

Utilising forest inventory data for biodiversity assessment

Michael Heym^{a,c,*}, Enno Uhl^a, Ralf Moshhammer^b, Jochen Dieler^a, Kilian Stimm^a, Hans Pretzsch^a

^a Technical University of Munich, TUM School of Life Sciences, Chair of Forest Growth and Yield Science, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany

^b Technical University of Munich, TUM School of Life Sciences, Forest Science and Resource Management, Germany

^c Bavarian State Institute of Forestry (LWF), Department Silviculture and Mountain Forest, Germany

ARTICLE INFO

Keywords:

Biodiversity
Forest inventory
Spatial and temporal scales
Scale-overarching
Sustainable forest management planning

ABSTRACT

Currently the paradigm of sustainable forest management is extended to a broad range of ecological, economic, and social forest functions and services. In particular, biodiversity becomes a more and more important issue in the forest planning processes. However, its quantification, monitoring and assessment still remain complex and difficult although data from regional or national forest inventories might contribute valuable information for quantifying biodiversity. Here, we demonstrate how such data can be tapped and aggregated to different spatial and temporal scales for deriving indicators to support biodiversity assessment and monitoring. By focusing on tree species and structural related indices, our method allows the evaluation of spatial and temporal variation of diversity indicators by using inventory data. We present a practice-oriented approach on how to integrate such indicators into forest planning processes and thereby extend the paradigm of sustainability of forest management. We exemplify our approach by inventory data from the Bavarian State Forest Enterprise to show how inventory data can be utilised to (i) assess biodiversity aspects from stand to landscape scales and (ii) integrate such information into forest management at different spatial and temporal scales. Finally, we discuss how this information extracted from forest inventories may contribute to a more generalised assessment, monitoring and planning of biodiversity in managed forest ecosystems.

1. Introduction

Covering approximately one third of the global land surface (FAO, 2020), forests play an important role for biodiversity management and conservation. During the last decades the issue of considering biological diversity in forest ecosystems received raising awareness globally. Since the UN Conference on Environment and Development (UNCED) in Rio de Janeiro 1992 and the ratification of the Convention of Biological Diversity (CBD) in 1993, the relevance of sustaining and improving biodiversity has been continuously addressed in the respective declarations. The signature states committed not only to promote sustainable forest management, but in addition enhance the conservation of biological diversity in forest ecosystems. Certificates, e.g. Programme for the Endorsement of Forest Certification Schemes (PEFC) or Forest Stewardship Council (FSC), provide instruments to ensure that forests are managed in line with this extended sustainability paradigm (Pretzsch et al., 2008). Forest owners (e.g. state forest enterprises,

municipal or private owners) have to implement these new aspects of sustainability into their management approach at local, regional and landscape level. On the operational level this requires measures, indicators and management guidelines to fulfil these political requirements. In order to verify the compliance of indicators, specific data sets are required, e.g. to characterise the preservation of biotope trees or rare and threatened species. However, the quantification of biodiversity is complex, appears as a multidimensional characteristic and cannot be expressed by a single number (Purvis and Hector, 2000). Instead, specific aspects of biodiversity need to be addressed (Duelli and Obrist, 2003) and implemented in operational and strategic planning processes. One of the first attempts to assess biodiversity was the hierarchical framework developed by Noss (1990), which is based on three recognised primary attributes of biodiversity in forest ecosystems: composition, structure and function (Franklin et al., 1981). Here, for each component, appropriate indices can be applied across different scales (spatial and temporal) and levels of organisation (e.g. gene, species or

* Corresponding author.

E-mail addresses: michael.hey@tum.de, michael.hey@lwf.bayern.de (M. Heym), enno.uhl@tum.de (E. Uhl), ralf.moshhammer@tum.de (R. Moshhammer), jochen.dieler@tum.de (J. Dieler), kilian.stimm@tum.de (K. Stimm), hans.pretzsch@tum.de (H. Pretzsch).

<https://doi.org/10.1016/j.ecolind.2020.107196>

Received 4 October 2019; Received in revised form 10 November 2020; Accepted 16 November 2020

Available online 10 December 2020

1470-160X/© 2020 The Authors.

Published by Elsevier Ltd.

This is an open access article under the CC BY-NC-ND license

(<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

community). The use of indices is a prominent approach to overcome the complexity of biodiversity (e.g. Noss, 1999; Duelli and Obrist, 2003; Hagan, 2006). However, the choice of a set of appropriate indices strictly depends on specific aims (Noss, 1999) and data availability is often problematic due to the lack of large spatial gradients, temporal resolution and high costs associated with data collection. Moreover, the required data need to reflect effects of forest management activities, e.g. from small to larger scales with continuous measurements. Therefore, the use of national or regional forest inventory data provide a feasible alternative (Van Den Meersschaut and Vandekerckhove, 1998; Müller et al., 2009; Corona et al., 2011; Storch et al., 2018). These data sets provide reliable information, cover large environmental gradients, span a broad range of spatial scales and are usually characterised by repeated measurements to track temporal changes.

Despite their strong focus on planning and management (in particular volume and volume growth), forest inventory data provide additional valuable information which can be addressed for characterising aspects of biodiversity (Winter et al., 2008; Corona et al., 2011; Storch et al., 2018). Tree species and tree dimensions such as diameter at breast height, tree height or species-specific age are, usually, available from inventory data. Therefore, species composition and structural aspects can be derived, which provide important information for quantifying aspects of biodiversity (Noss, 1990; McElhinny et al., 2005; Gao et al., 2014). Tree species abundance and variation of tree dimensions can be used as a proxy for habitat quality or biotope trees, e.g. for saproxylic beetles, bryophytes, lichens and fungi (Berghlund et al., 2009; Uliczka and Angelstam, 1999), occurrence of related microhabitats (Larrieu et al., 2014) or for defining habitat types (Kovac et al., 2020). In addition, based on individual trees, structural indices can be calculated which characterize a forest's structural complexity and provide insights in niche differentiation and potential habitat variability. For example, stand density and vertical structure are important characteristics when describing habitat potential of birds (MacArthur and MacArthur, 1962) or potential occurrence of umbrella species, such as woodpecker (Fernandez and Azkona, 1996; Müller et al., 2009; Zahner and Sikora, 2012). However, the selection of appropriate indices remains challenging (McElhinny et al., 2005), in particular when using forest inventory data. Moreover, for such data sets, we see a lack of spatial scale overarching approaches to quantify biodiversity, a lack of approaches that may indicate changes in biodiversity over time, and the need for establishing a reference for the grading of both one-time and repeated biodiversity assessments.

In this study, we exemplarily tapped the potential use of regular forest grid-based inventory data from a state forest management enterprise in southern Germany for assessing key aspects of biodiversity within forest ecosystems. We focus on indices related to tree species composition and structural diversity. In detail, we (i) demonstrate the quantification of biodiversity by indicators at inventory plot level, (ii) extend the characterisation to larger spatial levels (from the inventory plot to the landscape), (iii) track the development of diversity indicators over time, and (iv) provide a concept for practice-oriented result aggregation.

We finally discuss the potential application of our approach for grid-based inventory data, the restrictions of our method, and also the next steps of development and application.

2. Material and methods

2.1. Data source

The Bavarian State Forest Enterprise (Bayerische Staatsforsten AöR) covers approximately 30% (778,000 ha) of the total forest area in the German federal state of Bavaria (Thünen-Institut, Third National Forest Inventory, 2012) and is organised by division into several smaller forest enterprise units. The strategic and operational silvicultural aim of the Bavarian State Forest Enterprise has a strong orientation towards close-

