



## Index of biodiversity potential (IBP) versus direct species monitoring in temperate forests

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### ABSTRACT

Effects of forest management on forest biodiversity have received increasing attention in both research and forestry practice. Despite advances in technology, monitoring of biodiversity remains time and cost-intensive and requires specific taxonomic expertise. In forest management, however, there is increasing interest and need to integrate biodiversity monitoring into forest inventories efficiently to estimate the potential effects of forest management on biodiversity. Forest management systems can differ greatly depending on management goals and the intensity and frequency of the applied silvicultural interventions. To identify management effects on biodiversity, an estimation of biodiversity using forest structural attributes may be a reasonable approach. Forest structure can – compared to conventional species-based monitoring – easily be captured during forest inventories and does not require specific taxonomic expertise. The IBP (Index of Biodiversity Potential) is a composite index aiming to provide practitioners with an efficient tool for estimating biodiversity at the local level. We recorded the IBP on 147 plots in three regions of Germany, where detailed biodiversity monitoring had been conducted. This study quantified the relationship between changes in the IBP scores and changes in species richness for 13 taxonomic groups. To determine this, we analyzed estimated relationships between the IBP and species richness using a count regression model. We found positive estimated relationships with species richness of birds, fungi, true bugs, lichens, and moths in at least 3 of 5 examined forest types. However, for spiders, bats, carabids, necrophagous and saproxylic beetles, either no relationship with the IBP or estimated relationships with only one forest type were found. Changes in scores for the IBP's factors number of vertical layers, large living trees, tree-related microhabitats, and proportion of gaps correlated with changes in the measured species richness in many cases. Even though the IBP is generally not adequate to predict actual presence or precise number of species, it can be utilized to depict a forest stand's potential in terms of species richness. Due to its easy and time-efficient application, it could be a useful proxy used in combination with species-based monitoring approaches.

### 1. Introduction

Most European forests are currently managed; pristine forests are rare (Sabatini et al., 2021). Since both production forestry and nature

conservation are needed to meet the various needs of modern society; forest management must therefore address both (Aggestam et al., 2020; Felipe-Lucia et al., 2018; Manning et al., 2018). The provision of multiple ecosystem functions and services can be achieved either through

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segregation or integration approaches (Kraus and Krumm, 2013; Simons et al., 2021). Segregation largely decouples timber production and other ecosystem services such as nature conservation, while integration aims to deliver multiple forest ecosystem services at the same time and place. Integrated forest use has been pursued in many parts of the world through close-to-nature forestry (Schütz et al., 2016), or continuous cover forestry (Pommerening and Murphy, 2004; von Gadow et al., 2002). Recent extreme climatic events with subsequent pest insect outbreaks or windthrow have emphasized the urgency of making forest ecosystems more stable and resilient. Furthermore, worldwide loss of forest biodiversity (FAO and UNEP, 2020; Tittensor et al., 2014), can have drastic negative effects on wood production and other ecosystem functions and services (Gamfeldt et al., 2013; Paquette and Messier, 2011).

Even though potential future economic losses induced by biodiversity reduction are difficult to measure, efforts are being made to quantify the value of benefits provided by well-functioning forest ecosystems (Hahn, 2006; Paul et al., 2020). Such approaches increase awareness of the need for ecosystem protection before they undergo irreversible damage. Politicians and forestry stakeholders have begun to react via regulations and certification schemes for sustainable forest management following the UN Conference on Environment and Development 1992 in Rio de Janeiro (Bundesministerium für Ernährung, Landwirtschaft und Verbraucherschutz (BMELV), 2011; MCPFE, 2015). In addition, forestry practices have begun to integrate biodiversity assessments into silvicultural management (BMUB, 2007). Due to the extent of its activities, forest management has a great impact on how forest ecosystems will develop in the future; it therefore has huge potential for tracking the state of our forests' biodiversity.

