.88 ± 0.20). Means with different letters are significantly different.

(SDI = 0.81) in class IV, and the highest variation was between C1D1 and S2C1 (SDI = 0.44) in class VI + VIII, between C1D1 and S1C1 (SDI = 0.48) in class VII, and between C1D1 and S1C1 (SDI = 0.49) and between S2D2 and S3C1 (SDI = 0.49) in soil class V (Fig. 5).

4. Discussion

The main aim of this study was to develop and test an indicator for assessing plant species diversity at stand level based on stand structure parameters collected in many large-scale forest inventory datasets. On the basis of 1290 forest sampling plots inventoried as part of the NILS programme in southern Sweden, the results showed that: (1) Large-scale forest inventory data can be used as a basis for assessing forest biodiversity at stand level, and (2) soil class, stand structure parameters and plant species diversity/composition are correlated and this correlation can be described by the stand structure types derived from a combination of four stand structure parameters.

4.1. Soil class, forest stand structure parameter and plant species diversity

Plant species diversity varied significantly in terms of soil class in the present study. Similarly, Pärtel et al. (2004) found that plant diversity had a strong positive association with soil pH in mesic to moist soil conditions in temperate and boreal regions. This has been attributed to decreased decomposition and nitrogen fixation in relatively acid and dry soil, affecting the survival of plant species (Slattery and Hollier, 2002; Hollier and Reid, 2005). The present study generally confirmed previous findings on the relationship between plant species diversity and soil class, but also demonstrated that the relationship between plant species diversity and stand structure parameters was rather consistent across soil classes (see Table 5). This suggests that while overall plant species diversity is affected by changes in soil class, different forest stand structure parameters have similar effects on plant species diversity within each soil class. An explanation could be that the soil class effect on overall plant species diversity in forest stand is rather constant, while its effect on individual plant species is highly variable (Eisenhauer et al., 2010).

4.2. Plant species diversity in relation to individual stand structure parameters

Use of GLMM together with the interaction test prevented the possibility of interdependence between stand structure parameters. Higher plant species diversity was observed in stands with a semi-open canopy than in stands with a closed canopy, and these stands were mostly young and middle-aged. This is likely to be explained by differences in light availability, as semi-open stand structures support both light-adapted and shade-adapted species.