to-nature forestry, which manifests itself with current silvicultural management guidelines (e.g. Bayerische Staatsforsten AöR, 2014, 2011a, 2009, 2008). However, monospecific forest stands established under classical silvicultural approaches, such as mono-layered even age forests, are still present and considered for conversion into multi-layered mixed forest stands. Regular forest inventories are conducted at 10-year intervals and are based on circular (three concentric circles) forest inventory plots. They are distributed on a raster grid varying in width. The systematic raster grid may vary between or within the forest enterprise units. For example, in natural forest reserve areas, which may be part of a Forest Enterprise unit, the density of inventory plots is usually higher (smaller grid width). Occurring grid sizes in the Bavarian State Forest vary from 50×50 m to 300×200 m. Therefore, the density of inventory plots ensures a level of detail that is appropriate to cover the variation of growth stages and silvicultural strategies well. Based on the metric raster grid width, an area of representation and spatial information (Gauss-Krueger-coordinates) are available for each inventory plot. Trees are recorded depending on their distance and dimension to the central point of the inventory plot; trees with a diameter at breast height (dbh, measurement height 1.3 m) ≤ 10 cm are recorded on the inner circle only (radius = 2.82 m), those with dbh ≤ 30 cm on the middle circle (radius = 5.05 m), while larger trees are recorded on the complete outer circle (radius = 12.62 m). For each sampled tree, its species affiliation is recorded by classification into 45 taxonomic (genus) groups, summarising specific taxa such as e.g. sessile oak and pedunculate oak. Dendrometric variables are recorded at tree level with diameter at breast height being measured for all trees with dbh > 5 cm using a calliper. Trees with dbh ≤ 5 cm are assigned to 1 cm dbh classes. Heights are measured for 1–3 trees per tree species and stand layer, which allows a standardised local height curve function for estimating the heights of all sampled trees to be applied (Franz et al., 1973). Merchantable wood volume without bark is calculated based on the form factors provided by Franz (1971) for Bavaria. Age is provided at species group level and may vary within the species group. For example, in order to consider a high age diversity per species group, different age values may appear. See the corresponding forest inventory guidelines for more details (Bayerische Staatsforsten AöR, 2011b). We demonstrate the method for one forest enterprise unit (comprising 4,395 permanent forest inventory plots) in the south of Bavaria (Fig. 1). This forest enterprise unit is characterised by favourable growing conditions, with in general rich soils and rather high levels of precipitation and temperature. Under natural conditions, beech-dominated forests would prevail on most sites of the area but due to the heterogeneity in terms of topography, alluvial forests have a relevant share. Forest management history resulted in a mixture of occurring age classes and close-to-nature forests. The overall data set (152,656 permanent forest inventory plots) are used as a benchmark (see section methods).

2.2. Quantification of biodiversity-relevant indices at inventory plot level

The smallest meaningful unit for calculating biodiversity-relevant indices is the single inventory plot. At the same time, this unit is most relevant for forest managers, since they can actively control their activities. Therefore, this scale is crucial to quantify and monitor effects of the management, in particular when monitoring success or failure of operational and strategic goals. As the management affects single tree development, tree species composition and forest structure, it directly influences indices associated with them. Consequently, we focus on indices which are related to tree size, tree species and structural diversity.

For tree species diversity, the simplest feature is the number of tree species S . Here, we did not focus on specific species or distinguish between native and non-native species. We rather quantify its general diversity which in turn is important for associated species. As a more sophisticated concept, we used the Shannon index H (Shannon, 1948, Eq. (1)) which provides an overproportional weight to species with

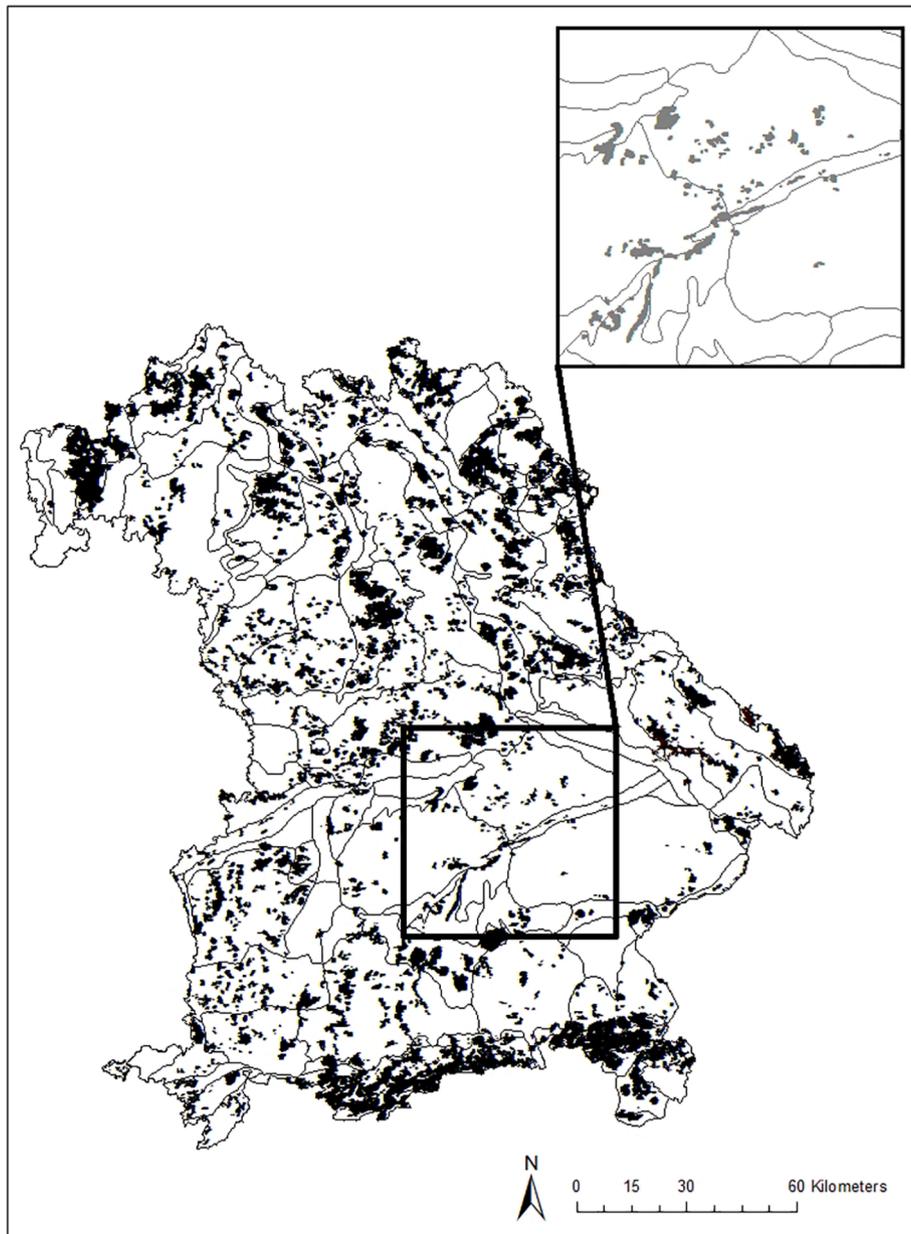


Fig. 1. Overview of considered permanent inventory plots of the Bavarian State Forest (black areas, number of plots: 152,656) and the selected forest enterprise unit (grey areas in the quadratic subplot, number of plots: 4,395). Due to scaling, the inventory grid is not visible; all black or grey areas are covered with such a grid.

small shares:

$$H = -1 * \sum_{i=1}^S p_i * \ln(p_i) \tag{1}$$

Where S is the number of species and p_i is the relative share of species i within the total tree number. With a given number of species S ($S > 1$) the maximum Shannon index is $H_{max} = \ln(S)$ (Pretzsch, 2009). Relating the Shannon index to this maximum, we obtain the species evenness E (Eq. (2)),

$$E = \frac{H}{\ln(S)} \tag{2}$$

With a potential range of $E = [0, 1]$ the Evenness informs how far a given diversity (as expressed by H) deviates from its theoretical maximum at the same number of species.

For structural diversity we considered the variability of species group age (V_{age} , Eq. (3)), tree height (V_h , Eq. (4)) and stand density. Variability

of age and height is expressed by their coefficients of variation.

$$V_{age} = \frac{sd(age)}{\bar{age}} \tag{3}$$

$$V_h = \frac{sd(h)}{\bar{h}} \tag{4}$$

V_{age} and V_h relate the standard deviation sd of a variable to its arithmetic mean (\bar{age} and \bar{h}). In addition, for age we characterise a frequency index at inventory plot level which expresses the occurrence of old trees. Coniferous and deciduous tree species differ in their potential age, in particular under management conditions. In order to take this into account, we applied a threshold of 120 years (age_{120+}) and 150 years (age_{150+}) while not distinguishing between the groups. For both the index is expressed as n_i/N , with N as the total number of inventory plots and n_i as the number of those with trees ≥ 120 years or ≥ 150 years, respectively. This index characterizes the proportion of inventory

plots with trees in old growth stages. For quantifying stand density we used the well-tried stand density index SDI (Reineke, 1933, Eq. (5))

$$SDI_i = N_i \cdot \left(\frac{d_{g_i}}{25} \right)^{-1.605} \quad (5)$$

N_i being the number of living trees per ha and d_{g_i} the quadratic mean diameter. The index i refers to the tree species and allows the aggregation to SDI ($SDI = \sum_1^i SDI_i$).