The meta-analyses of Chaudhary et al. (2016), Dieler et al. (2017), and Paillet et al. (2010) have improved our understanding of the management-biodiversity relationship. Since the effects of management intensity and management type vary greatly depending on the political framework, region, management aims, and local growing conditions, classification and quantification of management actions remain difficult. A simple comparison between managed and unmanaged forest stands therefore often falls short in specifying how different management regimes and actions can foster or hinder forest biodiversity in detail. Approaches to define pure and mixed-forest typologies have been made e.g. by de Cáceres et al. (2019), which would be useful in categorizing the outcome of different management regimes.

In any case, forest management directly influences stand structural attributes including composition, which in turn shape regeneration and further development of a forest stand (Stiers et al., 2018; Willim et al., 2019). Especially the hydraulic efficiency, which is of importance in times of frequent droughts, is influenced by species- and stand level mixing (De Cáceres et al., 2021). As forest biodiversity can be considered to consist of compositional, structural, and functional diversity at different spatial scales (Ćosović et al., 2020; Noss, 1990), within and between stand structural diversity can be seen as a direct link to biodiversity and ecosystem functioning (Schall et al., 2018a). The estimated relationship between forest structural attributes and biodiversity – regardless of whether that structure results from natural succession or forest management – has been studied in detail (Larrieu et al., 2019; Penone et al., 2019) and summarized by Burrascano et al. (2013). In addition to forest composition and thus stand type (Ammer and Schubert, 1999; Kriegel et al., 2021), type and amount of deadwood (Müller et al., 2015), tree-related microhabitats in large living trees (Winter and Möller, 2008), canopy openness (Bouget et al., 2014; Seibold et al., 2014), vertical structure (Knuff et al., 2020), and habitat heterogeneity in general (Begehold, 2017; Heidrich et al., 2020; Jung et al., 2012; Larrieu et al., 2015; Márialigeti et al., 2009), are important for species richness and species abundance.

Stand structural attributes can be quantified precisely (del Río et al., 2016; Schall et al., 2018b) during inventories and more easily than compositional or functional diversity. National forest inventories (NFIs)

such as the BWI (federal forest inventory) in Germany currently record structural attributes and habitat characteristics known to be relevant for biodiversity; e.g., amount of deadwood and tree species composition (BMEL, 2014). However, the validity of structural attributes or other forest inventory-based variables as proxies for biodiversity is controversial (Angelstam and Dönnz-Breuss, 2004; Noss, 1990). Some studies have found only weak links between structure and species diversity (Keren et al., 2020) while other studies have found positive correlations (Gao et al., 2014). These contradictory results have motivated researchers to learn more about structure-biodiversity relationships.

One attempt to capture the most important stand structures and context-related factors that potentially influence biodiversity was made by Larrieu and Gonin (2008). Their estimation-based index, the IBP (Index of Biodiversity Potential) was originally created as a tool to help forest managers take biodiversity into account during routine work (Larrieu et al., 2012). The IBP protocol consists of 10 factors considered among the most common structural drivers of forest biodiversity. They are easy and quick to record in the field, and do not require additional equipment or special taxonomic expertise to get the IBP score. This index, therefore, has great potential for practitioners and consultants. It is also used by scientists as rapid stand description protocol to analyze surrogacy patterns of presumed key attributes for biodiversity in both managed and unmanaged forests (Bouget et al., 2014). Due to its ease of recording, it also could be included in production-oriented forest inventories. Further research is needed, however, as comparisons of forest structure-based monitoring methods with taxonomic biodiversity monitoring are rare (Gao et al., 2015; Larrieu et al., 2019). Formerly conducted studies on the IBP aimed to calibrate the index with taxonomic data by quantifying the capacity of each of the factors gathered in the index to co-vary with empirical species richness and composition (Herrault et al., 2016; Larrieu et al., 2019). They used the number of items recorded in the field per factor, e.g. the total number of very large trees per ha, as dependent variables. This study is the first to assess whether changes in IBP scores reflect changes in species richness and therefore used IBP scores as dependent variables. Species of interest included spiders, bats, birds, bryophytes, carabids, fungi, true bugs, lichens, moths, necrophagous beetles, phytophagous beetles, plants, and saproxylic beetles. The research framework provided by the Biodiversity Exploratories provides valuable and unique data to compare the IBP to direct species monitoring. Our study therefore contributes to addressing the challenge of developing indices that shall depict biodiversity without actually sampling species. The following research questions were investigated:

- (I) Do variations in the IBP score reflect differences in species richness of the different taxonomic groups measured in conventional monitoring?
- (II) Are specific scores of the IBP's factors especially relevant in predicting species richness of different taxonomic groups?

