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Quantifying old-growthness of lowland European beech forests by a multivariate indicator for forest structure

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ABSTRACT

Quantifying the degree of old-growthness of forests is reasonable to assess their conservation value and guide management decisions. This study aimed at developing and applying an indicator to quantify the old-growthness of forest structure on potential beech forest sites in Central Europe which exhibit a long history of forest management. A set of structural variables was derived from sample plot inventories in European primeval beech forests in Eastern Slovakia (classified as old-growth) and 39 comparison stands of different management intensity, age and tree species composition in the North German lowlands. The comparison stands were arranged in triplets, consisting of i) a > 100 year old European beech forest left to natural development (ND), ii) 80 to 100 year old Scots pine forest with a certain amount of deciduous trees in the understory (OP), and iii) <80 year old Scots pine forest (YP).

The initial number of 134 attributes was condensed to 27 variables representing ten thematic groups. Selection criteria were, i) typical for the old-growth state, ii) widespread and meaningful, and iii) exhibiting no multicollinearity within the respective group. The developed old-growth indicator (OGI) measures the degree of overlap of the 5th–95th percentile ranges of a certain comparison stand with the primeval forests. OGI achieves values between 0 and 1 and allows the consideration of all thematic groups and variables separately as well as calculating an aggregated value.

We derived plausible OGI-values of between 0.71 and 0.74 for the primeval forests, 0.13 to 0.42 for the ND stands, and 0.07 to 0.30 for the OP and 0.03 to 0.26 for the YP stands. We postulated that OGI provides a comprehensive and reproducible indicator of the maturity of a forest stand on an empirical basis that allows for differentiated, as well as easy to handle, aggregated evaluations. An additional advantage is the implementation into the established workflow for forest surveys of national parks and strict forest reserves in Germany.

1. Introduction

The forest landscape of central Europe is a mosaic of forest types and management intensities ranging from production forests to strictly protected areas, such as national parks or strict forest reserves. Almost all European forests have been subject to major anthropogenic impacts in the past (Machado, 2004; Reif and Walentowski, 2008; Winter, 2012), resulting in large structural and compositional changes compared to the natural state (da Silva et al., 2019). Primeval forests are estimated to cover not more than 0.7% of the forest area in Europe (Sabatini et al., 2018). Important in this respect are the primeval beech forests of the Carpathians, a World Natural Heritage Site, together with ancient beech forest sites in the rest of Europe, inter alia in Germany (Kirchmeier and Kovarovics, 2016). Germany has a national responsibility for beech forests (BfN, 2008). Consequently, they play a major role in the German National Strategy on Biological Diversity (NBS). The NBS aims at a proportion of 2% to be dedicated as wilderness areas and 5% of the forested area to be left to natural development (BMU, 2007). National heritage sites have a high potential to contribute to these aims. They cover ca. 156,000 ha of the federal territory and are explicitly dedicated

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to nature protection. Many of them were previously military training areas, and they mainly comprise large, relatively undisturbed landscapes with a mixture of forests and open habitat. The majority of the forests are still managed in order to increase the degree of naturalness, with the ultimate goal being to leave them to natural development in future (Culmsee et al., 2015).

In forestry and nature conservation the degree of naturalness is an important measure (Angermeier, 2000; Reif and Walentowski, 2008). However, naturalness is a difficult to operationalize and ambiguous term. Because of the complexity of nature and diverging notions of 'naturalness', different approaches have been suggested for its quantification (Gossner et al., 2014; Kahl and Bauhus, 2014; Kowarik, 1999; McRoberts et al., 2012; Rüdisser et al., 2011). The ambiguity in operationalizing a natural state of central European forests is also rooted in the fact that primeval forests are scarce or barely existent for certain forest types. Consequently, for central European forests, natural structures and processes, and in particular the natural disturbance regime, are largely unknown (Ammer et al., 2018). However, small remnants of pristine European beech forests exist in south-eastern Europe (Korpel, 1995; Leibundgut, 1993; Smejkal et al., 1997) and to a larger extent in the eastern part of central Europe (Sabatini et al., 2018). They can be used as reference sites for the old-growth state of natural forests.

Wirth et al. (2009) characterize old-growth forests as the climax state of a forest type that has developed under the absence of large disturbances (like wild-fire, insect outbreaks, major wind-throw or harvest). Spies (2004) defines the old-growth forest as a 'product of structures and processes associated with the maturation and senescence of a population of trees'. Although old-growth forests exhibit a maximum degree of naturalness (Peterken, 1996; Westphal et al., 2004), it should be pointed out, however, that other successional states of maximum naturalness also exist, e. g. early successional stages (Swanson et al., 2011). In small and alternating extent all phases of a forest life cycle are included in the old-growth forest which is the reason for its high value for all forms of life (Hilmers et al., 2018, Thorn et al., 2020)

We asked how the old-growthness of forest structure can be operationalized and measured on the basis of available survey data. Focussing on forest structure is advantageous, as there is wide consensus about typical old-growth structural attributes (Bauhus et al., 2009) and investigations into the structure of several European old-growth beech forests have been conducted (Alessandrini et al., 2011; Burrascano et al., 2013; Keren and Diaci, 2018; Kucbel et al., 2012; Vandekerkhove et al., 2018; Glatthorn et al., 2018). Typical attributes include the presence of large old trees, an irregular stand structure, advanced regeneration of shade-tolerant tree species, the presence of canopy gaps and a high volume of deadwood of different diameters and decay stages (Bauhus et al., 2009; Hobi et al., 2015; Nilsson et al., 2002; Motta et al., 2015; Zenner et al., 2014).

Our study aimed at developing an indicator for the degree of old-growthness of forest stand structure, which is i) multivariate (s. Franklin and Van Pelt, 2004), ii) considers the variability of the single attributes (s. Král et al., 2010), iii) allows for aggregated as well as overall evaluations, iv) is based on reference data of actual old-growth stands, and v) is implemented in an existing workflow of monitoring forest structure.

We drew on forest inventory data from three Slovakian primeval forests as old-growth reference sites and 13 forest sites in the northern German lowland as comparison stands with a lower degree of old-growthness, respectively.

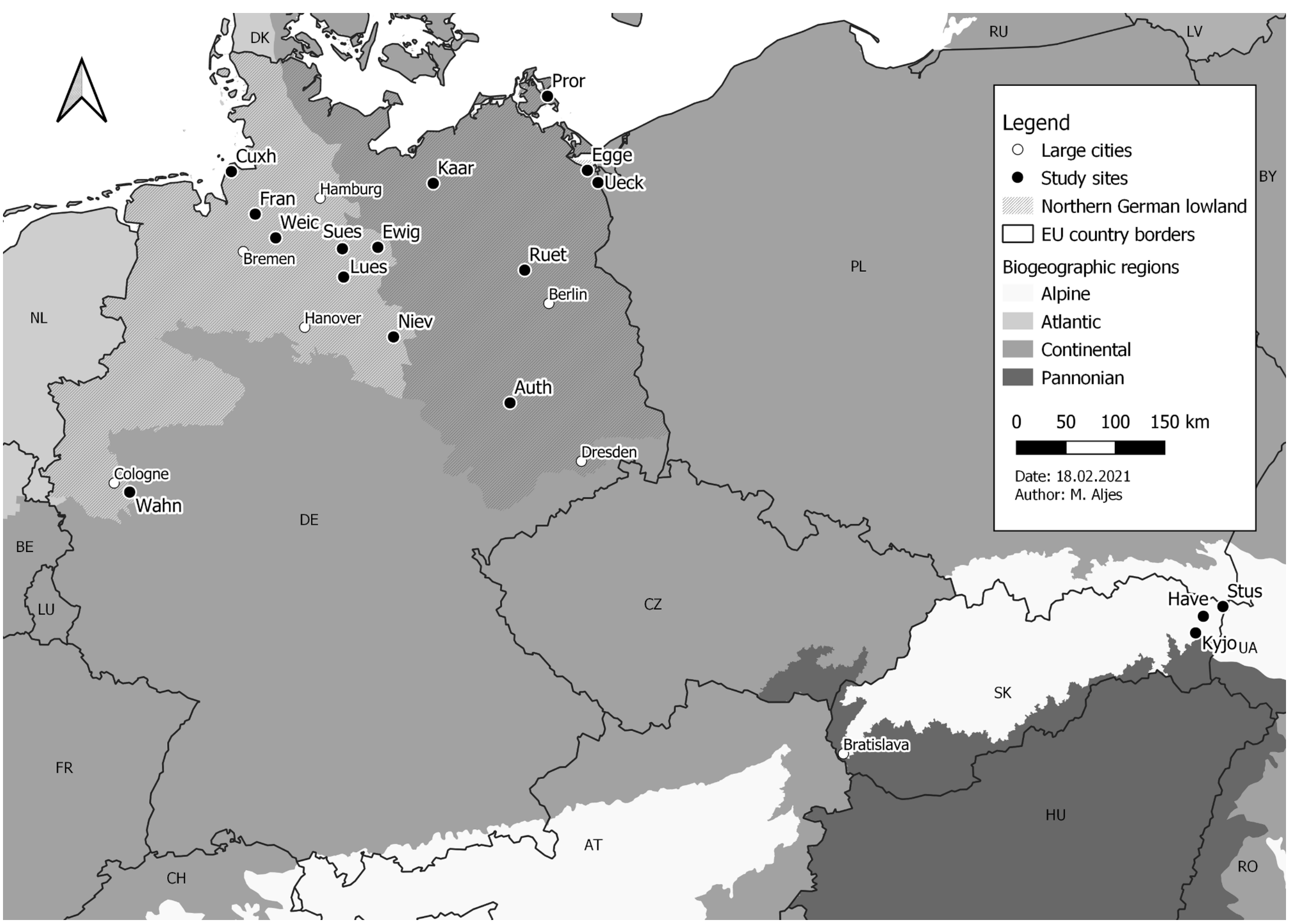

Fig. 1. Location of the 13 triplets in the northern German lowland (according to Gauer and Aldinger, 2005) consisting of a beech forest, an old and a young pine forest, respectively, and three old-growth reference beech forests in eastern Slovakia. For abbreviations see Table 1 in the Appendix.