In order to quantify maximum tree size, we took the maximum tree diameter at breast height, d_{max} of all living trees. Similarly to age, we added a frequency index at the plot level, which determines the occurrence of plots with trees ≥ 65 cm ($d_{65+} = n_i/N$, with N as the total number of inventory plots and n_i as the number of those with trees ≥ 65 cm). This threshold is approximately an upper border of target diameter in silvicultural guidelines, e.g. as for the Bavarian State Forest Enterprise for Norway spruce, European beech or Scots pine (Bayerische Staatsforsten AöR, 2009, 2011a, 2014). Moreover, in the literature large diameters are often considered as an indicator with respect to habitat potential of tree related microhabitats (Larrieu and Cabanettes, 2012) or for its general importance for biodiversity (Vuidot et al., 2011).

2.3. Quantification of biodiversity-relevant indices at different spatial and temporal scales

We extended the quantification of the biodiversity-relevant indices from inventory plot level to larger scales. Different spatial scales are determined by aggregating multiple inventory plots. Here, the smallest unit is a single inventory plot. By stepwise including n nearest neighbour plots (ordered by increasing distance to the original plot of interest) we created larger aggregation units. Through the distance dependent identification, this approach is applicable for different raster grid sizes within a landscape, e.g. 50×50 m change into 100×100 m. In order to determine the nearest neighbour, we applied a nearest neighbour search routine (Arya et al., 2018). The area represented by a specific aggregation unit is here defined by the sum of all contained inventory plots' representation areas. Fig. 2 represents a schematic depiction of how we defined increasing aggregation units for a 100×100 m grid size.

In order to characterise scale-overarching indicators, we determined for each inventory plot aggregation units by considering 1 to 25 plots and quantified for each unit the biodiversity-relevant indices as described above.

For describing temporal developments, the indices were calculated for two consecutive surveys, applying the same method, respectively. However, we only considered the subset (forest enterprise unit), not the overall data set. In addition, we only considered inventory plots with a second survey and applied Welch's t -test (paired) to test for significant changes along the spatial scales.

2.4. Practice-oriented result aggregation

In order to summarise the results for the forest enterprise unit, we grouped all aggregation units of the same size, e.g. all units containing the same number of inventory plots. Thus, we considered 25 groups each containing 4,395 aggregation units (corresponding to the number of inventory plots). Here, each group represents a different spatial scale based on the involved number of inventory plots per aggregation unit. We then determined an index-specific average and scale-overarching behaviour which expresses the change from small to larger scales within the forest enterprise unit. Here, the results for each group were summarised by calculating the average index value, its standard error and the average area of representation. Due to the potential variation in raster grid widths within a landscape, the distances between the single plots may differ and consequently also their areas of representation. We therefore did not use the calculation of beta diversity measures as a characteristic of similarity or dissimilarity between the samples (Whittaker, 1972). We feel that this concept may need additional correction when applying to forest inventory data and believe that the average better reflects this variation.

In order to facilitate result interpretation, we further defined a reference system to provide a benchmark. Instead of applying the same method for all current forest enterprise units (41 in total) and then averaging their results, we rather considered all inventory plots within the whole Bavarian State Forest Enterprise (152,656 permanent forest inventory plots) and applied the same method as described above. In addition to the index specific average, its lower and upper extremes, expressed by the 5% and 95% percentiles, were determined for each group. We prioritised the use of all inventory plots, since then the reference system is independent from artificial management boundaries (Forest Enterprise units), which may change over time, e.g. due to political or organisational reasons. Moreover, the quantification of temporal changes of the reference is more straightforward, although this was not part of this study. Therefore, this benchmark can be seen as a common average behaviour across the state forest in Bavaria. The grid density across the state forest varies from 50×50 m to 300×200 m and affects the average area of representation per group. Consequently, it differs from a specific forest enterprise unit. For example, for the latter we may find a large grid width of 200×200 m which results in larger areas of representation per group than we expect for the reference with a smaller average grid density. Due to such a variation of the raster grid widths, we favoured the average area of representation against the number of involved inventory plots. Consequently, comparisons between both data sets are only meaningful for the common area of representation.

For visualisation of the results, we plotted the group-specific (average) indices for both data sets against the corresponding area of representation. Furthermore, to test whether the index-specific scale-

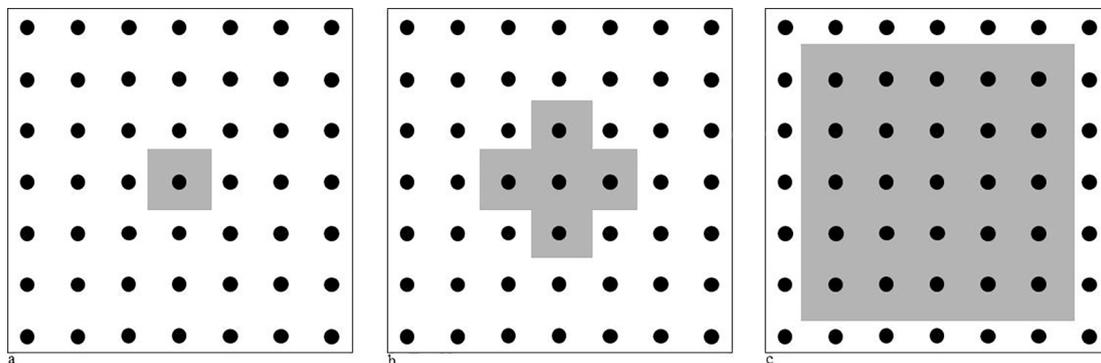


Fig. 2. Exemplarily schematic representation of defining aggregation units of different size, e.g. 1, 5 and 25 inventory plots (a: single plot level; b: aggregating 5 inventory plots; c: aggregating 25 inventory plots) considering a 100×100 m grid size. Black points represent individual inventory plots and grey is the area of representation of the aggregation unit.

overarching behaviour differs between the forest enterprise unit and the reference, we applied an ordinary least squares linear regression analysis (Eq. (6)):

$$\ln(y_i) = a_0 + a_1 \cdot \log \text{area}_i + a_2 \cdot \text{ref} + a_3 \cdot \log \text{area}_i \cdot \text{ref} + \epsilon \quad (6)$$

where y_i refers to the average index value per level of aggregation i , area_i to the corresponding average area of representation, ref refers to a dummy coded with 0 (reference) or 1 (Forest Enterprise unit) and ϵ refers to the error term. Thus, we test whether the increase of an index differs between the forest enterprise unit and the reference. For the forest enterprise unit, we applied Welch's t -test (paired) for each aggregation unit i to test the difference of the means between the previous and the most recent survey. Therefore, for each aggregation unit the success or failure of temporal development can be determined.

Besides the indices described above, we used two frequency indices which simply consider all inventory plots of the forest enterprise unit and reference, respectively.

First, tree species frequency (SF, Eq. (7)) described the relative occurrence of a given tree species:

$$\text{SF}_i = \frac{n_i}{N} \quad (7)$$

where N is the number of inventory plots considered and index i characterises tree species i . Thus, n_i represents the number of inventory plots where tree species i occurs. SF_i represents the relative occurrence of a certain tree species. We applied Eq. (7) for both data sets (forest enterprise unit and reference) and compared both graphically (Fig. 7a).

Second, besides V_h to quantify structural diversity, we used another more complex indicator for the vertical structure, which is essentially a vector that expresses the frequency of occupied height classes i (height class frequency, HCF, Eq. (8)):

$$\text{HCF}_i = \frac{n_i}{N} \quad (8)$$

where N is the total number of inventory plots considered and index i characterises height i . Thus, with n_i being the number of the plots with occupied height class i , HCF_i represents the relative occurrence of a certain height class. The following height classes were defined and assigned at each inventory plot: 0–2 m, 2.1–5 m, 5.1–15 m, 15.1–25 m, 25.1–35 m and > 35 m, and represents common thresholds for silvicultural strategies. If a tree's top range is inside a specific height class, this class is considered.

The inventory data evaluation routines including graphical outputs were programmed in the free data analysis language R (R Core Team, 2018).