## 2. Materials and methods

### 2.1. Study regions and experimental plots

To test the sensibility by comparing the IBP to conventionally monitored biodiversity data, we recorded the IBP at 147 experimental forest plots in three regions of Germany (<https://www.biodiversity-exploratories.de/en/regions/overview/>), within the Biodiversity Exploratories' framework (Biodiversity Exploratories, 2020; Fischer et al., 2010). These regions are: 1) The UNESCO Biosphere Reserve Schorfheide-Chorin in northwest Germany, 2) the Hainich-Dün Region including the Hainich National Park and surrounding managed forests, and 3) the UNESCO Biosphere reserve Swabian Alb in southwestern Germany, which are henceforth called "Schorfheide", "Hainich", and "Alb". The 3 regions as influencing variables were categorically scaled to be included in the model function as 3 levels.

Each of the three locations contains 50 experimental plots,

**Table 1**

IBP categories and factor definitions of the ten factors that constitute the Index of Biodiversity Potential (IBP; Larrieu and Gonin, 2008) v.3 Atlantic and Continental lowland context, and scoring system; dbh: diameter at breast height.

Categories	Type of factor	Factor	Succinct definition	Scoring system
Stand and its current management	compositional	A: Tree richness	Number of autochthonous tree genera (dead or living trees)	1 or 2 genera: 0 points 3 or 4 genera: 2 5 genera and more: 5
	structural	B: Vertical structure	Number of vegetation layers (max 5 layers)	1 layers: 0 2 layers: 1 3 or 4 layers: 2 5 layers: 5
		C: Standing deadwood	Number of small snags (SS; 17.5 cm < dbh < 37.5 cm) and large snags (LS; dbh ≥ 40 cm)	LS/ha < 1 and SS/ha < 1 : 0 LS/ha < 1 and SS/ha ≥ 1 : 1 1 ≤ LS/ha < 3 : 2 LS/ha ≥ 3 : 5
		D: Lying deadwood	Number of small logs (SL; 17.5 cm < d < 37.5 cm) and large logs (LL; d ≥ 40 cm); diameter at the larger end	LL/ha < 1 and SL/ha < 1 : 0 LL/ha < 1 and SL/ha ≥ 1 : 1 1 ≤ LL/ha < 3 : 2 LL/ha ≥ 3 : 5
	E: Very large trees	Number of trees with 47.5 cm < dbh < 67.5 cm (LT) and dbh ≥ 70 cm (VLT)	VLT/ha < 1 et LT/ha < 1 : 0 VLT/ha < 1 et LT/ha ≥ 1 : 1 1 ≤ VLT/ha < 5 : 2 VLT/ha ≥ 5 : 5	
	F: Habitat-trees (HT)	Number of live trees with at least one tree-related microhabitat (reference list of tree-microhabitats to observe)	<1 HT/ha: 0 ≥ 1 and < 2 HT /ha: 1 ≥ 2 and < 6 HT/ha: 2 At least 6 HT /ha: 5	
	G: Openness	% per ha of open areas (clearings, edges and other areas with a well-developed herb layer composed of flowering plants)	0% : 0 < 1% or > 5% : 2 1 to 5%: 5	
Context	historical	H: Temporal continuity of the woody state	Presence of the stand on an ancient map (19th c.)	Absence: 0 Edge of an ancient forest: 1 Ancient forest partially cleared or replanted after tillage: 2 Ancient forest never cleared: 5
	structural	I: Wet macrohabitats	Number of wet-habitat types (reference list of macrohabitats to observe)	none: 0 only 1 type: 2 2 or more types : 5
		J: Rocky macrohabitats	Number of rocky-habitat types (reference list of macrohabitats to observe)	none: 0 only 1 type: 2 2 or more types: 5

**Table 2**

Region and forest type overview.