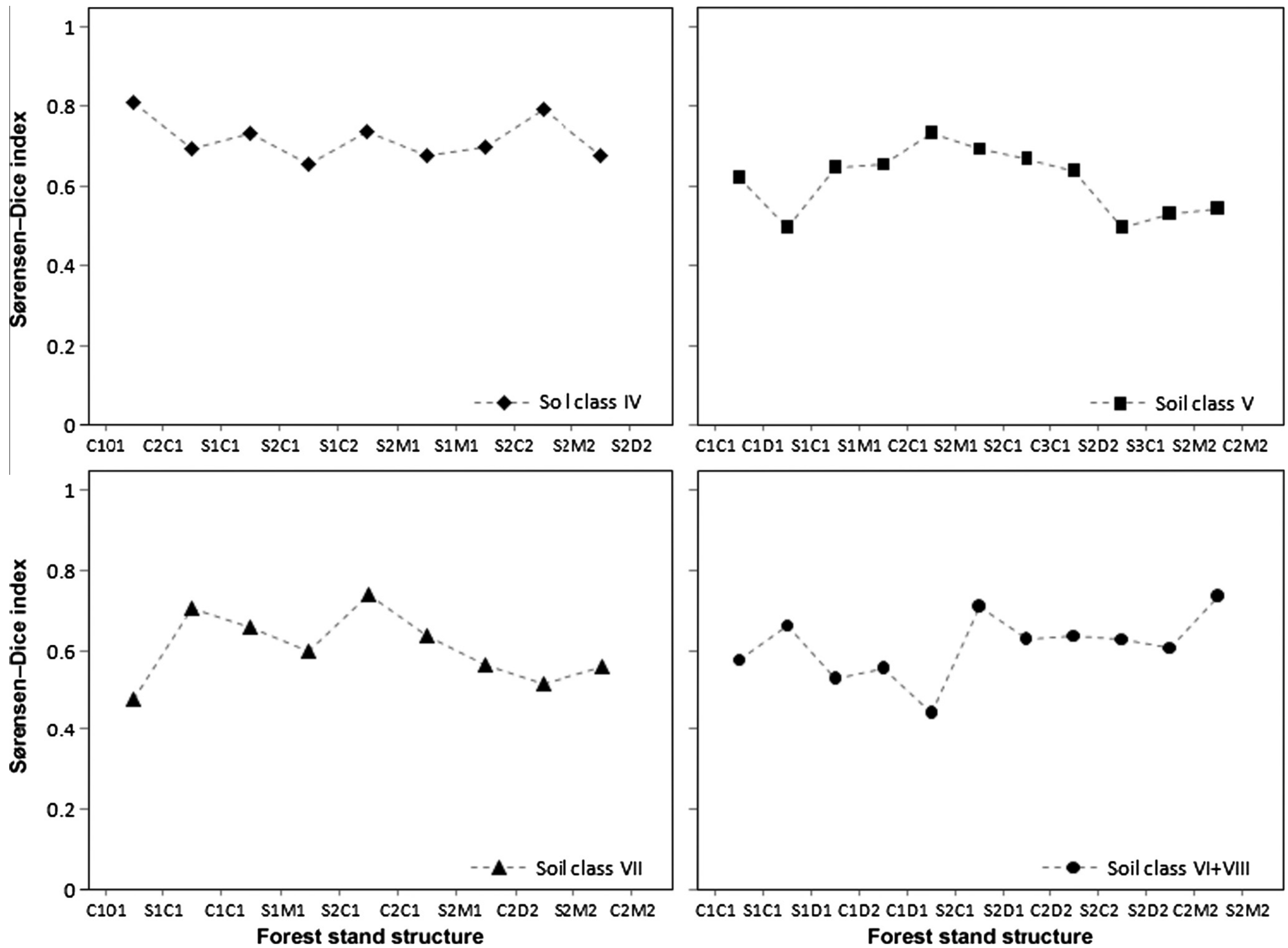

Fig. 5. Variations in Sørensen-Dice index value (*y*-axis) along stand structure gradient of Shannon value increase in soil classes IV, V, VII and VI + VIII.

Sagar et al. (2008) found that the canopy type exhibiting intermediate levels of light intensity reflected the greatest herbaceous diversity. However, a study in Sweden showed that the total cover of bryophytes did not show significant response to the changes in canopy cover (Hedwall et al., 2010). Coote et al. (2013) found that canopy coverage has a positive relationship with bryophyte diversity before the canopy fully closed. But from an overall plant species diversity perspective the increased bryophyte diversity maybe not compensate sufficiently for the losses arising through shading of other species, for example vascular plants and lichens (Hedwall et al., 2010).

Across the soil classes, plant species diversity was higher in mature and old stands than in young stands. However, due to the very limited number of old stands and the dominance of mature stands with semi-open canopy, which are likely to support both shade-tolerant species and light-adapted species, this finding should be interpreted with caution. Nevertheless, a previous study conducted in southern Sweden found that epiphytic species richness increased with stand age to 65 years (Johansson et al., 2007). Other studies in the Nordic countries have found conflicting results. Uotila and Kouki (2005) found that young spruce-dominated forest in eastern Finland and adjoining parts of Russia had higher total species richness of vascular plants, bryophytes and lichens than old spruce forest, regardless of intensity of human disturbance. In contrast, a study in Norway on lichen colonisation in forests showed that the major lichen species are confined to old forest (Hilmo and Såstad, 2001). Halpern and Spies (1995) found that forests in the Pacific Northwest of North America, vascular plant species diversity tends to increase with time, peaking in old growth. An explanation could be fewer disturbances in mature and old stands (Halpern and Spies, 1995; Torras and Saura, 2008).