2. Material and methods

2.1. Study areas and forest stand selection

The comparison stands were situated in the northern German lowlands, spanning an oceanic-continental gradient of 580 km between the most distant sites (Fig. 1). Mean annual rainfall and temperature varied between 555 and 908 mm and between 8.1 and 10.3 °C, respectively (Appendix Table 1). The soils developed from sandy glacial deposits of the last (Weichselian) or penultimate (Saalian) Ice Age. The soil types were dystric to spodo-dystric Cambisols and Cambisol-Luvisols with high acidity and low to medium nutrient availability without groundwater influence. A basic selection criterion was the classification as potential oligotrophic to mesotrophic beech and mixed beech forests according to Suck et al. (2010). The aim was to cover the current characteristics of naturally developing beech forests in the northern German lowlands, whereas the time since abandonment varied from 4 to 43 years (see Table 1 in the appendix). The selected stands were either part of the strict forest reserves network of the states of Lower Saxony and Saxony-Anhalt or of the natural heritage sites, which is property of the German Federal Environmental Foundation (Culmsee et al., 2015).

Within each study area, one forest stand was selected to represent each of the three management categories developed for natural heritage sites (Culmsee et al., 2015, Table 1) to form a so-called triplet consisting of young pine forest (YP), older pine forest (OP) and broadleaved forest dedicated to natural development (ND) (Fig. 2). Within a triplet the stand sites were sought to be comparable according to the local site mapping. The size of a stand unit had to be at least 2 ha. For category ND, we selected strict forest reserves and natural heritage sites with beech (Fagus sylvatica L.) stands aged > 100 years, except for one oak stand on a potential natural beech site ('Rüthnicker Heide'). All stands exhibited at least 200 years of forest continuity. In close vicinity, matching YP and OP stands were selected. Overall, our study consisted of 13 triplets, comprising 39 forest stands. Beech stands of the category ND were mainly in the mid optimum to late optimum phase of forest succession stages (acc. to Hilmers et al., 2018) and are visibly influenced by earlier forest management. Since true old-growth beech forests do not exist in northern central Europe, we applied data on forest structure from three primeval forests in the Carpathians of eastern Slovakia (Havešová, Kyjov, Stužica, s. Appendix Table 1) as reference sites for maximum achievable old-growthness. In these reserves, there has been no known direct human interference for centuries (Korpel, 1995). The three beech-dominated (F. sylvatica) forests at montane elevation (from 550 m a.s.l. to 950 m a.s.l) are protected as National Nature Reserves; two of them are listed in UNESCO's World Heritage. The stands belong to some of the last remnants of temperate broad-leaved virgin forests in the western Carpathians. The reserves Havešová and Kyjov are pure beech stands and although Stužica contains a considerable proportion (11% by stem numbers) of silver fir (*Abies alba*), all three stands belong to the *Fagetum dentarietosum glandulosae* forest community (Bohn et al., 2003). Though climatic and soil conditions differ to a certain degree between the old-growth reference sites and the comparison stands, according to Markgraf (1931) and Peters (1992), we hypothesized that the structure of European beech forests on non-extreme sites is highly comparable.

Table 1
Main characteristics of the three forest management categories (taken from Culmsee et al., 2015).

Category	Forest with natural development (ND)	Old pine forests (OP)	Young pine forests (YP)
Stand attributes	Broadleaf forests following natural development with beech forest associations as the potential natural vegetation	Old Scots pine forests ≥ 80 years old (main stand), and a few ingrowing broadleaf trees, understory dominated by broadleaf species (70–89% of cover)	Young Scots pine forests < 80 years old (main stand), indigenous broadleaf trees occur only in some stands in the understory
Management	Natural development, past management ceased 10 to 40 years ago	Silvicultural management in the near past, current interventions only for battling invading non-native tree species	Silvicultural management in the near past, current interventions only for battling invading non-native tree species

3. Forest inventory

In 2015, forest structure was sampled on 10 randomly distributed 0.1 ha circular plots for each of the forest categories ND, OP and YP at all 13 German sites (390 plots in total), following mainly the protocol for strict forest reserves in Hesse (Meyer et al., 2021). The minimum distances between the borders of the plots, as well as between the plot and forest borders and roads, was 30 m (see Fig. 3). In each of the three reference sites in Slovakia 12 plots were inventoried in 2013, largely according to the same protocol (Glatthorn et al., 2017, Feldmann et al., 2018). Methodological deviations from Meyer et al. (2013) were, i) plots in the Slovakian old-growth forest sites were selected by choosing 4 plots with the majority of the plot being in one of the successional stages 'Initial', 'Optimum' and 'Terminal' at each site according to Feldmann et al. (2018), ii) circular plot radius was 12.62 m (0.05 ha) and iii) tree regeneration was recorded on two subplots.

All standing trees and snags with a diameter at breast height (dbh) ≥ 7 cm, as well as lying deadwood with a diameter ≥ 20 cm at the butt end, were recorded on the whole sample plot area. Tree regeneration was assessed in the northeast quarter of the sample plot for all plants ≥ 1.5 m height and < 7 cm dbh. Plants < 1.5 m were assessed on a subplot of 25 m^2 in the comparison stands. In the primeval forests the census of tree regeneration was carried out on two subplots of 13 m^2 per sample plot for all plants < 7 cm dbh. A wide range of stand attributes was collected, such as dbh, tree species, tree height (sample), microhabitats and decay stage of deadwood (for details s. Meyer et al., 2021). Forest inventories were performed using the computer aided forest data collection software Field-Map (IFER, Jílové u Prahy, Czech Republic). Data processing, statistical analysis and graphical representation were carried out using SAS 9.4 and R version 3.5.1 (R Core Team, 2018).

4. Development of the old-growth indicator (OGI)

As a first step, 134 structural variables were calculated for all 36 plots (12 replicates on three sites) for the reference sites (see Appendix Table 2). They were further condensed by the authors' opinion to 41 variables that are meaningful to describe forest structure, are easy to calculate and to interpret. We tested all 41 variables for significant differences between the three Slovakian reference sites using a non-parametric Kruskal-Wallis rank-sum test ($p \leq 0.05$), and kept only those variables which did not exhibit a significant difference (s. Appendix Table 3). These variables were arranged into 10 thematic groups that we considered essential for a coherent description of forest structure (Table 2).

In order to reduce redundancy, we conducted multicollinearity analysis within these groups (proc reg under SAS 9.4, options vif collin). To ensure comparable variable selection as a rule of thumb we took a variance inflation factor > 10 and/or a tolerance < 0.2 as threshold values (for discussion of threshold values s. Wooldridge, 2013). If different variables characterized the same aspect only the more widely applied and/or the variables that are easier to calculate were retained. This procedure resulted in 27 retained variables for the old-growth indicator (OGI) calculation (Table 2). Finally, the variables were operationalized per thematic group as follows:

Successional status: The dominance of late successional tree species,

Fig. 2. View into the structurally rich old beech forest at Prora natural heritage site. Picture by N. Rosing. Copyright DBU Naturerbe GmbH.

and their advanced regeneration is typical for beech old-growth stands (Korpel, 1995). The actual successional status of the living tree stand ≥ 7 cm dbh, as well as that of the regeneration layer, was calculated by multiplying the stem number proportion of tree species by 1 for pioneer species (e.g. birch, aspen, pine), 2 for intermediate tree species (e.g. oak, maple, ash), and 3 for shade-tolerant climax species (beech). The sum of the respective values yielded the successional status.

Forest development stage: To calculate the forest development stage of a plot, all trees of the living stand ≥ 7 cm dbh were classified into 'natural age classes' (NFP, 2001) on the basis of their dbh, namely 1 (<20 cm), 2 (20–35 cm), 3 (>35–50 cm), 4 (>50–80 cm), and 5 (≥80 cm). Again, the mean of the numbers weighted by the stem number proportions resulted in the respective variable.

Because a small-scale mosaic texture is typical for beech old-growth forests, the number of different development stages was included as a second variable in this thematic group.

Number of tree species: Beech old-growth stands are characterized by a low tree species diversity (Leuschner, 2015). This feature is expressed by the variable 'number of tree species'.

Native tree species: It is self-explanatory that natural old-growth stands consist solely of native tree species. The share of non-native species was used as indicator for the degree of human interventions in the past in both the living stand ≥ 7 cm dbh and the regeneration layer.

Differentiation of tree dimensions: The characteristic diameter distribution of old-growth stands is often found to be a rotated-sigmoid function (Feldmann et al., 2018; Goff and West, 1975; Westphal et al., 2006), which indicates a multi-cohort age structure and results in a high differentiation of tree dimensions and a rather high number of trees in small diameter classes. As proxies for these features we applied several dbh measures: maximum and minimum dbh, dbh span, mean dbh and number of giant trees.

Density: As density measures, both the number and volume of living trees per ha were selected. Although the stand density index (Zeide, 2005) would provide a density measure which is independent from site conditions and tree age, we opted for the easier to calculate and frequently used classical parameters.

Density of regeneration: Advanced regeneration is another typical feature of beech old-growth stands (Korpel, 1995). Three variables were selected, one quantifying the overall density of regeneration, as well as of two development stages defined by tree height.

Deadwood: Because of natural maturation and tree mortality, high levels of large deadwood are a typical feature of old-growth forests (Bauhus et al., 2009). We selected 6 different variables to indicate the old-growthness in this thematic group. While in the old-growth the number of large snags was high, standing dead trees and snags in the low dbh-classes were not very frequent. This can be explained by a rather low rate of self-thinning within the stand ≥ 7 cm dbh because beech trees are known to survive for very long periods even under a closed canopy. The group also contains total deadwood volume, as this parameter is widely used in studies on forest ecology.

Decay stage: Deadwood passes through different more or less distinct decay stages. We multiplied the numbers 1 to 5 of the decay stages of downed dead logs between freshly dead (1) and wood completely soft (5) by the relative frequency of the respective objects. The sum of the resulting values indicated the mean decay stage. A high mean value is typical for beech old-growth because passing the later stages takes much more time than passing the early ones (Müller-Using and Bartsch 2009).

Microhabitats: This thematic group is represented by the density of three microhabitat types which are typical for beech old-growth. The number of trees with cavities and with conks of fungi is quite high while the number of root plates exhibited large variation.