Region	Forest type (n plots)	Total species richness of the 13 examined species groups		IBP score	
		mean	sd	mean	sd
ALB	Spruce (12)	249.85	32.69	21.05	4.11
ALB	Beech (38)	232.74	48.03	21.17	5.13
HAI	Spruce (1)	305.00	n.a.	31.00	n.a.
HAI	Beech (46)	196.37	30.95	23.63	5.28
SCH	Pine (15)	243.00	22.81	17.40	4.07
SCH	Oak (7)	221.20	35.45	23.84	3.87
SCH	Pine/Beech (7)	213.38	27.26	17.20	3.64
SCH	Beech (21)	216.66	32.91	22.68	4.49

henceforth called “plots”, with a plot size of 1 ha each (100\*100 m), resulting in total 150 plots. We excluded 3 plots due to recent storm events that had severely affected stand structure by throwing nearly all mature trees and ended up with 147 plots, leading to 147 levels for the different plots in the model function. The research framework offers plots managed by different forest management regimes allowing for comparisons between the different plots, which was not our focus in this study. For purely comparing the IBP with species richness monitored on the same plots, it was irrelevant to know if the structures captured in the IBP resulted from management or natural succession. The regions are dominated by Scots pine (*Pinus sylvestris* L.), European beech (*Fagus sylvatica* L.), sessile and pedunculate oak (*Quercus petraea* and *Quercus robur*) (Schorfheide), European beech (Hainich), and European beech and Norway spruce (*Picea abies* (L.) Karst.) (Alb). Most of the examined 147 experimental plots were dominated by beech (104), while the

**Table 3**

Species richness per species group.

Species group	Year of sampling	Species richness per species group at plot level	
		mean	sd
Spiders	2008	21.93	6.67
Bats	2008–2010	4.00	2.65
Birds	2008–2010	11.03	3.47
Bryophytes	2007	14.13	7.15
Carabids	2008	15.10	3.13
Fungi	2010	13.75	4.89
True bugs	2008	4.19	3.02
Lichens	2007	10.59	8.28
Moths	2018	68.17	17.17
Necrophagous beetles	2008	7.81	2.64
Phytophagous beetles	2008	11.75	4.62
Plants	2009–2010	26.02	15.51
Saproxyllic beetles	2008	20.82	12.82

remaining plots were dominated by pine (15), spruce (13), oak (8), and pine/beech (7) (see Table 2). The forest types, defined on the basis of the dominant tree species, were included in the model function as 5 different levels.

Since the plots were originally selected to be similar in their variation in land use intensity, soil depth, slope, and vegetation composition, among others, they provided a sound basis for testing the sensitivity of the IBP. The plots differ in upper soil pH, with a soil pH of around 5.5 (Alb), 4.6 (Hainich), and 3.5 (Schorfheide). The three regions are located at 3–140 m.a.s.l. (Schorfheide), 285–550 m.a.s.l. (Hainich), and 460–860 m.a.s.l. (Alb). Annual precipitation and mean annual

temperature are 520–580 mm and 8.0–8.5 °C (Schorfheide), 500–800 mm and 6.5–8.0 °C (Hainich), and 700–1000 mm and 6.0–7.0 °C (Alb) (Fischer et al., 2010).