Plant species diversity was slightly higher in broadleaved stands than in coniferous stands. Light availability, plantation of introduced species, management practices designed to reduce pests, competition from other plants and timber production activities such as intensive timber extraction, clearcut, etc. may reduce the plant species diversity of coniferous forest (Alexander et al., 2006). However, it should by no means be assumed that coniferous stands have little value for plant species conservation, because coniferous forest often contains a range of different species to those found in broadleaved forest, including rare and endangered species (Zerbe, 1993; Budde et al., 2011; Boch et al., 2013). This is consistent with our SDI results, which showed distinctly different species composition between coniferous and broadleaved stands. Across the soil classes in the present study, mixed stands had significantly higher SHDI values than coniferous or broadleaved stands, most likely because mixed forests harbour both coniferous-dependent and broadleaved-dependent species groups. Zhang et al. (2014) found that the mixed forest revealed compositional and structural features between its adjacent broadleaved and coniferous stands. The existence of different tree species in the canopy is associated with provision of a greater diversity of microhabitats allowing for the addition of understory plant species associated with each canopy species (Cavard et al., 2011).

In all soil classes, plant species diversity was higher in multilayered forest than in single-layered forest. It is generally accepted that a vertically complex forest generally supports more species than a simple forest, but most evidence to date relates to animal species such as birds (Díaz et al., 2005; Patthey et al., 2012), mammals (Williams et al., 2002; Grelle, 2003), reptiles (Bell and Donnelly, 2006) etc., which rely on specific layers of vegetation for food, nesting and cover. However, few previous studies have examined the relationship between plant species diversity itself and vertical structure. Thus our results make a novel empirical contribution in this regard by indicating that vertical structure provides a range of habitats used by plant species and that the layer per se represents different plant species groups.

4.3. Stand structure types and plant species diversity

Combining four stand structure parameters in a model for classifying forest stands into different structural types allowed us to go beyond the individual parameters and achieve a more nuanced understanding of how they jointly shape the plant species diversity of forest stands. For example, the results showed that mature stands with a multi-layered structure always had higher plant species diversity, particularly if they were also mixed broadleaved and coniferous and/or had a semi-open canopy (e.g. S2M2 and C2M2 in Table 2). In contrast, young, one-layered forest stands always had low plant species diversity, particularly if they were also coniferous and/or had a closed canopy (e.g. C1C1 and C1D1). Other forest stand structures (e.g. S2D1, S2C1, C1D2, C2M1 etc.) were intermediate in terms of plant species diversity. Although there were no statistical interactions between the four parameters and plant species diversity, their combined effects presumably determine the gradient of plant species diversity in forest stands (Berger and Puettmann, 2000; Barbier et al., 2008; Chávez and MacDonald, 2012). Caution is needed, however, because the national inventory dataset used in the present study it is not a full plant species inventory but limited to a range of trees, shrubs and field layer herbs, grasses, ferns and graminoids ($n = 286$) selected to indicate habitat characteristics or species turnover. Therefore further studies using full plant species inventories as data input would be desirable to determine whether the stand structure parameters combined in the model can also predict total plant species diversity between different stand structures.

4.4. Stand structure types and plant species composition

The SDI values obtained revealed that different stand structure types represented different species composition, regardless of soil classes and their species diversity (SHDI value). Species turnover is most likely related to differences in light conditions in stands (canopy coverage and stratification), successional stage (age of canopy trees) and type of stand (tree species composition) (Hilmo and Såstad, 2001; Johansson et al., 2007; Smith et al., 2008; Coote et al., 2013). However, most SDI values were higher than 0.5, indicating that fewer than 50% of species changed between stand structure types. This may be partly due to the removal of environmental affects, i.e. the comparisons within each soil class, and partly to the age structure being dominated by trees under 80 years of age, with nearly all sampling plots located in managed forest. Thus, Zobel et al. (1993) found that managed forest communities have low variance in diversity between their biotopes.

4.5. Implications for forest planning and management

In Sweden and many other countries, there is national legislation to protect the value of forests and forest land for production and at the same time safeguard biodiversity (Swedish Ministry of Environment, 2012). However, it should be remembered in this context that although methods may be devised for measuring biodiversity in forests, these are useless unless the specific goals of forest management are known. If the goal is to promote biodiversity in general on stand level, the results of the present study demonstrate that mature and well-stratified stand structure profiles with a semi-open canopy of mixed coniferous and broadleaved trees host high plant species diversity. Management actions should therefore aim to retain old trees in order to increase the variation in tree size in the stand and, when possible, have approximately equal foliage volumes in the lower, middle and upper canopy layers (Crawford and Frank, 1987). These structures could be maintained by selective cutting, allowing continuous forest cover. When regenerating stands, our results suggest that mixtures of broadleaved trees and conifers should preferably be planted where site conditions allow and subjected to early thinning, as a means of enhancing below-canopy structural diversity (Moore, 2012).