As a second step, after variable selection a bootstrapping procedure (proc surveyselect under SAS 9.4, method = urs (unrestricted random sampling with replacement)) with 5000 iterations was employed, i) within all 36 old-growth samples, ii) within each of the three old growth stands and iii) within each of the 39 comparison stands. This stochastic approach overcomes uncertainties resulting from small sample sizes, as long as the samples are representative of the whole population (Efron and Tibshirani, 1993). The number of samples to be drawn in every bootstrap iteration was set to the number of plots available (i.e. 36 for i), 12 for ii) and 10 for iii)). For the single reference sites, as well as for all reference sites combined, and for each comparison stand, the 5th and 95th percentile boundaries were calculated and the communality between the respective ranges was used as measure for old-growthness. We distinguished two general forms of communality between a comparison stand and the old-growth reference site, i) overlap with the 90%

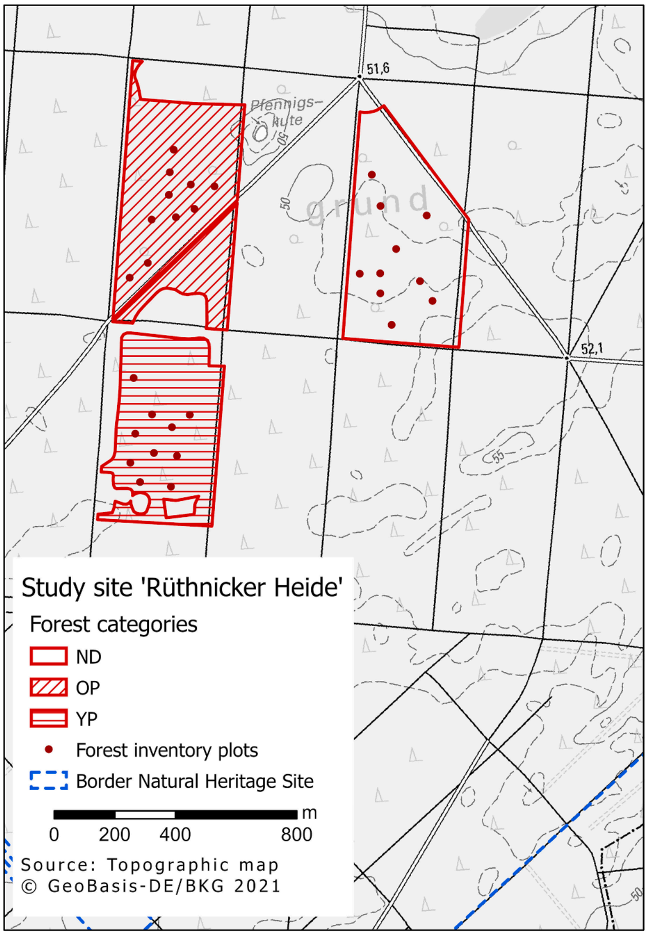

Fig. 3. Distribution of forest inventory plots on the natural heritage site Rüthnicker Heide. For each forest category (ND = natural development, OP = old pine forest, YP = young pine forest) ten circular plots were randomly distributed over the selected stand.

confidence interval of the reference site (Eq. (1)), and ii) excess variability outside the 90% confidence interval of the reference site, in the sense of negative communality (Eq. (2)).

$$OGI_{com} = \frac{R_{com}}{R_{OG}} \quad (1)$$

where:

OGI_{com} = common variability between the old-growth reference and the comparison stand

R_{com} = common range between comparison stand and old-growth

R_{OG} = old-growth range

$$OGI_{exc} = 1 - \frac{R_{exc}}{R_{CS}} \quad (2)$$

where:

OGI_{exc} = excess variability of the comparison stand outside the old-growth range

R_{exc} = range of comparison stand outside the old-growth range

R_{CS} = total range of comparison stand

The final OGI was calculated according to Eq. (3):

$$OGI = \frac{OGI_{com} + OGI_{exc}}{2} \quad (3)$$

Overall, 11 different cases of continuous or point values, of full and partial overlap and of excess variability occurred (Fig. 4, Table 3).

The resulting single OGI values for each variable varied between 0 and 1. To give equal weights to all thematic variable groups, each

Table 2
Thematic groups and variables used in the old-growth indicator (OGI) and the 5th and 95th percentile range in the old-growth reference sites (bootstrapping result from all 36 sample plots combined).

Group	Variable	Characteristics in old-growth-stands	5th–95th percentile of old-growth
Successional status	Successional status in the living stand ≥ 7 cm dbh between 1 (pioneer) and 3 (climax)	High proportion of climax species	2.98–3
	Successional status in the regeneration layer between 1 (pioneer) and 3 (climax)	High proportion of climax species	2.85–2.95
Forest development stage	Mean development stage in the living stand ≥ 7 cm dbh between 1 (pole stage) and 5 (over-mature trees)	Multi-cohort structure results in low values because the proportion of small trees is high	2.03–2.29
	number of different forest development stages	high value as a result of occurrence of several development stages at small scale	4.06–4.44
Tree species diversity	Number of tree species in the living stand ≥ 7 cm dbh	Low as a result of beech dominance	1.28–1.58
Native tree species	Proportion of native central European tree species in the living stand ≥ 7 cm dbh [%]	Exclusively native central European tree species	100
	Proportion of native central European tree species in the regenerating layer [%]	Exclusively native central European tree species	100
Differentiation of tree dimensions	dbh-span in the living stand ≥ 7 cm dbh	Large as a result of the multi-cohort structure	69.6–77.75
	Minimum dbh in the living stand ≥ 7 cm dbh	Very low	8.48–9.69
	Maximum dbh in the living stand ≥ 7 cm dbh	Very high	78.57–86.91
	dbh of the mean basal area stem in the living stand ≥ 7 cm dbh	More or less low due to a high number of small dimension trees	36.01–41.14
	Number of trees with dbh ≥ 80 cm ha^{-1}	Large	7.5–12.78
Density	Number of living trees ≥ 7 cm dbh ha^{-1}	Moderate	294.44–363.33
	Volume of living trees ≥ 7 cm dbh ha^{-1}	High	527.8–655.31
Density regeneration layer	Total number of woody plants in the regeneration layer ha^{-1}	High due to advanced regeneration	24,345–43,380
	Number of woody plants ≥ 0.5 and < 1.5 m height ha^{-1}	High due to advanced regeneration	3838–7174
	Number of woody plants ≥ 1,5 m height ha^{-1}	High due to advanced regeneration	1370–3926
Dead wood			122.38–185.38

(continued on next page)

Table 2 (*continued*)

Group	Variable	Characteristics in old-growth-stands	5th–95th percentile of old-growth
	Dead wood volume in m^3 per ha	High total dead wood volume	
	Number of snags and standing dead trees with dbh ≥ 7 and < 20 cm	Low because of low rate of self-thinning in early development stages	5.56–16.67
	Number of snags and standing dead trees with dbh ≥ 20 cm and < 50 cm	Rather low because of low rate of self-thinning in mid development stages	6.11–15.56
	Number of snags and standing dead trees with dbh ≥ 50 cm	High because of natural mortality of mature and over mature trees	7.22–17.22
	Number of downed logs with diameter at the butt end ≥ 20 cm and < 50 cm	high because of natural mortality and decay processes	40.56–63.33
	Number of downed logs with diameter at the butt end ≥ 50 cm	High because of natural mortality and decay processes	18.33–35.56
Decay stage	Mean decay stage of downed logs between 1 (freshly dead) and 5 (wood completely soft, mouldered)	High due to long duration of later decay stages	3.74–4.22
Microhabitats	Number of trees with fruiting bodies of polypore fungi ha^{-1}	Moderate - high due to natural mortality	5–10.83
	Number of trees with cavities ha^{-1}	High due to natural cavity formation and high number of mature and over mature trees	18.33–30.28
	Number of root plates ha^{-1}	Wide span due to spatially different impact of wind throw	1.67–7.78

variable was weighted by the inverse of the number of variables per group divided by 10 (e. g. multiplier in a group of 4 variables = 1/40). As a result, the maximum value for each group is 0.1 and the maximum value for the OGI adds up to 1.

5. Results

Total OGI scores of the old-growth stands varied only slightly between 0.71 and 0.74. Although in the comparison stands many OGI variables varied largely within a management category (Fig. 5), the OGI scores exhibited plausible and significant differences between the categories (Fig. 6). The ND stands reached OGI scores between 0.13 and 0.42 with a mean of 0.27, the OP stands values between 0.*07* and 0.3 with a mean of 0.2, and the YP stands values between 0.03 and 0.26 with a mean of 0.14.

The plausible ranking of the management categories along the OGI range is also shown when the single stands and the different thematic groups are depicted (Fig. 7). As a general trend, the high proportion of native tree species and the presence of microhabitats contributed most to old-growthness across all categories. The least similarity in respect of microhabitats was found for stem cavities, which are closely associated with later development stages of a tree. The OP stands were separated from the YP stands mainly by the thematic groups 'forest development stage' and 'deadwood'. The higher old-growthness of the ND stands compared to the OP stands resulted largely from the thematic groups 'successional status' and 'number of tree species'. The OGI scores of the thematic groups 'differentiation of tree dimensions' and 'successional status', which are mainly driven by stand age and tree species composition, decreased strongly from ND to YP. Mean decay stages of downed logs were in general much lower in the comparison stands than in old-growth forests, but there was a higher score in the ND stands, presumably as a result of the extended time span in which deadwood could accumulate and decay on the ground. In regard to density, the number of stems is higher in the YP and OP stands, while volume per ha is lower, which is also reflected in a lower OGI score. For the thematic group 'forest development stage', OP stands reached the highest OGI scores because they exhibited several vertical tree layers. With respect to tree regeneration, the categories ND and YP reached higher OGI values than OP. Taking a look into deadwood features the occurrence of snags and logs is more similar to old-growth in OP stands than in the categories ND and YP. However, total deadwood volume remains far below the levels of the Slovakian old-growth forests.

6. Discussion

Defining naturalness in an objective, comprehensive and widely accepted way is a problem in forest ecology (McRoberts et al., 2012), as well as in forestry and nature conservation (Angermeier, 2000; Reif and Walentowski, 2008). To our knowledge, the approach we devised and applied is the first to use inventory data of forest structure from actual old-growth stands as reference against which to measure naturalness. In a direct way OGI quantifies the similarity of forest structure to an old-growth state. Insofar, the indicator follows a different approach than taking the management intensity as an indirect measure (Gossner et al., 2014; Kahl and Bauhus, 2014). As a general rule high degrees of old-growthness should coincide with low management intensity.