## 2.2. Taxonomic data and diversity measures

Species data was recorded from 2007 to 2018 (Heidrich et al., 2020), covering 13 taxonomic groups including about 2600 species. Most of the taxonomic groups were recorded on all 150 experimental plots once within that time frame (Table 3). Details of the sampling methods are given in Heidrich et al. (2020). We used the resulting species richness per taxonomic group to test the IBP through regression analysis. In this study, species richness at the level of the taxonomic groups spiders, bats, birds, bryophytes, carabids, fungi, true bugs, lichens, moths, necrophagous beetles, phytophagous beetles, saproxylic beetles, and plants (Heidrich et al., 2020) was retrieved from the data set 25126 (Aggregated species richness and habitat heterogeneity variables for testing the habitat-heterogeneity hypothesis, 2006–2018) (Heidrich et al., 2019), which is available to the public (Biodiversity Exploratories, 2020) and which builds on the following datasets (IDs): 4141 (Müller et al., 2009), 4060 (Boch et al.), 15386 (Kahl and Bauhus, 2012), 16866 (Gossner et al., 2017a), 16867 (Gossner et al., 2017b), and 16868 (Gossner et al., 2017c), 18547 (Blaser and Fischer, 2017), 19848 (Jung and Tschapka, 2016a), 19849 (Jung and Tschapka, 2016b), 19850 (Jung and Tschapka, 2016c), 21446 (Renner et al., 2017a), 21447 (Renner et al., 2017b), 21448 (Renner et al., 2017c). The different species groups were included in the model function as 13 different levels. Species richness was defined as the total number of species per species group and was used in this study as a surrogate for biodiversity. The forest type classification of the experimental plots was used according to the data set 17706 (Schall and Ammer, 2021).

## 2.3. The IBP

The IBP (Index of Biodiversity Potential) by Larrieu and Gonin (2008) is an estimation-based index, which was originally created for the routine work of forest managers. With the help of the index they are able to integrate biodiversity into their assessment tasks. The 147 plots of 1 ha each (100 m × 100 m) were examined by 3 different observers following the protocol for the IBP (v3) (Larrieu and Gonin, 2008). Each of the observers recorded all plots belonging to 1 of the 3 regions Schorfheide, Hainich, and Alb. Gosselin & Larrieu (2020) assessed the impact of observer effect on IBP scores and found a moderate number of systematic random observer variations for 5 factors. Therefore, potential differences in recording and unexplained variations between the regions were accounted for in the regression model by a grouping effect. Field observations of stands were recorded following a standardized route. The IBP protocol is composed of 10 factors (A–J) that are either management-related (factors A–G) or context-related (H–J) (Larrieu and Gonin, 2008). Under management-related factors, number of native tree species, vertical structure in terms of canopy layers, standing and fallen deadwood, large living trees, TreM-bearing (tree-related microhabitat-bearing) living trees, and percentage of gaps providing flower resources, were recorded. Context-related factors address the temporal continuity of forested area as well as aquatic and rocky habitats. By encompassing different types of factors, the IBP corresponds to the concept of “biodiversity evaluation tools” described by Larsson (2001). All factors except temporal continuity were recorded in the field and rated afterwards according to the IBP protocol. By comparing field observations with threshold values, a scoring system awards a score of 0, 2 or 5 per factor (Table 1). Therefore, the IBP scores ranged from 0 to 50.

All examined plots reached the highest score for factor H (temporal continuity of forest) since all plots have been forest land of one type or another over the past 300 years. Some plots had been forested as shelterwood systems with grazing and some had been clear cut and replanted in the past. None of the plots had been deforested and used for agriculture (Fischer et al., 2010).

## 2.4. Applied regression model

We used Bayesian modelling for our regression analyses to investigate the relationship of explanatory variable *IBPscore* with the response variable *species richness per species group*. This response is denoted  $y_{ij}$ , storing species richness  $n_{ij}$  per species group  $j$  at plot  $i$  with  $n_{ij} = 1, \dots, n_i$ .

For each of the plots  $n_i$ , the number of observed species in each of the  $n_j$  species groups is given by  $y_{ij}$ , a count variable taking positive integer values including 0.

To investigate the data-generating process leading to these counts, we applied a count regression model based on the negative binomial distribution. This type of distribution is able to directly incorporate overdispersion – occurring when a random variable contains larger variance than granted by the applied distribution – by estimation of dispersion parameter  $\theta$  next to expectation parameter  $\mu$  (Zeileis et al., 2008).

We modelled the response variable *species richness* as a negative binomially distributed outcome, with  $\mu$  and  $\theta$  as observation-unit specific parameters composed of parameter-specific linear predictors  $\eta_{\mu,ij}$  and  $\eta_{\theta,ij}$ . Further, we used the natural logarithm as a link-function Eq. (1), i.e.,

$$\mu_{ij} = \exp(\eta_{\mu,ij}), \theta_{ij} = \exp(\eta_{\theta,ij}) \quad (1)$$

which guarantees that both distributional parameters hold their positivity constraints.