In Sweden, studies on boreal forests have showed that thinning had little effect on the cover of individual species, except *Vaccinium myrtillus* (Bergstedt and Milberg, 2001). However, studies in Canada showed that structural diversity induced by pre-commercial thinning enhances the abundance and species diversity of the plant community in even-aged commercial forest stands (Lindgren et al., 2006). Moreover, decreased availability of light, as an indirect effect of fertilisation through increased tree canopy cover, was found to be the most important factor behind the change in species diversity and composition of vascular plants and lichens in a study of different fertilisation regimes in Sweden (Hedwall et al., 2010). This is in accordance with another study demonstrating that the influence on understory vegetation of other growth-limiting factors e.g. nutrients etc. become less important as the density of the tree layer increases (VanderSchaaf, 2008). Therefore, stand structure types seem parent to certain management regimes such as thinning and fertilisation for promoting forest biodiversity, at least in Sweden.

Nevertheless, if the goal is to promote biodiversity on a landscape level, forests should be managed in a way that supports as many forest stand structure types as possible, in order to maximise beta-diversity and maintain viable populations for species. Thus, many species need several stand structure types in an area in order to complete their life cycle (Fuller and DeStefano, 2003). Forest planning that permits the development of a mosaic of many different forest stand structures representing different successional stages (young, mature and old) would most likely support the highest biodiversity at landscape level.

5. Conclusions

Use of large-scale forest inventory data for assessing forest biodiversity can greatly reduce costs and save time. By using a new model combining four stand structure parameters, we found clear and consistent differences in plant species diversity between managed forest stands with varying structure characteristics (canopy coverage, age of canopy trees, tree species composition and canopy stratification). These findings indicate that it is possible to classify forests in terms of species diversity based on stand structure. According to the impact on plant species diversity, the existing model for stand classification may need to be modified, with age of canopy trees as level 1, canopy stratification as level 2, tree species composition as level 3 and canopy coverage as level 4. The results indicate the potential of the model to support decision-making on sustainable forest management and biodiversity conservation. The stand structure parameters included in the model can be extracted from National Forest Inventories in most countries and understood without the need for specialist taxonomic knowledge, facilitating potential implementation in practice. The most interesting field for further validation of the model for classifying stand structure types would be to test it in old managed stands and unmanaged forests and in comparisons of managed and unmanaged forests.

Acknowledgments

This research was funded by the Northwest A & F University and the Swedish University of Agricultural Sciences postgraduate program. We are grateful to Jan-Eric Englund for valuable suggestions on data analysis of the manuscript.

Appendix A. Configuration of soil classes (I–IX) based on Ellenberg's indicator values concerning water conditions and pH value.

<table>
<tr><td colspan="3" rowspan="3">pH
SWC</td><td colspan="9">Soil pH (Score 1-9)</td></tr>
<tr><td colspan="3">Low</td><td colspan="3">Medium</td><td colspan="3">High</td></tr>
<tr><td>1</td><td>2</td><td>3</td><td>4</td><td>5</td><td>6</td><td>7</td><td>8</td><td>9</td></tr>
<tr><td rowspan="9">Soil water conditions (Score 1-9)</td><td rowspan="4">Dry</td><td>1</td><td colspan="3" rowspan="4">Soil class I:
SWC 1--Indicator of extreme dryness, restricted to soils that often dry out for some time.
SWC 2 - Between 1 and 3.
SWC 3 - Dry site indicator, more often found on dry ground than in moist places.
SWC 4 - Between 3 and 5.
pH 1 - Indicator of extreme acidity, never found on weakly acid or basic soils.
pH 2 - Between 1 and 3.
pH 3 - Acidity indicator, mainly acid soils, but exceptionally also nearly neutral soils.</td><td colspan="3" rowspan="4">Soil class II:
SWC 1, SWC 2, SWC 3, SWC 4