With our approach it was possible to meet all five predefined criteria. Firstly, we designed a multivariate indicator that, secondly, considered the variability of attributes. Thirdly, OGI allows for differentiated as well as aggregated evaluations of the many features which characterise old-growth stands in contrast to managed forests (Blasi et al., 2010; Burrascano et al., 2013; Chiavetta et al., 2012; Keren and Diaci, 2018; Liira and Sepp, 2009). It solves the problem of combining many attributes into a coherent indicator without losing the ability for differentiated evaluations (Kunttu et al., 2015). Fourthly, in contrast to the approach of the potential natural vegetation (Kowarik, 1999; Suck et al., 2010) and of biodiversity-related indicators (Geburek et al., 2010; Larrieu and Gonin, 2008; Larrieu et al., 2019) OGI is based on empirical reference data. Taking true old-growth stands as reference facilitated to overcome the problem of reference sites which are still largely influenced by human intervention (Winter, 2012). In this context it is advantageous that the old-growth state of a forest is comparably well defined (Bauhus et al., 2009; Wirth et al., 2009) and several relicts can still be found throughout Europe. Fifthly, the indicator is implemented in an existing workflow, namely the monitoring scheme for strict forest reserves of the North-western German Forest Research Institute (Meyer, 2020).

It should be mentioned that in natural forest landscapes, besides old-growth, other natural states also occur, in particular early successional stages after large infrequent disturbances. Several studies show that it is challenging to quantify the natural extent, turnover and effects of large infrequent disturbances in a region without extensive areas of natural forests, like central Europe (Nagel et al., 2006, 2007; Jaloviar et al., 2017; Šamonil et al., 2009; Svoboda et al., 2014). Furthermore, the disturbance regime is expected to undergo alterations caused by climate change and other anthropogenic drivers (Seidl et al., 2017), making it questionable whether an exact definition of a natural disturbance regime is a reasonable concept at all. However, it is beyond doubt that the old-growth state resulting from small-scale disturbances and maturation is a central element of a natural forest landscape. Although we do not claim that our approach is sufficient to cover all aspects of the complex notion of naturalness, at least it contributes a solution to

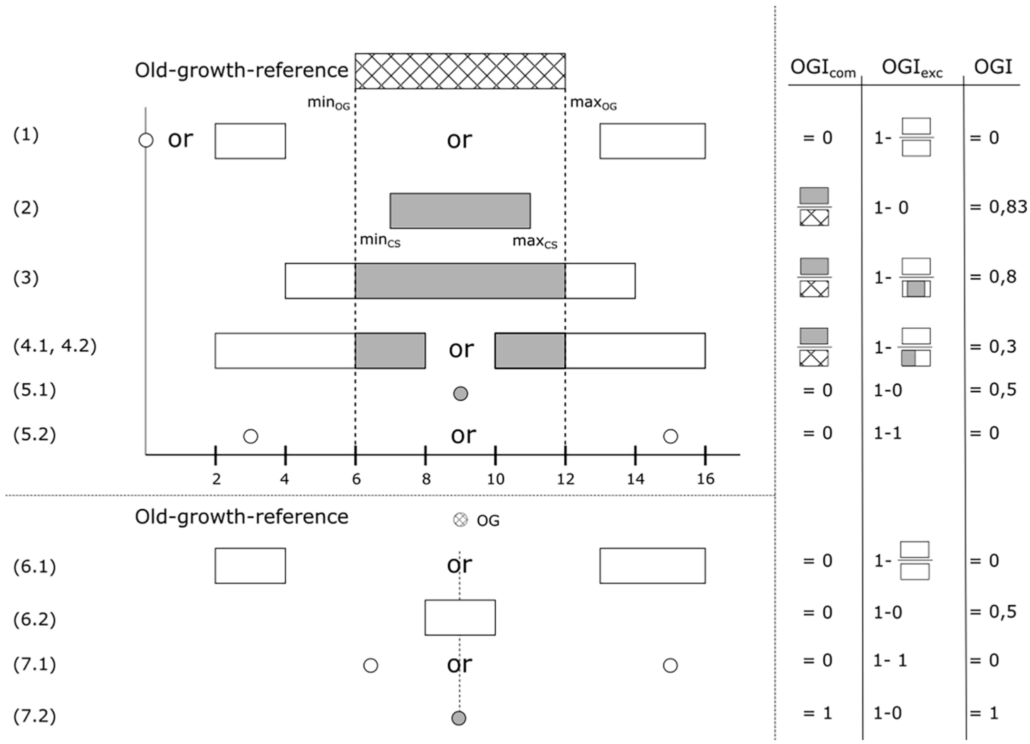

Fig. 4. Calculation of the old-growth indicator (OGI) resulting from the overlap (OGIcom, grey bars) and excess (OGIexc, white bars) variability between the comparison stands and references sites (true old-growth stand) (cross-hatched bar and dot, respectively). Numeration on the left side refers to the different cases explained in the text. The left side of each bar is the value of the 5th, the right side of the bar the value of the 95th percentile. The scale on the x-axis is exemplary for a value of one attribute, to make the calculation examples on the right side comprehensible. Where more than one case is depicted in one line the calculation examples are valid for both sides.

Table 3
The two components of the OGI (OGI_{com} and OGI_{exc}) were calculated according to the following rules (abbreviations: min, max = 5th and 95th percentile of the bootstrap result for every variable; CS = comparison stand, OG = old-growth reference site).

Case	Prerequisite	Prerequisite (expression)	Formula
1	No overlap between the 90% confidence intervals of the comparison stand and of the old-growth reference site	$min_{CS} < min_{OG} or min_{CS} > max_{OG}$	$OGI_{com} = 0, OGI_{exc} = 1 - 1 = 0$
2	The 90% confidence interval of the comparison stand lies within the 90% confidence interval of the old-growth reference site	$min_{CS} \geq min_{OG} and max_{CS} \leq max_{OG}$	$OGI_{com} = \frac{R_{CS}}{R_{OG}}, OGI_{exc} = 1 - 0$
3	The 90% confidence interval of the old-growth reference site lies within the 90% confidence interval of the comparison stand	$min_{CS} \leq min_{OG} and max_{CS} \geq max_{OG}$	$OGI_{com} = 1, OGI_{exc} = 1 - \frac{R_{CS} - R_{OG}}{R_{CS}}$
4.1	Partial overlap of the 90% confidence interval of the comparison stand with the 90% confidence interval of the old-growth reference site on one side Left side	$min_{CS} < min_{OG}\ and (max_{CS} \geq min_{OG}\ and max_{CS} \leq max_{OG})$	$OGI_{com} = \frac{(max_{CS} - min_{OG})}{R_{OG}}, OGI_{exc} = 1 - \frac{(min_{OG} - min_{CS})}{R_{CS}}$
4.2	Partial overlap of the 90% confidence interval of the comparison stand with the 90% confidence interval of the old-growth reference site on one side Right side	$min_{CS} \leq max_{OG}\ and (min_{CS} \geq min_{OG}\ and max_{CS} > max_{OG})$	$OGI_{com} = \frac{(max_{OG} - min_{CS})}{R_{OG}}, OGI_{exc} = 1 - \frac{(max_{CS} - max_{OG})}{R_{CS}}$
5.1	Point value of the comparison stand lies within the 90% confidence interval of the old-growth reference site	$min_{CS} = max_{CS} and min_{OG} \neq max_{OG}\ and (min/max_{CS} \geq min_{OG}\ and min/max_{CS} \leq max_{OG})$	$OGI_{com} = 0, OGI_{exc} = 1 - 0$
5.2	Point value of the comparison stand lies outside of the 90% confidence interval of the old-growth-reference site	$min_{CS} = max_{CS} and min_{OG} \neq max_{OG}\ and (min/max_{CS} < min_{OG} or min/max_{CS} > max_{OG})$	$OGI_{com} = 0, OGI_{exc} = 1 - 1$
6.1	Point value for the old-growth reference site but 90% confidence interval > 0 for the comparison stand The 90% confidence interval of the comparison stand has no overlap with the old-growth reference site point	$min_{OG} = max_{OG}\ and (\frac{min}{max_{OG}} < min_{CS}\ or min/max_{OG} > max_{CS})$	$OGI_{com} = 0, OGI_{exc} = 1 - 1$
6.2	Point value for the old-growth reference site but 90% confidence interval > 0 for the comparison stand The old-growth reference site point lies within the 90% confidence interval of the comparison stand	$min_{OG} = max_{OG}\ and (\frac{min}{max_{OG}} \geq min_{CS}\ and min/max_{OG} \leq max_{CS}$	$OGI_{com} = 1, OGI_{exc} = 1 - 1$
7.1	Point value for the old-growth reference site and the comparison stand Values not identical	$min_{CS} = max_{CS}\ and min_{OG} = max_{OG}\ and (min/max_{CS} \neq min/max_{OG})$	$OGI_{com} = 0, OGI_{exc} = 1 - 1$
7.2	Point value for the old-growth reference site and the comparison stand Values identical	$min_{CS} = max_{CS}\ and min_{OG} = max_{OG}\ and min_{CS} = min_{OG}$	$OGI_{com} = 1, OGI_{exc} = 1 - 0$

quantify naturalness in respect of a certain state of natural forests that is highly important for the conservation of biodiversity (Wirth et al., 2009).