### 2.4.1. Linear predictor specification and variables

We normalized explanatory variable *IBPscore* by subtraction of its empirical mean by its standard deviation Eq. (2):

$$IBP_{sca,ij} = \frac{IBP_{score,ij} - \text{mean}(IBP_{score})}{sd(IBP_{score})} \quad (2)$$

which led to facilitated estimation of the intercept parameters and application of default prior statements for estimation of the influence of *IBPscore* on *species richness*.

Potential influencing variables were categorically scaled: *region* (3 levels for Alb, Hainich, Schorfheide), *species group* (13 levels for the different species groups), *plot id* (147 levels for the different plots), and *forest type* (5 levels for the different forest types according to the dominant tree species). In the second part of the analysis, we examined the effect of the single factors of the *IBPscore* (leading to explanatory variables A, B, C, ..., G) on the response *species richness*. Each of the explanatory variables, A, B, C, ..., G, was normalized in the same way as the full *IBPscore* (subtraction of respective empirical mean and division by respective empirical standard deviation).

For variable *region* we used dummy coding with region *Alb* as the reference factor. The variables *species group* and *forest type* were included as grouped coefficients, also called random intercepts. The potential variation of the influence of *IBPscore* with varying levels of *species group* and *forest type* was also modeled – as so-called random slopes.

As notational helper, we introduced the indicator function Eq. (3):

$$I_{(conditional)} = \begin{cases} 1, & \text{if condition is met,} \\ 0, & \text{else.} \end{cases} \quad (3)$$