3. Results

3.1. Number of tree species (S), Shannon index (H) and species Evenness (E)

The average number of tree species (S) and its standard error for the forest enterprise unit and reference range from 3.06 ± 0.020 to 12.35 ± 0.045 and 2.72 ± 0.003 to 10.33 ± 0.008 (inventory plot level to highest level of aggregation), respectively (Table 1). At inventory plot level the Shannon index, H, and species Evenness, E, range from 0.61 ± 0.006 and 0.18 ± 0.002 for the forest enterprise unit and 0.54 ± 0.001 and 0.17 ± 0.001 for the reference. For the highest level of aggregation, we detect a range of 1.33 ± 0.01 (H) and 0.35 ± 0.001 (E) for forest enterprise unit and 1.19 ± 0.001 (H) and 0.32 ± 0.001 (E) for the reference. The corresponding areas of representation are similar at smaller scales, e.g. at inventory plot level with 3.6 ha (forest enterprise unit) and 2.4 ha (reference), but highly different at larger scales with 86.9 ha (forest enterprise unit) and 57.6 ha (reference). The higher difference towards larger scales is caused by the different raster grid widths of the forest

Table 1

Overview of average and standard error (se) when considering 1 (AG1), 15 (AG15) and 25 (AG25) inventory plots as aggregation units. Shown are the average values for number of tree species; S, Shannon index; H, species Evenness; E, coefficient of variation of tree height; V_h , and age; V_a , maximum diameter; d_{Max} , and stand density; SDI for the forest enterprise and reference. In addition, for the landscape the corresponding minimum and maximum values are shown, respectively.

Indices	Level of aggregation	forest enterprise mean \pm se	min	max	Reference mean \pm se
S	AG1	3.06 ± 0.020	1	10	2.72 ± 0.003
	AG15	10.41 ± 0.044	2	20	8.76 ± 0.008
	AG25	12.35 ± 0.045	4	21	10.33 ± 0.008
H	AG1	0.61 ± 0.006	0	1.93	0.54 ± 0.001
	AG15	1.25 ± 0.006	0.19	2.31	1.13 ± 0.001
	AG25	1.33 ± 0.006	0.27	2.35	1.19 ± 0.001
E	AG1	0.18 ± 0.002	0	0.51	0.17 ± 0.001
	AG15	0.33 ± 0.002	0.05	0.61	0.3 ± 0.001
	AG25	0.35 ± 0.001	0.07	0.63	0.32 ± 0.001
V_h	AG1	69.14 ± 0.799	0	349.41	66.86 ± 0.171
	AG15	100.24 ± 0.357	5.69	178.88	109.92 ± 0.083
	AG25	101.58 ± 0.319	28.06	163.64	111.74 ± 0.087
V_a	AG1	124.61 ± 1.587	0	563.01	122.88 ± 0.312
	AG15	163.79 ± 0.790	13.99	354.95	174.11 ± 0.164
	AG25	164.63 ± 0.701	38.78	346.54	176.52 ± 0.150
d_{Max}	AG1	47.42 ± 0.265	0	138.50	44.59 ± 0.043
	AG15	74.12 ± 0.191	27.5	138.50	68.17 ± 0.037
	AG25	78.55 ± 0.198	43.5	138.50	71.79 ± 0.041
SDI	AG1	793.00 ± 5.972	0	2881	840.90 ± 1.057
	AG15	881.70 ± 2.908	325	1510	957.30 ± 0.540
	AG25	885.10 ± 2.692	427	1381	964.70 ± 0.502

enterprise unit and reference.

Fig. 3a–c illustrates the average index values and corresponding areas per aggregated group for the forest enterprise unit and reference.

The solid black lines in Fig. 3 represents the average change for number of tree species, Shannon index and species Evenness for the forest enterprise unit when the area of interest increases (integrating multiple inventory plots). While for the number of tree species no clear saturation effect appears, the flattening of the curves in the case of the other two indicate saturation at areas of approximately 50 ha. The same tendency can be observed for the reference curve (grey lines). In all cases, the reference appears with higher values at smaller scales. Steeper slopes of the forest enterprise unit curves, however, result in an area of intersection at 10–20 ha (number of tree species) and 5–10 ha (Shannon index and species Evenness) and yield in a turnover beyond these scales. The results of Equation (6) (Supplement Table 1) indicate significant positive effects in the case of the scale (area, a_1). For S and E, we detect a tendency of a higher difference (superiority of the forest enterprise unit) towards larger areas. In the case of H, this effect seems to diminish slightly.

3.2. Coefficient of variation for tree height (V_h), tree species age ($V_{age_{120+}}$ and age_{150+})

The average values and standard error for V_h and V_a and of the forest enterprise unit range from 69.14 ± 0.799 and 124.61 ± 1.587 (inventory plot level) to 101.58 ± 0.319 and 164.63 ± 0.701 (the highest level of

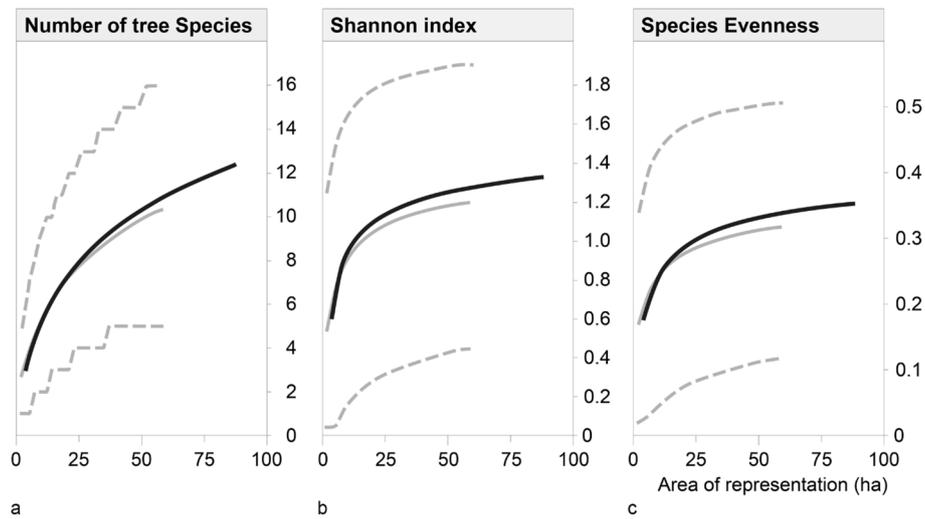


Fig. 3. a–c: Illustration of the average indices and areas of representation across all scales considered (aggregating 1–25 inventory plots) for number of tree species S (a), Shannon index H (b) and species Evenness E (c). Solid black lines represent the forest enterprise unit and solid grey lines the reference. Dotted grey lines refer to the upper (95%) and lower (5%) percentiles of the reference.

aggregation), respectively. In contrast, the average values for the reference range from 66.86 ± 0.171 and 122.88 ± 0.312 (inventory plot level) to 111.74 ± 0.087 and 176.52 ± 0.150 (the highest level of aggregation) for V_h and V_{age} , respectively. Fig. 4 illustrate the average index values of the Forest Enterprise unit and reference across all scales, respectively. The areas of representation are identical to those from Fig. 3a–c.

The two curves (solid black line: landscape and solid grey line: reference) in Fig. 4a (V_h) and 4b (V_{age}) differ and indicate an absolute difference across the considered scales. In both cases, the reference occurs with higher variability along all scales while for V_{age} this effect is higher than for V_h . For variability of tree heights (V_h ; Fig. 4a), the discrepancy stabilises at an area of 15–20 ha, V_{age} (Fig. 4b) shows an increasing divergence from small towards larger scales. Equation (6)

predicts a significant positive effect with increasing scale with higher effects for the reference (Supplement Table 1), in particular in the case of V_{age} . For tree height variability, only at small scales does similarity between both data sets occur, while at scales beyond 7 ha, the reference shows a significantly higher variability. For V_{age} the results are comparable, however, the difference increases more towards larger scales and starts at areas beyond 6 ha.

For the forest enterprise unit, approximately 17% of the inventory plots contain trees older than or equal to 120 years while at 6% of the plots we observe trees older than or equal to 150 years (Supplement Fig. 4). Again, we did not distinguish between coniferous and deciduous species.

3.3. Maximum diameter (d_{max}), large tree diameter (d_{65+}) and stand density (SDI)

For the forest enterprise unit, the average d_{max} and standard error range from 47.02 ± 0.265 cm (inventory plot level) to 78.55 ± 0.198 cm (the highest level of aggregation). In the case of SDI the values range from 793.00 ± 5.972 (inventory plot level) to 885.10 ± 2.692 (the highest level of aggregation). For the reference, the values occur with 44.59 ± 0.043 and 840.90 ± 1.057 (stand level) and with 71.79 ± 0.041 and 964.70 ± 0.502 (highest level of aggregation) for d_{max} and SDI, respectively. In the case of the forest enterprise unit, 14% of the inventory plots consist of trees which are equal to or exceed a diameter at breast height of 65 cm (Supplement Fig. 4).