At first sight it seems odd that the old-growth stands did not reach maximum old-growthness. This can be attributed to the concept of taking the 5th to 95th percentile range as a reference measure. Consequently, if one of the stands reaches extreme values for a certain feature (e.g. very dense regeneration), these are not included in the pooled

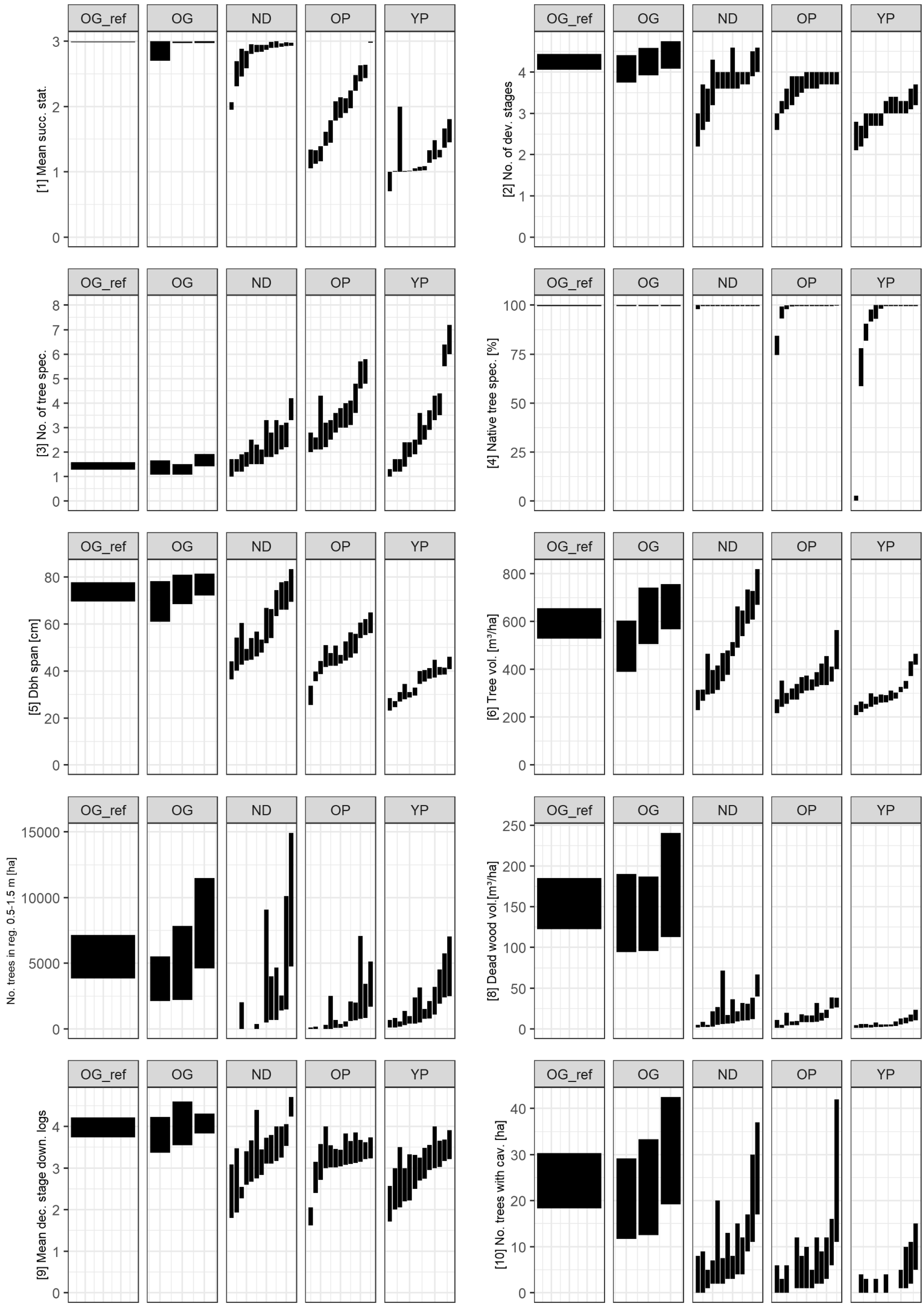

Fig. 5. 5th to 95th percentile ranges for selected OGI variables (for detailed definition s. text and Table 2) of the old-growth reference (OG_ref), the three single old-growth stands (OG) and the comparison stands (ND = natural development, OP = old pine stands, YP = young pine stands).

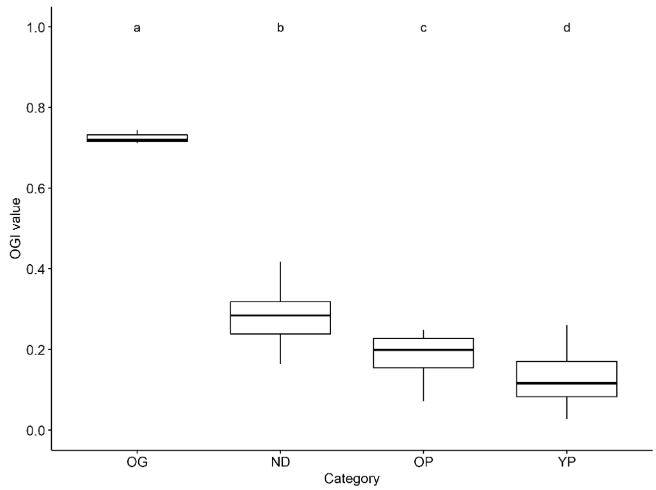

Fig. 6. Value ranges of OGI scores of the old-growth stands and the comparison stands in the northern German lowlands (abbreviations s. text) with median and error bars. Different letters indicate significant differences ($p < 0.05$) between the medians of the groups according to a non-parametric pairwise Wilcoxon rank-sum test.

range, which, in turn results in OGI scores below 1. The low variability between the three Slovakian old-growth sites seems also surprising, as one feature of old-growth stands is structural heterogeneity. But interestingly, this heterogeneity can be found on a very small scale. For the reference stands Feldmann et al. (2018) showed that there actually is low variability of forest structure between the three Slovakian old-growth sites. They developed an index to quantify the share of a certain development stage on each plot and found a quite similar distribution of all development stages throughout the plots of all sites. Other structural characteristics were tested for significant differences between the sites and with few exceptions they were also quite similar.

The OGI score rates common variability positive and excess variability negative, an approach which was also proposed by Machado (2004) and is in line with the target to preserve the typical natural diversity (Lindenmayer and Hunter, 2010). In that respect old-growthness is characterized by both high and low levels of certain features, e. g. high deadwood amount contrasting with low number of tree species. This may result in the negative rating of structures with high conservation value. For instance, as a result of active promotion of seed trees in the past the ND stand 'Authausener Wald' showed higher numbers of giant trees than the old-growth reference. This example shows that the OGI score should not be taken as an exhaustive measure of the conservation value of forest structures.

Our results indicate that the ND stands generally exhibit higher OGI scores than the OP and YP stands. However, the ND stands are also lacking many old-growth features in respect of deadwood quality and quantity, density of the living stand, development stage, dimension and regeneration. All of these features are likely to approach the old-growth levels with further maturation. In the absence of large-scale disturbances, the disintegration of the dominant tree layer and the following tree regeneration is likely to proceed over many decades to centuries (Jönsson et al., 2009; Svoboda et al., 2010). There are considerable differences in the time of abandonment of the ND stands. Some of the strict forest reserves are without management since the early 70 s, whereas natural heritage sites became legally protected in 2009. Still, time since abandonment alone does not ultimately lead to a higher OGI score. All natural heritage sites in our study have been former military training areas, thus timber production was not the main focus in management. However, forests are still being managed until they fall into the category of ND. To interpret the OGI results for the comparison sites,

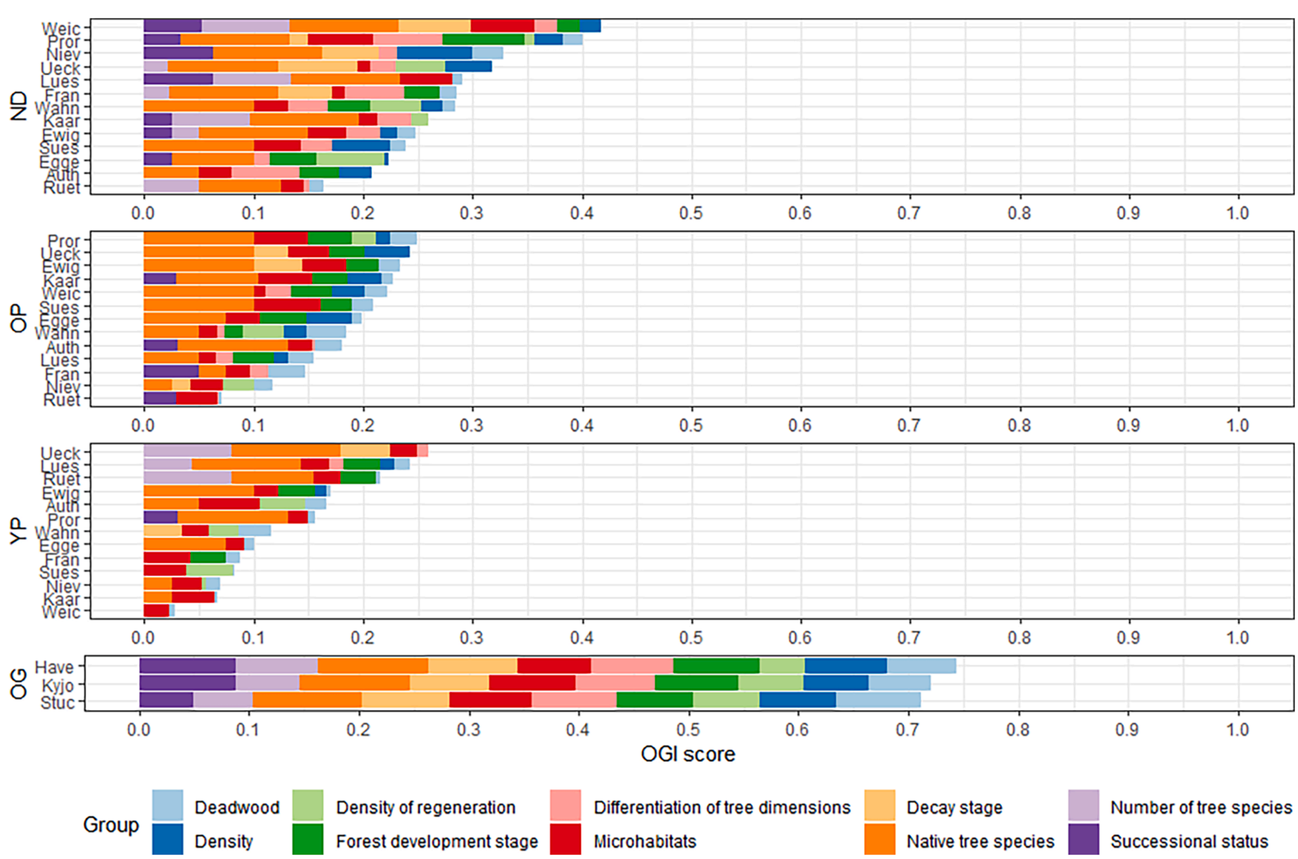

Fig. 7. Single and aggregated OGI scores for the three old-growth forest stands (OG) and the comparison stands in categories ND, OP and YP with equal weight of the ten thematic groups (abbreviations s. text).

forest management history has to be taken into account.

An even better foundation of the OGI approach, beyond the actual set of reference data, is highly desirable, as it can be assumed that there is considerable variability across and between single beech old-growth stands of different regions. There are several more ancient beech forests in Europe that are worth to include in a reference dataset (see Kirchmeier and Kovarovics (2016)). Thus, we would highly appreciate extending the reference data base by incorporating more stands and samples. For further research it would be very interesting to use forest inventory data from German forests with a long history of non-intervention, e.g. national park Kellerwald-Edersee, Grumsin forest, or national park Jasmund, and see how they resemble the old-growth reference sites according to the OGI.