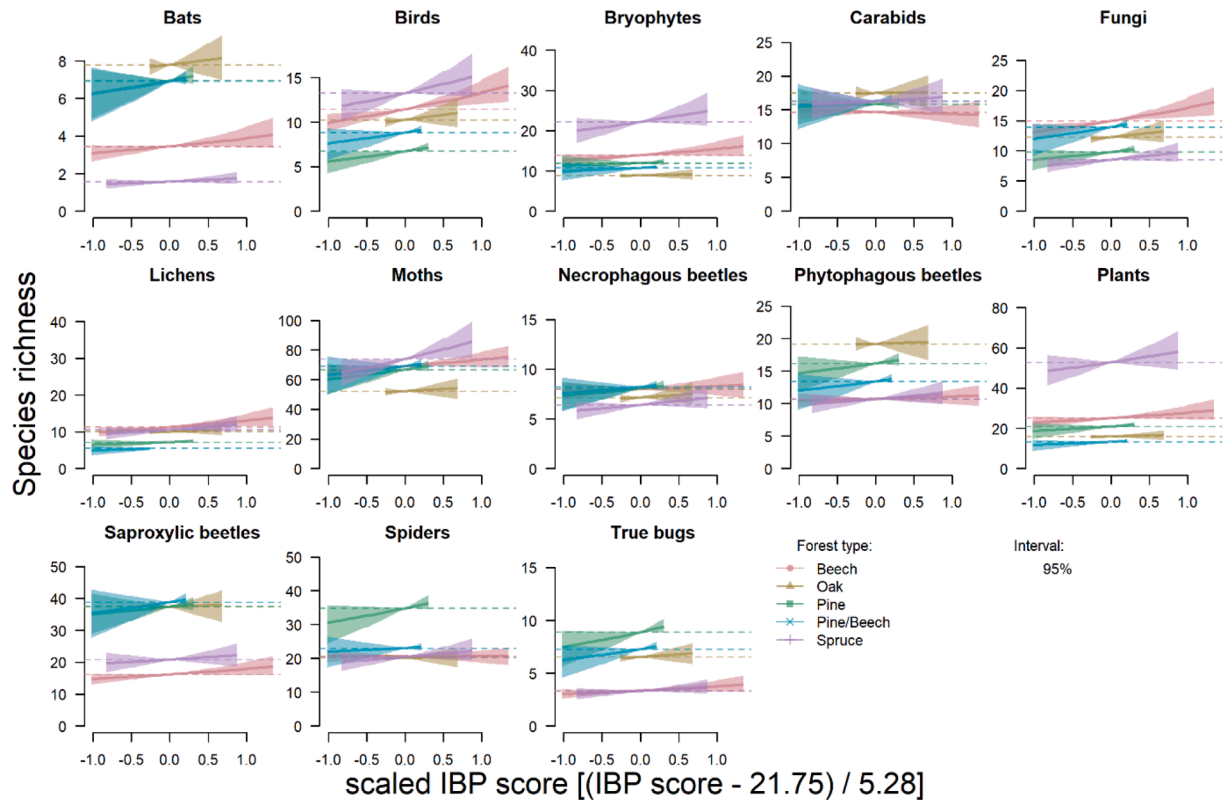


Fig. 1. Estimated relationship between IBP score and species richness per species group and forest type. Horizontal lines representing mean species richness per species group and forest type. Intervals at 95% probability.

For the model function Eqs. (4) and (5) we used:

$$\begin{aligned}
 \eta_{\mu,i,j} &= \beta_{\mu,0} + \beta_{\mu,1}IBP sca_{i,j} + \beta_{\mu,2}I_{\{region_{i,j}=HA\}} + \beta_{\mu,3}I_{\{region_{i,j}=SCH\}} + \beta_{\mu,4}IBP sca_{i,j}I_{\{region_{i,j}=HA\}} + \beta_{\mu,5}IBP sca_{i,j}I_{\{region_{i,j}=SCH\}} + \sum_{r=1}^5 \gamma_{A,r}I_{\{foresttype_{i,j}=foresttype^{[r]}\}} \\
 &+ \sum_{r=1}^{147} \gamma_{B,r}I_{\{plotid_{i,j}=plotid^{[r]}\}} + \sum_{r=1}^{13} \gamma_{C,r}I_{\{speciesgroup_{i,j}=speciesgroup^{[r]}\}} + \sum_{r=1}^{13} \left( \sum_{r=1}^5 \gamma_{D,r,s}I_{\{speciesgroup_{i,j}=speciesgroup^{[r]}\}} I_{\{foresttype_{i,j}=foresttype^{[s]}\}} \right) \\
 &+ \sum_{r=1}^{13} \left( \sum_{r=1}^5 \gamma_{E,k,l}I_{\{speciesgroup_{i,j}=speciesgroup^{[r]}\}} I_{\{region_{i,j}=region^{[k]}\}} \right) + IBP sca_{i,j} \sum_{r=1}^5 \gamma F, r^l \{foresttype_{i,j} \\
 &= foresttype^{[r]}\} + IBP sca_{i,j} \sum_{r=1}^{13} \gamma G, r^l \{speciesgroup_{i,j} = speciesgroup^{[r]}\} + IBP sca_{i,j} \sum_{r=1}^{13} \left( \sum_{r=1}^5 \gamma_{H,k,l}I_{\{speciesgroup_{i,j}=speciesgroup^{[r]}\}} I_{\{foresttype_{i,j}=foresttype^{[k]}\}} \right) \quad (4)
 \end{aligned}$$

and:

$$\begin{aligned}
 \eta_{\theta,i,j} &= \beta_{\theta,0} + \beta_{\theta,1}IBP sca_{i,j} + \beta_{\theta,2}I_{\{region_{i,j}=HA\}} + \beta_{\theta,3}I_{\{region_{i,j}=SCH\}} + \beta_{\theta,4}IBP sca_{i,j}I_{\{region_{i,j}=HA\}} + \beta_{\theta,5}IBP sca_{i,j}I_{\{region_{i,j}=SCH\}} + \sum_{r=1}^{13} \gamma_{I,r,s}I_{\{speciesgroup_{i,j}=speciesgroup^{[r]}\}} \\
 &+ \sum_{r=1}^5 \gamma_{J,r}I_{\{foresttype_{i,j}=foresttype^{[r]}\}} + \sum_{r=1}^{39} \gamma_{K,r}I_{\{speciesgroup:region_{i,j}=speciesgroup:region^{[r]}\}} \quad (5)
 \end{aligned}$$