pH 4 - Between 3 and 5.
pH 5 - Indicator of moderately acid soils, only occasionally found on very acid or on neutral to basic soils.
pH 6 - Between 5 and 7.</td><td colspan="3" rowspan="4">Soil class III:
SWC 1, SWC 2, SWC 3, SWC 4

pH 7 - Indicator of weakly acid to weakly basic conditions; never found on very acid soils.
pH 8 - Between 7 and 9.
pH 9 - Indicator of basic reaction, always found on calcareous or other high-pH soils.</td></tr>
<tr><td>2</td></tr>
<tr><td>3</td></tr>
<tr><td>4</td></tr>
<tr><td rowspan="2">Mesic</td><td>5</td><td colspan="3" rowspan="2">Soil class IV:
SWC 5 - Moist site indicator, mainly fresh soils of average dampness.
SWC 6 - Between 5 and 7.

pH 1, pH 2, pH 3</td><td colspan="3" rowspan="2">Soil class V:
SWC 5, SWC 6

pH 4, pH 5, pH 6</td><td colspan="3" rowspan="2">Soil class VI:
SWC 5, SWC 6

pH 7, pH 8, pH 9</td></tr>
<tr><td>6</td></tr>
<tr><td rowspan="3">Wet</td><td>7</td><td colspan="3" rowspan="3">Soil class VII:
SWC 7 - Dampness indicator, mainly constantly moist or damp, but not wet soils.
SWC 8 - Between 7 and 9.
SWC 9 - Wet-site indicator, often water-saturated, badly aerated soils.

pH 1, pH 2, pH 3</td><td colspan="3" rowspan="3">Soil class VIII:
SWC 7, SWC 8, SWC 9

pH 4, pH 5, pH 6</td><td colspan="3" rowspan="3">Soil class IX:
SWC 7, SWC 8, SWC 9

pH 7, pH 8, pH 9</td></tr>
<tr><td>8</td></tr>
<tr><td>9</td></tr>
</table>

References

Alexander, A., Butler, J., Green, T., 2006. The value of different tree and shrub species to wildlife. Br. Wildlife 18, 18–28.

Arnan, X., Gracia, M., Comas, L., Retana, J., 2009. Forest management conditioning ground ant community structure and composition in temperate conifer forests in the Pyrenees Mountains. For. Ecol. Manage. 258, 51–59.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. For. Ecol. Manage. 254, 1–15.

Bell, K.E., Donnelly, M.A., 2006. Influence of forest fragmentation on community structure of frogs and lizards in North eastern Costa Rica. Conserv. Biol. 20, 1750–1760.