Fig. 5a–b illustrate the index-specific average values of d_{max} and SDI along all scales. Solid black lines correspond to the forest enterprise unit and grey lines to the reference, respectively.

For maximum diameter, the reference shows higher values at smaller scales. The steeper slopes of the forest enterprise unit result in an area of intersection at approximately 7–9 ha and a turn-over with increasingly higher values of the latter towards larger areas (when aggregating multiple inventory plots). Stand density is lower for the forest enterprise unit across all scales considered, while the divergence indicates a further increase towards larger scales (Fig. 5b). Equation (6) predicts a significant positive effect with increasing scales for both indices (Supplement Table 1). For d_{max} , the results (Equation (6)) confirm the tendency of higher values for the forest enterprise unit towards larger scales. For stand density, we detect a significant superiority of the reference towards larger scales (Supplement Table 1).

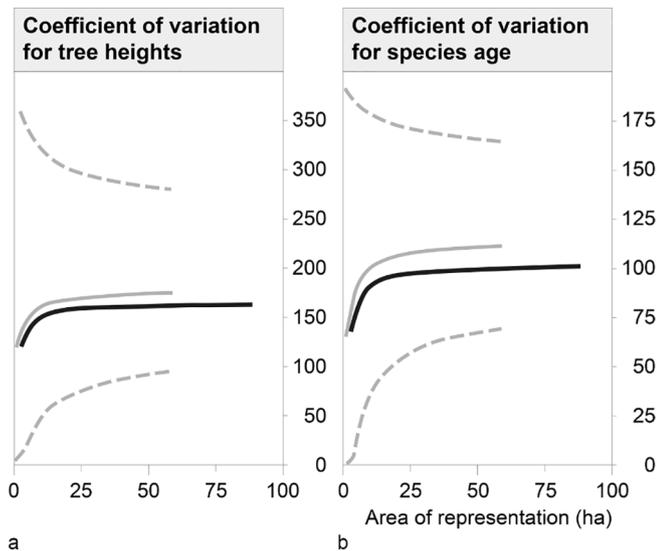


Fig. 4. a–b: Illustration of the average indices and areas of representation across all scales considered (aggregating 1–25 inventory plots) for coefficient of variation of tree height V_h (a) and tree species group age V_{age} (b). Solid black lines represent the forest enterprise unit and solid grey lines the reference. Dotted grey lines refer to the upper (95%) and lower (5%) percentiles of the reference.

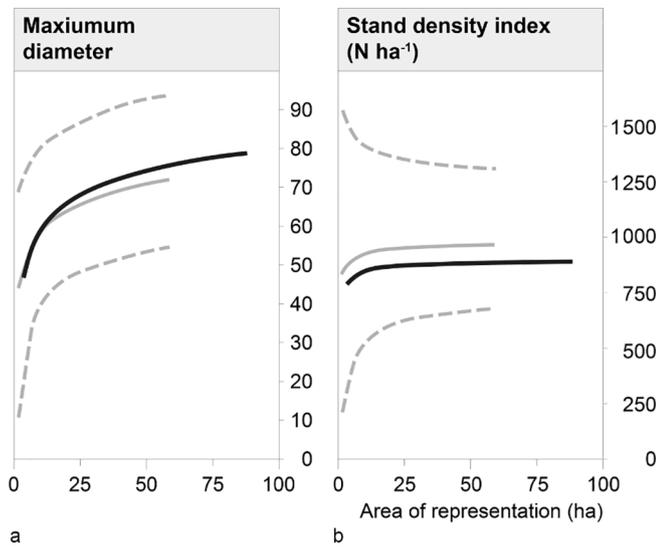


Fig. 5. a–b: Illustration of the average indices and areas of representation across all scales considered (aggregating 1–25 inventory plots) for maximum diameter (a) and stand density index (b). Solid black lines represent the forest enterprise unit and solid grey lines the reference. Dotted grey lines refer to the upper (95%) and lower (5%) percentiles of the reference.

3.4. Species frequency (SF) and height class frequency (HCF)

Species frequency (SF) for the forest enterprise unit illustrates the importance of Norway spruce (*Picea abies* (KARST.) L.) and higher tree species diversity when compared with the reference (Fig. 6a). The species at x-axis are shown in ascending order based on the reference’s frequencies. The main tree species of the reference are less frequent in the forest enterprise unit, e.g. Norway spruce or European beech (*Fagus*

sylvatica L.). However, higher occurrence appears for tree species which are characteristic for alluvial forests, e.g. ash (*Fraxinus* sp.), alder (*Alnus* sp.), elm (*Ulmus* sp.) or willow (*Salix* sp.).

Height class frequency (HCF), characterised at inventory plot level, indicates a higher vertical variability for the forest enterprise unit (Fig. 6b, black colour). For the forest enterprise unit four height classes occur with a frequency > 50%. In addition, height classes 0–2 m, 3–5 m, 6–15 m and 16–25 m occur with higher frequencies than the reference (+6.01%, +12.55%, +13.13% and + 8.37%, respectively). For height classes 26–35 m (-2.67%) and > 35 m (-0.03%) slightly lower frequencies exist for the forest enterprise unit.

3.5. Temporal change within the landscape

The result of temporal change for the forest enterprise unit shows a significantly higher number of tree species S across all scales for the recent inventory. Here, the discrepancy increases from stand level towards the highest level of aggregation (Table 2, Supplement Fig. 1a). For the Shannon index, H, and species Evenness, E, the average index values across the scales are significantly higher for the recent survey (Table 2, Supplement Fig. 1b and c). Here, for both indices, the difference increases towards larger scales.

For the coefficients of variation of tree height and age, the temporal change indicates a different behaviour (Supplement Fig. 2a–c). For both, at smaller scales (up to approximately 10 ha) we detect a significant superiority for the recent inventory, however, the steeper slopes for the previous inventory result in a turnover. Beyond approximately 15 ha, the differences between the two surveys become significant and show a tendency to increase with superiority for the previous inventory. For maximum diameter, the difference between the recent and previous survey appears significant across all scales with superiority of the recent inventory (Table 2, Supplement Fig. 3a). In contrast, stand density, SDI, indicates a significant reduction along all considered scales (Table 2, Supplement Fig. 3b). Here, the differences slightly increase towards larger scales.

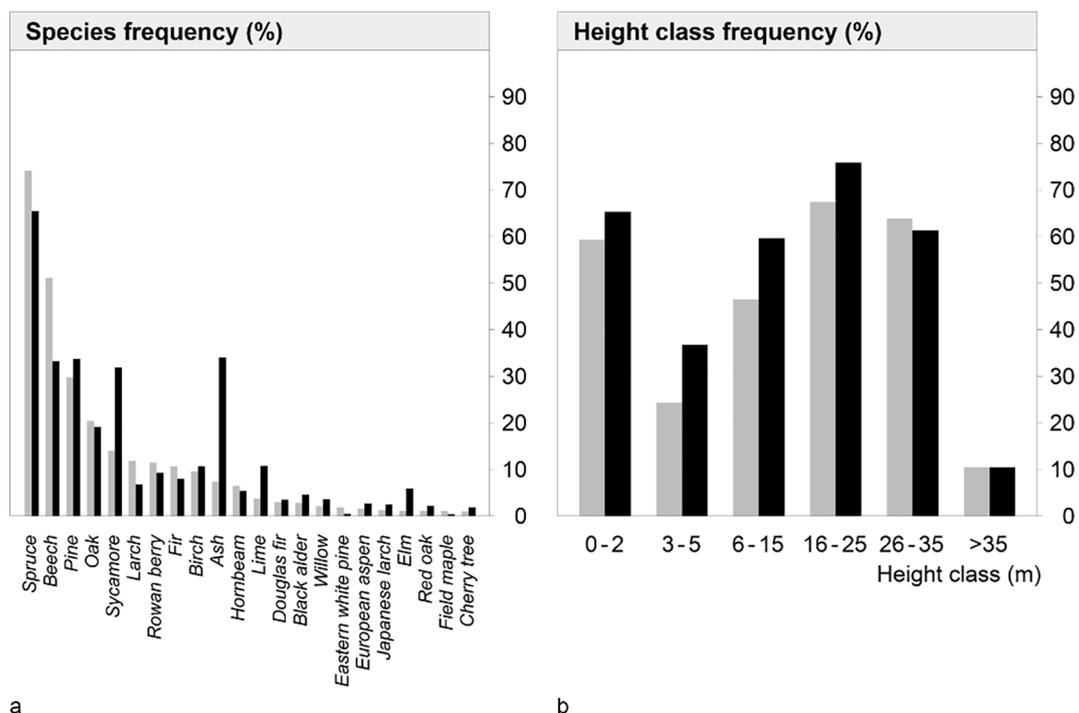


Fig. 6. a–b: Illustration of species frequency (a) and height class frequency (b) at stand level. Shown are the reference (grey colour) and forest enterprise unit (black colour), respectively.