We explicitly focused on the potential natural distribution range of beech forests. However, transferring the methodological approach to other forest types should be possible, provided that a comparable protocol is applied when collecting data from the respective old-growth reference stands. It is, however, not advisable to use the beech old-growth reference for other natural forest types, since parameter ranges may differ considerably. To further improve and generalize the indicator it could be worth to choose a set of variables that are applying not only to old-growth beech forests but to old-growth forests in general. Therefore a review of universally applicable old-growth forest attribute values and their value ranges in European old-growth forest remnants could be an interesting task to pursue in the future.

7. Conclusions

Larger areas of unaltered beech forests in the lowlands of central Europe are inexistent. Leaving a proportion of managed beech forests to natural succession and monitoring the development can help to better understand the passive restoration of a natural, self-regulated state (Meyer, 2020; Vandekerkhove et al., 2018). In Germany, the forests included in the national heritage sites have a great potential to become old-growth hotspots in future. They often provide the spatial extent that is necessary to allow natural spatio-temporal dynamics of beech forests. To improve the as yet poor understanding of natural forest dynamics, monitoring and research should be conducted in these forests. In this context, the OGI score could serve as an indicator for the development over time. It can also be applied for assessing the effectiveness of different conservation-oriented management regimes and restoration measures, e.g. leaving or creating deadwood or planting late-successional tree species. The sound evaluation of these often costly measures seems to be necessary (Culmsee et al. in prep.; Storch et al. 2020). In this context, it needs to be stressed that OGI does not provide a complete assessment of naturalness, as several other important facets, such as species diversity and composition or large-scale disturbances (Brumelis et al., 2011), are not covered. The indicator should, however, be suitable to monitor the pace and direction of forest development towards old-growthness. A great advantage of the OGI approach can be seen in its immediate application in an already well established work flow. Thus, data to calculate the OGI are already available for a large number of strict forest reserves, and also for several national parks and biosphere reserves (Meyer, 2020).

CRediT authorship contribution statement

Peter Meyer: Conceptualization, Methodology, Software. **Maria Aljes:** Visualization, Validation. **Heike Culmsee:** Project administration, Funding acquisition. **Eike Feldmann:** Investigation. **Jonas Glatthorn:** Investigation. **Christoph Leuschner:** Funding acquisition. **Heike Schneider:** Investigation.

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.

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Appendix Table 1. Characteristics of the 39 sampled stands in 13 study areas in the northern German lowlands, and the three Slovakian old-growth beech reference forests. Soil nutrient conditions based on information of forest site mapping. Predominant potential natural vegetation (PNV) follows Suck et al. (2010). Climate data (mean annual temperature and rainfall) from German national meteorological Service, DWD, based on the reference period 1981–2010

Study area (abbreviation)	Category	Potential natural vegetation	Dominant tree species	Mean stand age (years)	Last silvicultural intervention (year)	Soil nutrient conditions	Mean annual precipitation (mm yr^{-1})	Mean annual temperature (°C)
Wahner Heide (Wahn)	ND	*Stellario-Carpinetum*	European beech	146	<1995	Poor	866	10.3
	OP	*Milio-Fagetum*	Scots pine	133	2012		879	10.1
	YP	*Milio-Fagetum*	Scots pine	81	<1995		882	10.1
Franzhorn (Fran) (ND) and Cuxhavener Küstenheiden (Cuxh) (OP and YP)	ND	*Deschampsio-Fagetum*	European Beech	156	1972	Medium	857	9.1
	OP	*Deschampsio-Fagetum*	Black pine	100	2008		908	9.3
	YP	*Deschampsio-Fagetum*	Black pine	60	2014		884	9.4
Weichel (Weic)	ND	*Molinio-Fagetum*	European Beech	144	1986	Rich/ Medium	797	9.3

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Study area (abbreviation)	Category	Potential natural vegetation	Dominant tree species	Mean stand age (years)	Last silvicultural intervention (year)	Soil nutrient conditions	Mean annual precipitation (mm yr^{-1})	Mean annual temperature (°C)
	OP	*Molinio-Fagetum*	Scots pine	95	2013		798	9.2
	YP	*Deschampsio-Fagetum*	Scots pine	68	2012		822	9.2
Lüßberg (Lues)	ND	*Deschampsio-Fagetum*	European Beech	195	1972	Medium	813	8.7
	OP	*Deschampsio-Fagetum*	Scots pine	125	1992		809	9.0
	YP	*Deschampsio-Fagetum*	Scots pine	66	2015		808	8.7
Süsing (Sues)	ND	*Deschampsio-Fagetum*	European Beech	139	1996	Medium	775	8.9
	OP	*Deschampsio-Fagetum*	Scots pine	144	2015		795	8.9
	YP	*Deschampsio-Fagetum*	Scots pine	64	<2008		799	8.9
Ewige Route (Ewig)	ND	*Deschampsio-Fagetum*	European Beech	134	1996	Medium	728	8.9
	OP	*Deschampsio-Fagetum*	Scots pine	125	1996		724	8.8
	YP	*Deschampsio-Fagetum*	Scots pine	66	2003		712	8.9
Nievoldhagen (Niev)	ND	*Stellario-Carpinetum*	European Beech	124	1999	Rich/ Medium	624	9.1
	OP	*Milio-Fagetum*	Scots pine	93	n.a.		634	9.1
	YP	*Milio-Fagetum*	Scots pine	64	2011		605	9.4
Kaarzer Holz (Kaar)	ND	*Galio-Fagetum*	European beech	112	2004	Medium	659	8.9
	OP	*Galio-Fagetum*	Scots pine	155	2012		650	8.9
	YP	*Galio-Fagetum*	Scots pine	68	2006		653	8.9
Authausener Wald (Auth)	ND	*Luzulo-Fagetum*	European beech	166	2006	Medium	657	9.3
	OP	*Luzulo-Fagetum*	Scots pine	96	2011		651	9.3
	YP	*Luzulo-Fagetum*	Scots pine	55	2013		653	9.3
Rüthnicker Heide (Ruet)	ND	*Maianthemo-Fagetum*	Sessile Oak	119	<2001	Medium	587	9.2
	OP	*Maianthemo-Fagetum*	Scots pine	126	2012		581	9.3
	YP	*Maianthemo-Fagetum*	Scots pine	63	2010		585	9.3
Prora (Pror)	ND	*Milio-Fagetum*	European beech	142	2004	Medium	660	8.7
	OP	*Milio-Fagetum*	Scots pine	102	2011		661	8.6
	YP	*Milio-Fagetum*	Scots pine	63	2013		674	8.6
Eggesiner Forst (Egge)	ND	*Maianthemo-Fagetum*	European beech	104	2011	Poor	566	8.1
	OP	*Maianthemo-Fagetum*	Scots pine	115	2009		567	8.8
	YP	*Milio-Fagetum*	Scots pine	62	2013		555	8.8
Ueckermünder Heide (Ueck)	ND	*Galio-Fagetum*	European beech	150	2005	Medium	571	8.7
	OP	*Maianthemo-Fagetum*	Scots pine	90	2009			8.9
	YP	*Milio-Fagetum*	Scots pine	62	2008		558	8.8
Havešová (Have)		*Fagetum dentariosum glandulosae*	European beech	app. 400	none	Rich/ Medium	825	6.3
Kyjov (Kyjo)		*Fagetum dentariosum glandulosae*	European beech	app. 400	none	Medium	975	5.5
Stužica (Stuz)		*Fagetum dentariosum glandulosae*	European beech	app. 400	none	Rich/ Medium	1050	4.5

Appendix Table 2. 134 structural attributes calculated from forest inventory data

Number	Forest structural attribute
1	Stem number n per ha in living stand with dbh ≥ 7 cm
2	Basal area in m^2 per ha in living stand with dbh ≥ 7 cm
3	Wood volume in m^3 per ha in living stand with dbh ≥ 7 cm
4	Stand Density Index (according to Zeide, 2005)

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Number	Forest structural attribute
5–6	Number of tree species in regeneration and number of tree species in living stand
7	Number of trees in regeneration < 0.5 m height per ha
8	Number of trees in regeneration between 0.5 m and < 1.5 m height per ha
9	Number of trees in regeneration ≥ 1.5 m height and dbh < 7 cm per ha
10	Diameter of stem with mean basal area in cm
11–12	Minimum diameter in cm and maximum diameter in cm
13	Standard deviation of mean diameter in the living stand with dbh > 7 cm
14	Stem number n per ha of standing deadwood with dbh ≥ 7 cm and < 20 cm
15	Volume m^3 per ha standing deadwood with dbh ≥ 7 cm and < 20 cm
16	Stem number n per ha of standing deadwood with dbh ≥ 20 cm and < 50 cm
17	Volume m^3 per ha standing deadwood with dbh ≥ 20 cm and < 50 cm
18	Stem number n per ha of standing deadwood with dbh ≥ 50 cm
19	Volume m^3 per ha standing deadwood with dbh ≥ 50
20	Stem number n per ha of lying deadwood with led ≥ 20 cm and < 50 cm
21	Volume m^3 per ha lying deadwood with led ≥ 20 cm and < 50 cm
22	Stem number n per ha of standing deadwood with led ≥ 50 cm
23	Volume m^3 per ha standing deadwood with led ≥ 50
24	Volume standing and lying deadwood in m^3 per ha
25	Number of root plates per ha
26	Number of stems with cavities per ha
27	Number of stems with trunk cavity per ha
28	Number of stems with conks of fungi per ha
29	Number of trees with dbh ≥ 80 cm
30–34	Percentage of number of stems in forest development stage 1, 2, 3, 4 and 5
35–39	Percentage of basal area of stems in forest development stage 1, 2, 3, 4 and 5
40–56	Share of beech, hornbeam, oak, maple species, ash, elm, lime, bird cherry, shrubs, pioneer species, native tree species, neophytic tree species, spruce, fir, douglas fir, pine and larch as percentage of total stem number
57–73	Share of beech, hornbeam, oak, maple species, ash, elm, lime, bird cherry, shrubs, pioneer species, native tree species, neophytic tree species, spruce, fir, douglas fir, pine and larch as percentage of total basal area
74–90	Number of beech, hornbeam, oak, maple species, ash, elm, lime, bird cherry, shrubs, pioneer species, native tree species, neophytic tree species, spruce, fir, douglas fir, pine and larch trees < 0.5 m height per ha
91–107	Number of beech, hornbeam, oak, maple species, ash, elm, lime, bird cherry, shrubs, pioneer species, native tree species, neophytic tree species, spruce, fir, douglas fir, pine and larch trees between 0.5 m and 1.5 m height per ha
108–124	Number of beech, hornbeam, oak, maple species, ash, elm, lime, bird cherry, shrubs, pioneer species, native tree species, neophytic tree species, spruce, fir, douglas fir, pine and larch trees ≥ 1.5 m height per ha
125–129	Percentage of lying deadwood in decay stage 1, 2, 3a, 3b and 4 per total number of pieces
130–134	Percentage of lying deadwood in decay stage 1, 2, 3a, 3b and 4 per total volume of pieces

Appendix Table 3. Overview of the 41 forest structural attributes tested for significant differences between the three old-growth stands ($p \leq 0.05$) and tested for multicolinearity and intercorrelation within their thematic group. Attributes showing no significant differences between old-growth stands and are not correlated within the group are indicated by +, those which do are indicated by – If both criteria were met with a +, the attribute was included in the final selection for the old-growth indicator.