Berger, A.L., Puettmann, K.J., 2000. Overstory composition and stand structure influence herbaceous plant diversity in the mixed Aspen forest of northern Minnesota. Am. Midland Nat. 143, 111–125.
Berglund, H., Jonsson, B.G., 2001. Predictability of plant and fungal species richness of old-growth boreal forest islands. J. Veg. Sci. 12, 857–866.
Bergstedt, J., Milberg, P., 2001. The impact of logging intensity on field-layer vegetation in Swedish boreal forests. For. Ecol. Manage. 154, 105–115.
Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.-D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic Appl. Ecol. 14, 496–505.
Boutin, S., Haughland, D.L., Schieck, J., Herbers, J., Bayne, E., 2009. A new approach to forest biodiversity monitoring in Canada. For. Ecol. Manage. 258, S168–S175.
Bräuniger, C., Knapp, S., Kuhn, I., Klotz, S., 2010. Testing taxonomic and landscape surrogates for biodiversity in an urban setting. Landsc. Urban Plan. 97, 283–295.
Brunialti, G., Frati, L., Aleffi, M., Marignani, M., Rosati, L., Burrascano, S., Ravera, S., 2010. Lichens and bryophytes as indicators of old-growth features in Mediterranean forests. Plant Biosyst. 144, 221–233.
Budde, S., Schmidt, W., Weckesser, M., 2011. Impact of admixture of European beech (Fagus sylvatica L.) on plant species diversity and naturalness of conifer stands of Lower Saxony. Waldökologie, Landschaftsforschung und Naturschutz 11, 49–61.
Cavard, X., Macdonald, S.E., Bergeron, Y., Chen, H.Y.H., 2011. Importance of mixedwoods for biodiversity conservation: evidence for understory plants, songbirds, soil fauna, and ectomycorrhizae in northern forests. Environ. Rev. 19, 142–161.
Chávez, V., MacDonald, S.E., 2012. Partitioning vascular understory diversity in mixed wood boreal forests: the importance of mixed canopies for diversity conservation. For. Ecol. Manage. 271, 19–26.
Chirici, G., McRoberts, R.E., Winter, S., Bertini, R., Brändli, U.-B., Asensio, I.A., Bastrup-Birk, A., Rondeux, J., Barsoum, N., Marchetti, M., 2012. National forest inventory contributions to forest biodiversity monitoring. For. Sci. 58, 257–268.
Coote, L., Dietzsch, A.C., Wilson, M.W., Graham, C.T., Fuller, L., Walsh, A.T., Irwin, S., Kelly, D.L., Mitchell, F.J.G., Kelly, T.C., O'Halloran, J., 2013. Testing indicators of biodiversity for plantation forests. Ecol. Indic. 32, 107–115.
Crawford, H.S., Frank, R.M., 1987. Wildlife habitat responses to silvicultural practices in spruce-fir forests. Trans. 52nd N.A. Wildl. Nat. Res. Conf., pp. 92–100.
Díaz, I.A., Armesto, J.J., Reid, S., Sieving, K.E., Willson, M.F., 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloe Island, Chile. Biol. Conserv. 123, 91–101.
Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. Annu. Rev. Environ. Resour. 28, 137–167.
Dumortier, M., Butaye, J., Jacquemyn, H., Van Camp, N., Lust, N., Hermy, M., 2002. Predicting vascular plant species richness of fragmented forests in agricultural landscapes in central Belgium. For. Ecol. Manage. 158, 85–102.
Eisenhauer, N., Beßler, H., Engels, C., Gleixner, G., Habekost, M., Milcu, A., Partsch, S., Sabais, A.C.W., Scherber, C., Steinbeiss, S., Weigelt, A., Weisser, W.W., Scheu, S., 2010. Plant diversity effects on soil microorganisms support the singular hypothesis. Ecology 91, 485–496.
Fritz, O., Gustafsson, L., Larsson, K., 2008. Does forest continuity matter in conservation? A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. Biol. Conserv. 141, 655–668.
Fuller, T.K., DeStefano, S., 2003. Relative importance of early-successional forests and shrubland habitats to mammals in the northeastern United States. For. Ecol. Manage. 185, 75–79.
Gao, T., Qiu, L., Hammer, M., Gunnarsson, A., 2012. The importance of temporal and spatial vegetation structure information in biotope mapping schemes: a case study in Helsingborg, Sweden. Environ. Manage. 49, 459–742.
Gaston, K.J., 1996. What is biodiversity? In: Gaston, K.J. (Ed.), Biodiversity. A Biology of Numbers and Difference. Blackwell Sciences, London, pp. 1–9.
Gil-tena, A., Brotons, L., Saura, S., 2009. Mediterranean forest dynamics and forest bird distribution changes in the late 20th century. Global Change Biol. 15, 474–485.
Green, R.E., Balmford, A., Crane, P.R., Mace, G.M., Reynolds, J.D., Turner, R.K., 2005. A framework for improved monitoring of biodiversity: responses to the world summit on sustainable development. Conserv. Biol. 19, 56–65.
Grelle, C.E.V., 2003. Forest structure and vertical stratification of small mammals in a secondary Atlantic Forest, South eastern Brazil. Stud. Neotrop. Fauna Environ. 38, 81–85.
Gustafsson, L., Ahlén, I., (Eds.), 1996. Växter och Djur. Sveriges National Atlas. 44p. (in Swedish).
Hägglund, B., Lundmark, J.E., 1982. Handledning i bonitering med skogshögskolans boniteringssystem. Del 1 Definitioner och anvisningar. Skogsstyrelsen, Jönköping. ISBN 91-85748-11-0.
Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5, 913–934.
Hedwall, P.-O., Nordin, A., Brunet, J., Bergh, J., 2010. Compositional changes of forest-floor vegetation in young stands of Norway spruce as an effect of repeated fertilisation. For. Ecol. Manage. 259, 2418–2425.
Heilmann-Clausen, J., Christensen, M., 2005. Wood-inhabiting macrofungi in Danish beech-forests – conflicting diversity patterns and their implications in a conservation perspective. Biol. Conserv. 122, 633–642.
Hill, M.O., Mountford, J.O., Roy, D.B., Bunce, R.G.H., 1999. Ellenberg's indicator values for British plants. ECOFACT Volume 2 Technical Annex. Huntingdon, Institute of Terrestrial Ecology.