Table 2

Shown are the average values most recent (*Recent*) and consecutive (*Previous*) survey of the forest enterprise unit, exemplarily for aggregating 1, 15 and 25 inventory plots, respectively. CI_{lower} and CI_{upper} refer to the lower and upper confidence intervals, based on Welch's *t*-test. Bold average values indicate a significant difference of the mean (the range of CI_{lower} and CI_{upper} does not include 0, CI refers to the test *Previous-Recent*, respectively). Shown are the average values for the number of tree species; S, Shannon index; H, species Evenness; E, coefficient of variation of tree height; V_h , and age; V_{age} , maximum diameter; d_{max} , and stand density; SDI.

Indices	Level of aggregation	Previous mean	Recent mean	CI_{lower}	CI_{upper}
S	AG1	2.75	3.06	-0.37	-0.26
	AG15	9.69	10.43	-0.86	-0.62
	AG25	11.63	12.37	-0.87	-0.61
H	AG1	0.53	0.61	-0.1	-0.07
	AG15	1.19	1.25	-0.08	-0.04
	AG25	1.28	1.33	-0.07	-0.04
E	AG1	0.17	0.18	-0.02	-0.01
	AG15	0.32	0.33	-0.02	-0.01
	AG25	0.34	0.35	-0.02	-0.01
V_h	AG1	117.38	124.67	-12.02	-2.57
	AG15	170.75	163.55	4.87	9.52
	AG25	172.98	164.42	6.52	10.61
V_a	AG1	62	69.13	-9.54	-4.72
	AG15	106.47	100.09	5.24	7.53
	AG25	108.14	101.4	5.71	7.77
d_{Max}	AG1	44.39	47.41	-3.78	-2.28
	AG15	71.78	74.14	-2.91	-1.82
	AG25	76.07	78.58	-3.07	-1.95
SDI	AG1	844.76	793.4	33.75	68.96
	AG15	959.9	880.56	70.06	88.62
	AG25	965.31	883.78	72.85	90.22

4. Discussion

4.1. Forest inventory data for biodiversity assessment

Within the last decades the need for monitoring aspects of biodiversity during forest planning activities has become increasingly important for forest managers. However, the lack of reliable data sets as a basis for planning and decision making can be considered as a limiting factor. Therefore, we utilise data from regular forest inventories to develop a method which supports the assessment and monitoring of biodiversity aspects and make them accessible for forest planning processes. We build on our idea of a generalised concept of characterising biodiversity (Franklin et al., 1981; Noss, 1990) and modified the method to be applicable for forest inventory data at a regional or landscape level. In particular, we extract tree species and structural diversity and extend their assessment to characterise a scale-overarching behaviour. Therefore, we determine their rate of change, from small to larger scales, and provide insights of transition and saturation effects. The starting point at the smallest scale is an important feature. For example, if diversity characteristics are high at these scales and the early saturation effect appear towards larger scales, it indicates a homogenous situation throughout the landscape. In contrast, low diversity at small scales in line with steep slopes and early saturation effects indicate a tendency of a spatially diverse situation within the region or landscape. Consequently, low tree species diversity or structural diversity across different spatial scales does not necessarily imply a negative situation. In monocultures, such as traditional age-class forest systems, the expected tree species diversity is at its minimum, e.g. close to or even zero in the case of the Shannon index. Consequently, any increase, even small, already indicates a positive effect and confirm a transition towards a higher potential for habitat diversity. However, for further interpretation, the historical starting point and development, current management perspectives and growing conditions are important attributes. In order to better interpret the expression of indices, we introduced a reference system, in which the region of interest is a part of it. The index's

information is described analogously and provides an overarching average of a higher region, e.g. state level. Therefore, any deviation confirms an expected or unexpected behaviour and better supports a judgement. In particular, when assessing multiple regions or landscapes, which differ in their growing conditions or silvicultural strategies, it is important to orientate on a general reference.

Finally, the temporal comparison of two consecutive surveys within a landscape allows the changes and control success or failure of forest management to be monitored. Therefore, it allows the effect of operational silvicultural activities (stand level) and strategic planning (enterprise level) to be tracked directly.

However, the proposed approach shows some methodological restrictions. For example, based on the nearest neighbour search (when characterising different spatial scales), some inventory plots are selected more often than others. In particular, this occur in highly scattered forest cover or at the border of the landscape. Due to the high number of samples used for averaging in the current study, we assume the bias to be negligible. So far, we did not consider a fixed distance search which would result in different sample sizes and unequal weights of the involved inventory plots for the same distance group.

Any change in the forest cover or inventory design over time may cause a change in the number of inventory plots between the two surveys. Thus, for temporal comparison we considered only plots which have been surveyed twice. When comparing with the reference, different sampling densities, e.g. variation in raster grid width, may occur. This may result in differences of the area representation of single inventory plots which have to be considered when interpreting the results.

4.2. Opportunities and drawbacks of applications for characterising the state of an enterprise by example

Tree species diversity is known to have positive effects on habitat potential, e.g. arthropods (Brändle and Brandl, 2001; Ulyshen, 2011) or productivity (Jingjing Liang et al., 2016). Therefore, its assessment is an import control factor, in particular at smaller spatial scales (Mergner, 2014; Gao et al., 2014). At these scales, the forest manager actively controls tree species composition (Müller, 2005) by planting, regulating mixed growth or thinning. In the present data set, non-native tree species also occur, e.g. Douglas fir or Red oak. We have not distinguished between native and non-native tree species as the latter might be important alternatives in the future, e.g. under changing climatic conditions or increasing biotic or abiotic stress. The results for the forest enterprise show no saturation effect for the number of tree species (Fig. 3a). Therefore, it can be concluded that within the landscape the occurrence of different tree species, S, is distributed throughout the landscape. In the case of the Shannon index, H, and tree species Evenness, E, (Fig. 3b and c), the steep slopes at smaller scales and the saturation effect indicate a high species admixture and balanced situation throughout the entire landscape. The continuous increase of S in line with the steep slopes of H and E, enable us to conclude that a significant occurrence and balanced species admixture already appears at smaller scales. In addition, our results demonstrate a tendency for higher species abundance and more balanced composition in the case of the forest enterprise unit when compared with the reference. The latter appears with smaller raster grid widths and allows comparisons up to 50 ha (Fig. 3a–c). Due to the wider raster grid size of the forest enterprise unit with a lower density of inventory plots, tree species abundance may be more underestimated than in the case of the reference (Gotelli and Chao, 2013). We argue that this fact led to the assumption of a rather conservative assessment. Again, we did not distinguish between native and non-native tree species. However, this concept can be applied likewise for the two groups and is of particular importance for landscapes with a high density of natural reserve areas. In such cases, the abundance of native tree species might be important to differentiate, e.g. studies show that a high tree species diversity should not be equated with a quality characteristic for naturalness (Fischer et al., 2003).

The occurrence of micro and macro habitats can be linked to a tree's dimension, e.g. potential habitats for lichens and saproxylic beetles (Uliczka and Angelstam, 1999; Nascimbene et al., 2009; Hilmo et al., 2009). Trees with a very large diameter at breast height are often considered as an important indicator for habitat potential (Van Den Meersschaut and Vandekerckhove, 1998; Larrieu and Cabanettes, 2012). For the forest enterprise unit, the occurrence of trees exceeding 65 cm (d_{65+}) indicate a high potential of tree-related habitats at small scales. In addition, the increase of large tree diameters (d_{max}) from small towards larger scales enables us to conclude that such trees are distributed throughout the entire landscape. Consequently, this provides important information for the forest manager to assess and compare this specific status with the overarching requirements or guidelines to foster large trees within a landscape.

In the case of resource availability, expressed by stand density index, the early saturation effect indicates a homogenous situation within the forest enterprise unit. When considering the results of tree species diversity, resource availability is widely influenced by tree species with lower maximum densities, such as pine, sycamore or ash. Thus, when compared with the reference, the total resource availability may be smaller but more diverse and can therefore be considered to have more positive effects.