Thematic group	Attribute	Typical for old-growth	No multicolinearity/not strongly correlated	Final selection
Deadwood	Stem number n per ha of standing deadwood with dbh ≥ 7 cm and < 20 cm	+	+	+
	Stem number n per ha of standing deadwood with dbh ≥ 20 cm and < 50 cm	+	+	+
	Stem number n per ha of standing deadwood with dbh ≥ 50 cm	+	+	+
	Stem number n per ha of lying deadwood with led ≥ 20 cm and < 50 cm	+	+	+
	Stem number n per ha of standing deadwood with led ≥ 50 cm	+	+	+
	Volume m^3 per ha standing deadwood with dbh ≥ 7 cm and < 20 cm	+	–	–
	Volume m^3 per ha standing deadwood with dbh ≥ 20 cm and < 50 cm	+	–	–
	Volume m^3 per ha standing deadwood with dbh ≥ 50	+	–	–
	Volume m^3 per ha lying deadwood with ≥ 20 cm and < 50 cm at butt end	+	–	–
	Volume m^3 per ha standing deadwood with ≥ 50 at butt end	+	–	–
	Volume standing and lying deadwood in m^3 per ha	+	+	+
Decay stage	Number of different decay stages of downed logs	–	+	–
	Mean decay stage of downed logs	+	+	+
Density	Stem number n per ha in living stand with dbh ≥ 7 cm	+		+
	Basal area in m^2 per ha in living stand with dbh ≥ 7 cm	+	–	–
	Wood volume in m^3 per ha in living stand with dbh ≥ 7 cm	+	+	+
	Stand Density Index (according to Zeide, 2005)	+	–	–
Differentiation of tree dimensions	Diameter span from minimum to maximum dbh	+	+	+
	Standard deviation of mean diameter in the living stand with dbh > 7 cm	+	–	–
	Minimum diameter in cm	+	+	+
	Maximum diameter in cm	+	+	+
	Diameter of stem with mean basal area in cm	+	+	+
	Number of trees with dbh ≥ 80 cm	+	+	+
Forest development stage	Number of different forest development stages	+	+	+
	Mean of the numbers 1 to 5 weighted by the basal area proportions in the respective forest development stage	+	–	–

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Thematic group	Attribute	Typical for old-growth	No multicolinearity/not strongly correlated	Final selection
	Mean of the numbers 1 to 5 weighted by the stem number proportions in the respective forest development stage	+	+	+
Microhabitats	Number of root plates per ha	+	+	+
	Number of stems with stem and/or trunk cavities per ha	+	+	+
	Number of stems with conks of fungi per ha	+	+	+
Native tree species	Share of native species in the living stand as percentage of total stem number	+	+	+
	Share of native species in the living stand as percentage of total basal area	+	–	–
	Share of native species in regeneration as percentage of total stem number	+	+	+
Number of tree species	Number of different tree species in the living stand	+	+	+
	Number of different tree species in regeneration	–	+	–
Successional status	Mean of successional status 1 to 3 weighted by stem number proportion of trees in the respective successional status of the living stand	+	+	+
	Mean of successional status 1 to 3 weighted by basal area proportion of trees in the respective successional status of the living stand	+	–	–
	Successional status of trees in regeneration	+	+	+
Density of regeneration	Number of trees < 0.5 m height per ha	–	+	–
	Number of trees ≥ 0.5 m and < 1.5 m height per ha	+	+	+
	Number of trees ≥ 1.5 m height per ha	+	+	+
	Total number of trees in regeneration per ha	+	+	+

References

Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E., Piovesan, G., 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. For. Ecol. Manage. 262, 1950–1962. https://doi.org/10.1016/j.foreco.2011.08.025.

Ammer, C., Fichtner, A., Fischer, A., Gossner, M.M., Meyer, P., Seidl, R., Wagner, S., 2018. Key ecological research questions for Central European forests. Basic Appl. Ecol. 32, 3–25. https://doi.org/10.1016/j.baae.2018.07.006.

Angermeier, P.L., 2000. The natural imperative for biological conservation. Conserv. Biol. 14, 373–381.

Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manage. 258, 525–537. https://doi.org/10.1016/j.foreco.2009.01.053.

Blasi, C., Marchetti, M., Chiavetta, U., Aleffi, M., Audisio, P., Azzella, M.M., Burrascano, S., 2010. Multi-taxon and forest structure sampling for identification of indicators and monitoring of old-growth forest. Plant Biosyst. 144, 160–170.

Bohn, U., Neuhäusl, R., Gollub, R., Hettwer, C., Neuhäuslova, Z., Schlüter, H., Weber, H., 2003. Karte der natürlichen Vegetation Europas. Teil 1: Erläuterungstext. Landwirtschaftsverlag, Münster.

Brumelis, G., Jonsson, B., Kouki, J., Kuuluvainen, T., Shorohova, E., 2011. Forest naturalness in northern Europe: perspectives on processes, structures and species diversity. Silva Fennica 45. https://doi.org/10.14214/sf.446.

Bundesamt für Naturschutz (BfN) (Ed.), 2008. Beech Forests - German contribution to the global forest biodiversity. BfN-Skripten 233, 86 pp.

Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit (BMU) (Ed.), 2007. Nationale Strategie zur biologischen Vielfalt.

Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. For. Ecol. Manage. 291, 458–479. https://doi.org/10.1016/j.foreco.2012.11.020.

Chiavetta, U., Sallustio, L., Garfì, V., Maesano, M., Marchetti, M., 2012. Classification of the oldgrowthness of forest inventory plots with dissimilarity metrics in Italian National Parks. Eur. J. Forest Res. 131, 1473–1483. https://doi.org/10.1007/s10342-012-0616-7.

Culmsee, H., Denstorf, H.O., Mann, P., Schmid, L., 2015. Wälder des Nationalen Naturerbes. Natur und Landschaft 90, 8.

da Silva, L.P., Heleno, R.H., Costa, J.M., Valente, M., Mata, V.A., Gonçalves, S.C., Ramos, J.A., 2019. Natural woodlands hold more diverse, abundant, and unique biota than novel anthropogenic forests: a multi-group assessment. Eur. J. Forest Res. 138, 461–472. https://doi.org/10.1007/s10342-019-01183-5.

Efron, E., Tibshirani, R.J. In: Efron, E. & Tibshirani, R.J., An Introduction to the Bootstrap. Chapmann & Hall, CRC. Boca Raton, Confidence intervals based on bootstrap percentiles 1993 London, New York, Washington D. C.

Feldmann, E., Glatthorn, J., Hauck, M., Leuschner, C., 2018. A novel empirical approach for determining the extension of forest development stages in temperate old-growth forests. Eur. J. Forest Res. 137, 321–335. https://doi.org/10.1007/s10342-018-1105-4.

Franklin, J.F., Van Pelt, R., 2004. Spatial aspects of structural complexity in old-growth forests. J. Forest. 22–28.

Gauer, J., Aldinger, E., 2005. Waldökologische Naturräume Deutschlands – Forstliche Wuchsgebiete und Wuchsbezirke mit Karte im Maßstab 1:1000.000. Verein für Forstliche Standortkunde und Forstpflanzenzüchtung, Freiburg, Germany.

Geburek, T., Milasowszky, N., Frank, G., Konrad, H., Schadauer, K., 2010. The Austrian Forest Biodiversity Index: All in one. Ecol. Ind. 10, 753–761. https://doi.org/10.1016/j.ecolind.2009.10.003.

Glatthorn, J., Pichler, V., Hauck, M., Leuschner, C., 2017. Effects of forest management on stand leaf area: Comparing beech production and primeval forests in Slovakia. For. Ecol. Manage. 389, 76–85. https://doi.org/10.1016/j.foreco.2016.12.025.

Glatthorn, J., Feldmann, E., Tabaku, V., Leuschner, C., Meyer, P., 2018. Classifying development stages of primeval European beech forests: is clustering a useful tool? BMC Ecol. 18, 47–60. https://doi.org/10.1186/s12898-018-0203-y.

Goff, F.G., West, D., 1975. Canopy-understory interaction effects on forest population structure. For. Sci. 21, 98–108.

Gossner, M.M., Schall, P., Ammer, C., Ammer, U., Engel, K., Schubert, H., Weisser, W.W., 2014. Forest management intensity measures as alternative to stand properties for quantifying effects on biodiversity. Ecosphere 5, 1–111. https://doi.org/10.1890/ES14-00177.1.

Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. J. Appl. Ecol. 55, 2756–2766.

Hobi, M.L., Commarmot, B., Bugmann, H., 2015. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). J. Veg. Sci. 26, 323–336. https://doi.org/10.1111/jvs.12234.

Institute of Forest Research (IFER). Field-Map. Jílové u Prahy, Czech Republic. www.field-map.com.

Jaloviar, P., Saniga, M., Kucbel, S., Pittner, J., Vencurik, J., Dovciak, M., 2017. Seven decades of change in a European old-growth forest following a stand-replacing wind disturbance: A long-term case study. For. Ecol. Manage. 399, 197–205. https://doi.org/10.1016/j.foreco.2017.05.036.

Jönsson, M.T., Fraver, S., Jonsson, B.G., 2009. Forest history and the development of old-growth characteristics in fragmented boreal forests. J. Veg. Sci. 20, 91–106. https://doi.org/10.1111/j.1654-1103.2009.05394.x.