Hilmo, O., Såstad, S.M., 2001. Colonization of old-forest lichens in a young and an old boreal *Piceaabies* forest: an experimental approach. Biol. Conserv. 102, 251–259.
Hollier, C., Reid, M., 2005. Acid Soils. DPI AgNote April 2005.
Jansson, U. (Ed.), 2011. Agriculture and Foretsry in Sweden Since 1900. National Atlas of Sweden. National Atlas, Växter och Djur.
Jansson, G., Andrén, H., 2003. Habitat composition and bird diversity in managed boreal forests. Scand. J. For. Res. 18, 225–236.
Johansson, P., Rydin, H., Thor, G., 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. Ecoscience 14, 81–91.
Jukes, M.R., Peace, A.J., Ferris, R., 2001. Carabid beetle communities associated with coniferous plantations in Britain: the influence of site, ground vegetation and stand structure. For. Ecol. Manage. 148, 271–286.
Kati, V., Dimopoulos, P., Papaioannou, H., Poirazidis, K., 2009. Ecological management of a Mediterranean mountainous reserve (Pindos National Park, Greece) using the bird community as an indicator. J. Nat. Conserv. 17, 47–59.
Lindenmayer, R.A., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14, 941–950.
Lindgren, P.M.F., Ransome, D.B., Sullivan, D.S., Sullivan, T.P., 2006. Plant community attributes 12 to 14 years following precommercial thinning in a young lodgepole pine forest. Can. J. For. Res. 36, 48–61.
Mace, G.M., Norris, K., Fitter, A.H., 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends Ecol. Evol. 27, 19–26.
Máliš, F., Vladovič, J., Čaboun, V., Vodálová, A., 2010. The influence of Picea abies on herb vegetation in forest plant communities of the Veporské vrchy Mts. J. For. Sci. 56, 58–67.
Moore, K.M., 2012. Manipulation of vegetation succession in forestry and applications for sustainable forest management, PhD thesis. University of Dublin, Trinity College, Dublin. Moore, K.M., 2012. Manipulation of vegetation succession in forestry and applications for sustainable forest management, PhD thesis. University of Dublin, Trinity College, Dublin.
Nordén, B., Paltto, H., 2001. Wood-decay fungi in hazel wood: species richness correlated to stand age and dead wood features. Biol. Conserv. 101, 1–8.
Ozanne, C.H.P., Anhuf, D., Boulter, S.L., Keller, M., Kitching, R.L., Körner, C., Meinzer, F.C., Mitchell, A.W., Nakashizuka, T., Silva Dias, P.L., Stork, N.E., Wright, S.J., Yoshimura, M., 2003. Biodiversity meets the atmosphere: a global view of forest canopies. Science 301, 183–186.
Pärtel, M., Helm, A., Ingerpuu, N., Reier, Ü., Tuvi, E.L., 2004. Conservation of Northern European plant diversity: the correspondence with soil pH. Biol. Conserv. 120, 525–531.
Patthey, P., Signorell, N., Rotelli, L., Arlettaz, R., 2012. Vegetation structural and compositional heterogeneity as a key feature in Alpine black grouse microhabitat selection: conservation management implications. Eur. J. Wildlife Res. 58, 59–70.
Rudolf, K., Morschhauser, T., Pál-Fám, F., 2012. Macrofungal diversity in disturbed vegetation types in North-East Hungary. Central Eur. J. Biol. 7, 634–647.
Sagar, R., Singh, A., Singh, J.S., 2008. Differential effect of woody plant canopies on species composition and diversity of ground vegetation: a case study. Trop. Ecol. 49, 189–197.
Sauberer, N., Zulka, K.P., Abensperg-Traun, M., Berg, H.-M., Bieringer, G., Milasowszky, N., Moser, D., Plutzar, C., Pollheimer, M., Storch, C., Tröstl, R., Zechmeister, H., Grabherr, G., 2004. Surrogate taxa for biodiversity in agricultural landscapes of eastern Austria. Biol. Conserv. 117, 181–190.
Simonson, S.E., Opler, P.A., Stohlgren, T.J., Chong, G.W., 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodivers. Conserv. 10, 1369–1386.
Singh, A., Shi, H., Foresman, T., Fosnight, E.A., 2001. Status of the world's remaining closed forests: an assessment using satellite data and policy options. Ambio 30, 67–69.
Slattery, B., Hollier, C., 2002. Impacts of Acid Soils in Victoria, A report for Department of Natural Resources and Environment, Goulburn Broken Catchment Management Authority and North East Catchment Management Authority.
Smith, G.F., Gittings, T., Wilson, M., French, L., Oxbrough, A., O'Donoghue, S., O'Halloran, J., Kelly, D.L., Mitchell, F.J.G., Kelly, T., Iremonger, S., McKee, A.-M., Giller, P., 2008. Identifying practical indicators of biodiversity for stand-level management of plantation forests. Biodivers. Conserv. 17, 991–1015.
Ståhl, G., Allard, A., Esseen, P.-A., Glimskär, A., Ringvall, A., Svensson, J., Sundquist, S., Christensen, P., Torell, Å.G., Högström, M., Lagerqvist, K., Marklund, L., Nilsson, B., Inghe, O., 2011. National Inventory of Landscapes in Sweden (NILS) – Scope, design, and experiences from establishing a multiscale biodiversity monitoring system. Ecol. Monit. Assess. 173, 579–595.
Swedish Ministry of Environment, 2012. Svenska miljömål – preciseringar avmiljökvalitetsmålen och en förstauppsättning etappmål. Ds 2012:23. Ministry of Environment. ISBN 978-91-38-23762-5. ISSN 0284-6012.
Swedish Statistical Yearbook of Forestry, 2012. Published by Swedish Forest Agency, Sweden. ISSN 0491–7847. ISBN 978-91-88462-97-8.
Titchenell, M.A., Williams, R.A., Gehrt, S.D., 2011. Bat response to shelter wood harvests and forest structure in oak-hickory forests. For. Ecol. Manage. 262, 980–988.
Torras, O., Saura, S., 2008. Effects of silvicultural treatments on forest biodiversity indicators in the Mediterranean. For. Ecol. Manage. 255, 3322–3330.
Uliczka, H., Angelstam, P., 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. Ecography 22, 396–405.