For the forest enterprise unit, the variation of tree species age and tree height indicates a wide range of different age classes and physiological stages. Due to this variation, we assume that there is a considerable high niche supply with positive effects on community composition (Gossner et al., 2014). In both cases, the steep slopes and early saturation effect indicate that a high variation at smaller scales throughout the landscape exists. In turn, it represents a high variability of potential habitats across the entire landscape. In addition, the number of trees with an age of 120 years or above (age_{120+}) and 150 years or above (age_{150+}) indicates a considerable proportion of potential habitat trees at small scales. This important feature can be used to monitor at the most relevant management scale, the success or failure to increase the number of old trees.

The high variation of height class frequency enables us to conclude that the high values of stand density, variation in tree height and tree age are significantly distributed across the vertical stand layer. Therefore, we can expect that the observed positive effects also occur in different height classes within a forest stand.

4.3. Application for detection of temporal changes at the enterprise level

The temporal change indicates the failure or success of management strategies with respect to the selected indices. In the case of the Bavarian State Forest Enterprise, the shift of the index values over time may reflect the ongoing strategic goal to pursue the concept of close-to-nature forestry. Therefore, monitoring the temporal change is crucial to demonstrating the progress towards achieving the management and strategic objectives. While the operational success is more important for the forest enterprise units, strategic success is more relevant for the overall state forest. However, the latter is only possible by controlling the former. Here, any significant boost of a specific index in the most recent survey is equivalent to an increase of its contribution to the biodiversity level. Of particular importance are the smallest scales because they usually represent the management units and can be most actively affected. Larger scales, however, are more important for the longer perspective. For example, the demonstrated increase of tree species diversity (Supplement Fig. 1a–c) may indicate an active promotion of tree species diversity at stand level. The significantly higher number of tree species in line with the higher Shannon index and species Evenness at smaller scales reveal a more balanced situation for the most recent inventory. In contrast, the lower SDI values do not necessarily imply a negative effect on diversity. Introducing tree species with lower maximum stand density may lower the SDI (Supplement Fig. 3b). Consequently, an early saturation effect, as found for the forest

enterprise unit, may indicate diverse resource availability throughout the entire landscape. The higher maximum diameter values are a natural phenomenon as trees increase their dimension over time. However, under a management perspective, harvesting often aims at a specific target diameter. Therefore, the increase over time, when considering the absolute dimension, implies a strategy of retaining trees with larger diameters within the entire forest enterprise unit.

To aggregate the findings, we illustrate the relative change over time for the smallest spatial scale for a set of indices (Fig. 7) as $Index_{recent}/Index_{previous}$ (with previous = previous survey and recent = recent survey). The smallest considered spatial scale is most important for operational management activities, therefore summarising this scale will support the planning process. However, larger spatial scales can be aggregated in the same way.

5. Conclusions

Data from regular forest inventories provide large and continuous information, which allow indices linked to biodiversity aspects to be derived. It further enables multiple spatial and temporal scales to be considered. In addition to National Forest Inventories, which are usually grid-based and available for many European countries, regional or local grid-based inventories may also be available. The demonstrated approach is not restricted to a specific raster grid size (grid size may vary between and within countries) and is also applicable for other forest inventory methods where spatial explicit information of the sampling units, e.g. forest stands, are available. The indices used in this study describe an example of common indices, as they refer to the most basic information in forest inventories. Therefore, a transfer to other regions, landscapes or countries with a different grid design or inventory method is possible and may provide a basis for harmonisation. Furthermore, in forest inventories the update of recorded attributes is a continuous process. In the last decades, specific indices which can be directly or indirectly linked to aspects of biodiversity, e.g. dead wood or dead wood

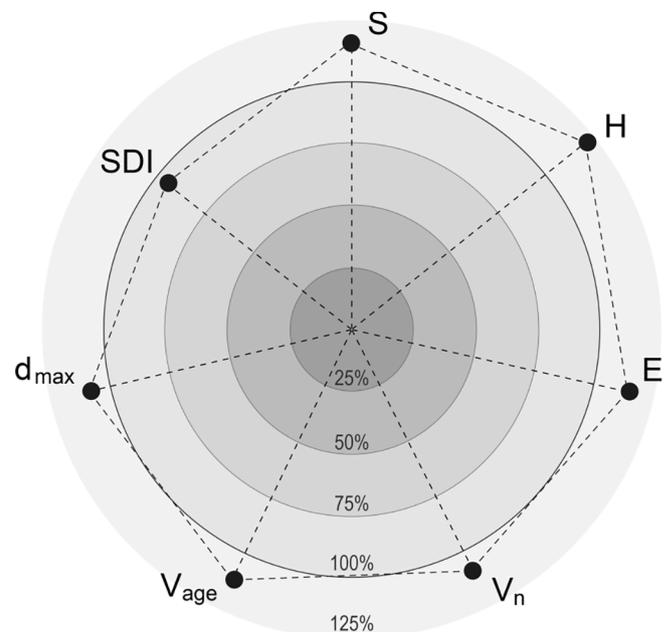


Fig. 7. Schematic overview of aggregating the results of temporal change as $Index_{recent}/Index_{previous}$, e.g. $S_{recent}/S_{previous}$. Illustrated is the relative change for the number of tree species S, Shannon index H, species Evenness E, coefficient of variation of tree height V_h and age V_{age} , maximum diameter d_{max} and stand density SDI. Solid black lines indicate the 100% line which means no change between the two surveys. The grey graduated colours represent values of change from 0 to 125% across the zones 0–25%, 25–50%, 50–75%, 75–100% and 100–125%, respectively.

composition, are part of the forest inventories. Besides, specific guidelines for recording trees with important features (habitat trees) or microhabitats will extend the potential set of indices to be used. Therefore, their implementation will further boost the strength of the method.

The reference system may be defined under multiple perspectives. We used a general reference, which allows multiple administrative regions, different in their growing conditions, to be compared with an expected average. However, when using natural reserves as a reference, a benchmark for specific management strategies, e.g. close-to-nature forestry can be provided.

The importance of characterising biodiversity aspects and implementing them in forest planning processes will become increasingly important. Thus, methods which enable the status and change of indices across multiple spatial and temporal scales are of special interest to be tracked. The continuous research of linking specific biodiversity aspects to more basic indices or specific threshold values, will increase the contribution to face upcoming challenges of monitoring the gain or loss of biodiversity within managed forest ecosystems.

Author contributions

M. Heym managed and analysed the data. M. Heym and E. Uhl wrote the manuscript. M. Moshhammer, J. Dieler and K. Stimm assisted with the interpretation. H. Pretzsch initiated the project and supervised the work.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors wish to thank the Bavarian State Forest Enterprise (Bayerische Staatsforsten AöR) for funding the development of the method and the access and use of the inventory data. In particular, we want to thank Markus Kölbl, Markus Neufanger and Alexander Schnell for the fruitful discussions regarding the practical relevance and use of the results. Special thanks go to Monika Bradatsch for the graphical artwork. We also thank Peter Biber, Erhard Dauber, Peter Wehl and Mathias Steckel for standardising the method and improving the manuscript. The authors thank the anonymous reviewers for their constructive criticism.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107196>.