Kahl, T., Bauhus, J., 2014. An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. Nature Conserv. 7, 15–27. https://doi.org/10.3897/natureconservation.7.7281.

Keren, S., Diaci, J., 2018. Comparing the quantity and structure of deadwood in selection managed and old-growth forests in south-East Europe. Forests 9, 76. https://doi.org/10.3390/f9020076.

Kirchmeier, H., Kovarovics, A. (Eds.), 2016. Nomination Dossier "Primeval Beech Forests of the Carpathians and Other Regions of Europe" as extension to the existing Natural World Heritage Site "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany". Klagenfurth.

Korpel, S., 1995. Die Urwälder der Westkarpaten. Gustav Fischer Verlag.

Kowarik, I., 1999. Natürlichkeit, Naturnähe und Hemerobie als Bewertungskriterien, in: Konold, W., Böcker, R., Hampicke, U. (Eds.). Handbuch Naturschutz und Landschaftspflege. ecomed-Verlag, Landsberg, 1-18.

Král, K., Janík, D., Vrška, T., Adam, D., Hort, L., Unar, P., Šamonil, P., 2010. Local variability of stand structural features in beech dominated natural forests of Central Europe: Implications for sampling. For. Ecol. Manage. 260, 2196–2203. https://doi.org/10.1016/j.foreco.2010.09.020.

Kucbel, S., Saniga, M., Jaloviar, P., Vencurik, J., 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective. For. Ecol. Manage. 264, 125–133. https://doi.org/10.1016/j.foreco.2011.10.011.

Kunttu, P., Junninen, K., Kouki, J., 2015. Dead wood as an indicator of forest naturalness: A comparison of methods. For. Ecol. Manage. 353, 30–40. https://doi.org/10.1016/j.foreco.2015.05.017.

Larrieu, L., Gonin, P., 2008. L'indice de Biodiversité Potentielle (IBP): une méthode simple et rapide pour évaluer la biodiversité potentielle des peuplements forestiers. Rev. For. Fr. 6, 727–748.

Larrieu, L., Gosselin, F., Archaux, F., Chevalier, R., Corriol, G., Dauffy-Richard, E., Bouget, C., 2019. Assessing the potential of routine stand variables from multi-taxon

data as habitat surrogates in European temperate forests. Ecol. Ind. 104, 116–126. https://doi.org/10.1016/j.ecolind.2019.04.085.
Leibundgut, H., 1993. Europäische Urwälder Wegweiser zur naturnahen Waldwirtschaft. Verlag Paul Haupt, Bern und Stuttgart.
Leuschner, C., 2015. Monospecific and mixed stands of Fagus and Nothofagus species in the temperate zones of the world. Berichte der Reinhold-Tüxen-Gesellschaft 27, 49–63.
Liira, J., Sepp, T., 2009. Indicators of structural and habitat natural quality in boreo-nemoral forests along the management gradient. Annales Botanici Fennici 46, 308–325. https://doi.org/10.5735/085.046.0407.
Lindenmayer, D., Hunter, M., 2010. Some guiding concepts for conservation biology. Conserv. Biol. 24, 1459–1468.
Machado, A., 2004. An index of naturalness. J. Nature Conserv. 12, 95–110. https://doi.org/10.1016/j.jnc.2003.12.002.
Markgraf, F., 1931. Aus den südosteuropäischen Urwäldern – Die Wälder Albaniens. Zeitschrift für das Forst- und Jagdwesen 73.
McRoberts, R.E., Winter, S., Chirici, G., LaPoint, E., 2012. Assessing forest naturalness. Forest Sci. 58, 294–309. https://doi.org/10.5849/forsci.10-075.
Meyer, P., 2020. Stubborn and adaptive – Five decades of monitoring and research of self-regulated tree demography. German J. Forest Res. 190 (5/6), 120–135.
Meyer, P., Brößling, S., Bedarff, U., Fricke, C., Tewes, C., Nagel, R., 2021. Monitoring of forest structure and vegetation in Hessian strict forst reserves. Hann. Münden, download under, Norwestdeutsche Forstliche Versuchsanstalt https://www.nw-fva.de/index.php?id=683.
Motta, R., Garbarino, M., Berretti, R., Meloni, F., Nosenzo, A., Vacchiano, G., 2015. Development of old-growth characteristics in uneven-aged forests of the Italian Alps. Eur. J. Forest Res. 134, 19–31. https://doi.org/10.1007/s10342-014-0830-6.
Müller-Using, S., Bartsch, N., 2009. Decay dynamic of coarse and fine woody debris of a beech (Fagus sylvatica L.) forest in Central Germany. Eur. J. Forest Res. 128, 287–296.
Nagel, T.A., Levanic, T., Diaci, J., 2007. A dendroecological reconstruction of disturbance in an old-growth Fagus-Abies forest in Slovenia. Ann. Forest Sci. 64, 891–897. https://doi.org/10.1051/forest:2007067.
Nagel, T.A., Svoboda, M., Diaci, J., 2006. Regeneration patterns after intermediate wind disturbance in an old-growth Fagus-Abies forest in southeastern Slovenia. For. Ecol. Manage. 226, 268–278. https://doi.org/10.1016/j.foreco.2006.01.039.
Forstplanungsamt, N., 2001. (NFP) Anweisung zur Betriebsinventur. Unpublished 88, pp.
Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ranius, T., 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. For. Ecol. Manage. 161, 189–204. https://doi.org/10.1016/S0378-1127(01)00480-7.
Peterken, G.F., 1996. Natural woodland: ecology and conservation in northern temperate regions. Cambridge University Press, New York.
Peters, R., 1992. Ecology of beech forests in the northern hemisphere. Wageningen.
R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Reif, A., Walentowski, H., 2008. The assessment of naturalness and its role for nature conservation and forestry in Europe. Waldökologie, Landschaftsforschung und Naturschutz 6, 63–76.
Rüdisser, J., Tasser, E., Tappeiner, U., 2011. Distance to nature – A new biodiversity relevant environmental indicator set at the landscape level. Ecol. Ind. 15, 208–216. https://doi.org/10.1016/j.ecolind.2011.09.027.
Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Kuemmerle, T., 2018. Where are Europe's last primary forests? Divers. Distrib. 24, 1426–1439. https://doi.org/10.1111/ddi.12778.
Šamonil, P., Antolík, L., Svoboda, M., Adam, D., 2009. Dynamics of wind throw events in a natural fir-beech forest in the Carpathian mountains. For. Ecol. Manage. 257, 1148–1156. https://doi.org/10.1016/j.foreco.2008.11.024.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Change 7, 395–402. https://doi.org/10.1038/nclimate3303.
Smejkal, G.M., Bindiu, C., Visoiu-Smejkal, D., 1997. Banater Urwälder - Ökologische Untersuchungen in Rumänien. Mirton Verlag, Temeswar.
Spies, T.A., 2004. Ecological concepts and diversity of old-growth forests. Forestry 14–20.
Storch, I., Penner, J., Asbeck, T., Basile, M., Bauhus, J., Braunisch, V., Yousefpour, R., 2020. Evaluating the effectiveness of retention forestry to enhance biodiversity in production forests of Central Europe using an interdisciplinary, multi-scale approach. Ecol. Evol. 10 (3), 1489–1509. https://doi.org/10.1002/ece3.6003. PMID: 32076529; PMCID: PMC7029101.
Suck, R., Bushart, M., Hofmann, G., Schröder, L., Bohn, U., 2010. Karte der Potentiellen Natürliche Vegetation Deutschlands im Maßstab 1: 500.000, Karten+ Legende. B. f. Naturschutz.
Svoboda, M., Fraver, S., Janda, P., Bace, R., Zenáhlíková, J., 2010. Natural development and regeneration of a Central European montane spruce forest. For. Ecol. Manage. 260, 707–714.
Svoboda, M., Janda, P., Bace, R., Fraver, S., Nagel, T.A., Rejzek, J., Lehejcek, J., 2014. Landscape-level variability in historical disturbance in primary Picea abies mountain forests of the Eastern Carpathians, Romania. J. Veg. Sci. 25, 386–401. https://doi.org/10.1111/jvs.12109.
Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Swanson, F.J., 2011. The forgotten stage of forest succession: Early-successional ecosystems on forest sites. Front. Ecol. Environ. 9, 117–125. https://doi.org/10.1890/090157.
Thorn, S., Seibold, S., Leverkus, A. B., Michler, T., Müller, J., Noss, R. F., Stork, N., Vogel, S., Lindemayer, D. B., 2020. The living dead: acknowledging life after tree death to stop forest degradation. Frontiers in Ecology and the Environment 18(9), pp. 505-512.
Vandekerkhove, K., Vanhellemont, M., Vrška, T., Meyer, P., Tabaku, V., Thomaes, A., … and Verheyen, K., 2018. Very large trees in a lowland old-growth beech (Fagus sylvatica L.) forest: Density, size, growth and spatial patterns in comparison to reference sites in Europe. Forest Ecology and Management 417, 1–17. https://doi.org/10.1016/j.foreco.2018.02.033.
Westphal, C., Härdtle, W., Oheimb v., G., 2004. Forest History, Continuity and Dynamic Naturalness, in O. Honnay K. Verheyen B. Bossuyt M. Hermy Forest Biodiversity 2004 CAB International 205 220.
Westphal, C., Tremer, N., Oheimb, V.G., Hansen, J., Gadow, V.K., Härdtle, W., 2006. Is the reserve J-shaped diameter distribution universally applicable in European virgin beech forests? For. Ecol. Manage. 223, 75–83.
Winter, S., 2012. Forest naturalness assessment as a component of biodiversity monitoring and conservation management. Forestry 85, 293–304. https://doi.org/10.1093/forestry/cps004.
Wirth, C., Messier, C., Bergeron, Y., Frank, D., Frankhänel, A., 2009. Old-growth forest definitions: a pragmatic view. Ecological Studies 209, 11–33.
Wooldridge, J.M., 2013. Introductory Econometrics. A modern approach, 5th edition. South Western, Cengage Learning, USA, p. 881.
Zeide, B., 2005. How to measure stand density. Trees 19, 1–14. https://doi.org/10.1007/s00468-004-0343-x.
Zenner, E.K., Peck, J.E., Hobi, M.L., Commarmot, B., 2014. The dynamics of structure across scale in a primeval European beech stand. Forestry 88, 180–189. https://doi.org/10.1093/forestry/cpu042.