Uliczka, H., Angelstam, P., 2000. Assessing conservation values of forest stands based on specialised lichens and birds. Biol. Conserv. 95, 343–351.
Uotila, A., Kouki, J., 2005. Understorey vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: successional patterns after anthropogenic and natural disturbances. For. Ecol. Manage. 215, 113–137.
VanderSchaaf, C.L., 2008. Estimating understory vegetation response to multi-nutrient fertilization in Douglas-fir and ponderosa pine stands. J. For. Res. 13, 43–51.
Williams, S.E., Marsh, H., Winter, J., 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. Ecology 83, 1317–1329.
Zerbe, S., 1993. Fichtenforste als Ersatzgesellschaften vonHainsimsen-Buchenwäldern. Vegetation, Struktur und Veg-etationsveränderungen eines Forstökosystems. Berichte desForschungszentrums Waldökosysteme 100, 1–173.
Zerbe, S., Schmidt, I., Betzin, J., 2007. Indicators for plant species richness in pine (Pinus sylvestris L.) forests of Germany. Biodivers. Conserv. 16, 3301–3316.
Zhang, J.Y., Cheng, K.W., Zang, R.G., Ding, Y., 2014. Changes in floristic composition, community structure and species diversity across a tropical coniferous-broadleaved forest ecotone. Trop. Conserv. Sci. 7, 126–144.
Zobel, K., Zobel, M., Peet, R.K., 1993. Change in pattern diversity during secondary succession in Estonian forests. J. Veg. Sci. 4, 489–498.