References

- Arya, S., Mount, D., Kemp, S.E., Jefferis, G., 2018. RANN: Fast Nearest Neighbour Search (Wraps ANN Library) Using L2 Metric. R package version 2.6. <https://CRAN.R-project.org/package=RANN>.
- Berglund, H., O'Hara, R.B., Jonsson, B.G., 2009. Quantifying habitat requirements of tree-living species in fragmented boreal forests with bayesian methods. *Conserv. Biol.* 23, 1127–1137. <https://doi.org/10.1111/j.1523-1739.2009.01209.x>.
- Brändle, M., Brandl, R., 2001. Species richness of insects and mites on trees: expanding Southwood. *J. Anim. Ecol.* 70, 41–504.
- Bayerische Staatsforsten AöR, 2014. Grundsätze für die Bewirtschaftung von Kiefern- und Kiefern-mischbeständen im Bayerischen Staatswald.
- Bayerische Staatsforsten AöR, 2011a. Waldbauhandbuch Bayerische Staatsforsten. Grundsätze für die Bewirtschaftung von Buchen – und Buchenmischbeständen im Bayerischen Staatswald.
- Bayerische Staatsforsten AöR, 2011b. Richtlinie für die mittel- und langfristige Forstbetriebsplanung in den Bayerischen Staatsforsten (Forsteinrichtungsrichtlinie — FER 2011). Regensburg, 2011.
- Bayerische Staatsforsten AöR, 2009. Bewirtschaftung von Fichten- und Fichtenmischbeständen im Bayerischen Staatswald.
- Bayerische Staatsforsten AöR, 2008. Waldbaugrundsätze der Bayerischen Staatsforsten.
- Corona, P., Chirici, G., McRoberts, R.E., Winter, S., Barbati, A., 2011. Contribution of large-scale forest inventories to biodiversity assessment and monitoring. *ISSN 0378-1127 For. Ecol. Manag.* 262 (11), 2061–2069. <https://doi.org/10.1016/j.foreco.2011.08.044>.
- Duelli, P., Obrist, M.K., 2003. Biodiversity indicators: the choice of values and measures. *Agric. Ecosyst. Environ.* 98 (1–3), 87–98. [https://doi.org/10.1016/S0167-8809\(03\)00072-0](https://doi.org/10.1016/S0167-8809(03)00072-0). ISSN 0167-8809.
- FAO, 2020. Global forest resources assessment 2020 – Key findings. Rome. <https://doi.org/10.4060/ca8753en>.
- Fernandez, C., Azkona, P., 1996. Influence of forest structure on the density and distribution of the White-backed Woodpecker *Dendrocopos leucotos* and Black Woodpecker *Dryocopus martius* in Quinto Real (Spanish western Pyrenees). *Bird Study* 1996 (43), 305–313.
- Fischer, A., Mayer, P., Schopf, R., Liepold, K., Gruppe, A., Chr. H., Agerer, R., 2003. Biodiversitätsforschung in ungenutzten und genutzten Wäldern. Sind ungenutzte Wälder artenreicher als Wirtschaftswälder? LWF aktuell 41, 4–5.
- Franz, F., 1971. Funktionen und Tabellen der Derbholzformhöhen für die wichtigsten Baumarten in Bayern. München, Manuskriptdruck, unveröffentlicht.
- Franz, F., Bachler, J., Deckelmann, E., Kennel, E., Kennel, R., Schmidt, A., Wotschikowsky, U., 1973. Bayerische Waldinventur 1970/71. Inventurabschnitt I: Großrauminventur Aufnahme- und Auswertungsverfahren, vol. 11. Forstliche Versuchsanstalt München, pp. 91–99.
- Franklin, J.F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA Forest Service General Technical Report PNW- 1 18. Pacific North.
- Gao, T., Hedblom, M., Emilsson, T., Nielsen, A.B., 2014. The role of forest stand structure as biodiversity indicator. *For. Ecol. Manag.* 330, 82–93. <https://doi.org/10.1016/j.foreco.2014.07.007>.
- Gotelli, N.J., Chao, A., 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Levin, S.A. (Ed.), *Encyclopedia of Biodiversity*, 2nd ed., Vol. 5, pp. 195–211. Waltham, MA, Academic Press.
- Gossner, M.M., Schall, P., Ammer, C., Ammer, U., Engel, K., Schubert, H., Simon, U., Utschick, H., Weisser, W.W., 2014. Forest management intensity measures as alternative to stand properties for quantifying effects on biodiversity. *Ecosphere* 5 (9), 113. <https://doi.org/10.1890/ES14-00177.1>.
- Hagan, J.M., Whitman, A.A., 2006. Biodiversity indicators for sustainable forestry: simplifying complexity. *J. For.* 104 (4), 203–210. <https://doi.org/10.1093/jof/104.4.203>.
- O. Hilmo, H., Holien, H., Hytteborn, H., Ely-Aalstrup, 2009. Richness of epiphytic lichens in differently aged *Picea abies* plantations situated in the oceanic region of Central Norway *Lichenologist*, 41 (2009) 97–108.
- Kovac, M., Gasparini, P., Notarangelo, M., Rizzo, M., Cañellas, I., Fernández-de-Uña, L., Alberdi, I., 2020. Towards a set of national forest inventory indicators to be used for assessing the conservation status of the habitats directive forest habitat types. *ISSN 1617-1381 J. Nat. Conserv.* 53, 125747. <https://doi.org/10.1016/j.jnc.2019.125747>.
- Larrieu, L., Cabanettes, A., 2012. Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. *Can. J. For. Res.* 42, 1433–1445.
- Larrieu, L., Cabanettes, A., Brin, A., et al., 2014. Tree microhabitats at the stand scale in montane beech-fir forests: practical information for taxa conservation in forestry. *Eur. J. For. Res.* 133, 355–367. <https://doi.org/10.1007/s10342-013-0767-1>.
- Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., et al., 2016. Positive biodiversity-productivity relationship predominant in global forests. *Science* 354, aaf8957.
- MacArthur, R.H., MacArthur, J.W., 1962. On bird species diversity. *Ecology* 42, 594–598.
- McElhinny, C., Gibbons, P., Brack, C., Bauhus, J., 2005. Forest and woodland stand structural complexity: its definition and measurement. *For. Ecol. Manag.* 218 (1–3), 1–24. <https://doi.org/10.1016/j.foreco.2005.08.034>. ISSN 0378-1127.
- Mergner, U., 2014. Small is beautiful. Ein Plädoyer für die kleinflächige Stilllegung in Wäldern. *AFZ - Der Wald* 3, 7–9.
- Müller, J., 2005. Waldstrukturen als Steuergröße für Artengemeinschaften in kollinen bis submontanen Buchenwäldern. Dissertation. Technische Universität München.
- Müller, J., Pöllath, J., Moshhammer, R., Schröder, B., 2009. Predicting the occurrence of Middle Spotted Woodpecker *Dendrocopos medius* on a regional scale, using forest inventory data. *For. Ecol. Manag.* 257, 502–509.
- Nascimbene, J., Marini, L., Motta, R., Nimis, P.L., 2009. Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. *Biodivers. Conserv.* 18, 1509–1522.
- Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4(4) (December 1990).
- Noss, R.F., 1999. Assessing and monitoring forest biodiversity: A suggested framework and indicators. *For. Ecol. Manag.* 115 (2–3), 135–146. [https://doi.org/10.1016/S0378-1127\(98\)00394-6](https://doi.org/10.1016/S0378-1127(98)00394-6).
- Pretzsch, H., Grote, R., Reineking, B., Rötzer, T.H., Seifert, S.T., 2008. Models for forest ecosystem management: a European perspective. *Ann. Bot.* 101 (8), 1065–1087.
- Pretzsch, H., 2009. *Forest Dynamics, Growth and Yield: From Measurement to Model*. Berlin, London, Springer, 2009.
- Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature* 405, 212–219.
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. *J. Agric. Res.* 46, 627–638.
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.

- Shannon, C.E., 1948. The mathematical theory of communication. In: Shannon, C.E., Weaver, W. (Eds.), *The Mathematical Theory of Communication*. Univ. of Illinois Press, Urbana, pp. 3–91.
- Storch, F., Dormann, C.F., Bauhus, J., 2018. Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. *For. Ecosyst.* 5(34). <https://doi.org/10.1186/s40663-018-0151-1>.
- Thünen-Institut, D.B., – Ergebnisdatenbank, 2012. Waldfläche [ha] nach Land und Eigentumsart. Jahr=2012, Filter.
- Uliczka, H., Angelstam, P., 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography* 22, 396–405. Copenhagen 1999.
- Ulyshen, M.D., 2011. Arthropod vertical stratification in temperate deciduous forests: Implications for conservation-oriented management. *For. Ecol. Manage.* 261 (9), 1479–1489. <https://doi.org/10.1016/j.foreco.2011.01.033>.
- Van Den Meerschaut, D., Vandekerkhove, K., 1998. Development of a stand-scale forest biodiversity index based on the State Forest Inventory. In: Hansen, M., Burk, T. (Eds.), *Integrated tools for Natural Resources Inventories in the 21st Century*. USDA, Boise, Idaho, pp. 340–349.
- Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. *Biol. Conserv.* 144 (1), 441–450. <https://doi.org/10.1016/j.biocon.2010.09.030>.
- Winter, S., Chirici, G., McRoberts, R.E., Hauk, E., Tomppo, E., 2008. Possibilities for harmonizing national forest inventory data for use in forest biodiversity assessments. *For. Int. J. For. Res.* 81 (1), 33–44. <https://doi.org/10.1093/forestry/cpm042>.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21 (2/3), 213–251.
- Zahner, V., Sikora, L., 2012. Ist der Schwarzspecht Zeiger oder Produzent von Stammfäule? *AFZ-DerWald* 12 (2012), 42–43.