**Table 4**  
Effect size - increase in n species per increase of 1 standard deviation (sd) of IBP score.

forest type	Beech		Oak		Pine		Pine/Beech		Spruce		
	absolute	%	absolute	%	absolute	%	absolute	%	absolute	%	
model probability (5)	>95	>90	>95	>90	>95	>90	>95	>90	>95	>90	
Spiders						2.54	7.57				
Bats	0.21	5.99									
Birds	0.90	7.73			0.71	12.24	0.73	8.81	1.06	7.79	
Bryophytes	0.77	5.47							1.58	7.13	
Carabids											
Fungi	1.08	7.09				0.76	8.57	1.18	8.79	0.69	8.31
True bugs		0.19	5.68		0.87	10.15	0.63	9.19			
Lichens	0.87	7.49					0.43	9.56	0.79	8.42	
Moths	2.22	3.21				3.89	6.1		6.73	9.17	
Necrophagous beetles									0.41	6.35	
Phytophagous beetles											
Plants		1.32	5.28								
Saproxylic beetles	0.84	5.2									

\*effect size = increase of n species per increase of 1\*sd of IBP score (5.28 points)

Here, the respective parameter-specific intercept parameters  $\beta_{\mu,0}$  and  $\beta_{\theta,0}$  specified the values of the respective parameter-specific linear predictors for region *Alb*. The main effect of  $IBP_{sca_{i,j}}$  is the effect conditional on region *Alb*.

The linear predictor for the parameter  $\theta$  is of reduced complexity in comparison to the linear predictor  $\mu$ , since, as described above, parameter  $\theta$  controls the relationship between expected value and variance in our response. It is therefore mandatory that each of the parameters included into the linear predictor  $\eta_{\mu,i,j}$  is based on sufficient data to permit a stable estimation of the respective conditional variance. As the variable forest type is unbalanced, e.g., the number of oak plots is very low compared to the number of beech plots, we therefore did not include any interactions of forest type into the term  $\eta_{\theta,i,j}$ .

For each of the coefficient groups  $\gamma_{\xi} = (\gamma_{\xi,1(1)}, \dots, \gamma_{\xi,R_{\xi}(S_{\xi})})$ ,  $\xi \in \{A, B, C, \dots, G\}$ , we made the following assumption Eq. (6):

$$\gamma_{\xi,r(s)} \sim Normal(0, \sigma_{\xi}^2) \tag{6}$$

For the intercept parameters, we have chosen non-informative priors Eqs. (7) and (8). By the use of flat priors, we considered the thoughts expressed in Section 7 of Greenland and Mansournia (2015):

$$\beta_{\mu,0} \sim Flat, \tag{7}$$

$$\beta_{\theta,0} \sim Flat, \tag{8}$$

and standard normal priors Eqs. (9) and (10) for the population-level coefficients (Gelman et al., 2015):

$$\beta_{\mu,j} \sim Normal(0, 1), j = 1, \dots, 5, \tag{9}$$

$$\beta_{\theta,j} \sim Normal(0, 1), j = 1, \dots, 5, \tag{10}$$

Considering priors for scale parameters of group coefficients  $\gamma$ , we preferred enough freedom to get large coefficients if there was strong support by the data, but also a stable solution with respect to the large number of parameters. We therefore chose a half-t-distribution (11) with a scale of 1 which is a less informative alternative to the half normal (Stan Development Team, 2021):

$$\sigma_{\xi} \sim t_{+}(v = 23, \mu = 0, \sigma = 1). \tag{11}$$

All analyses were performed in the R statistical software environment (R Core Team, 2019, version 3.6.3). We used the R package brms (Bürkner, 2017; Bürkner, 2018, version 2.13.3) for estimation of the models as described above.

### 3. Results

Mean species richness over all taxa and plots per region and forest type ranged from 196 to 305, while the IBP score ranged from 17 to 31 out of 50 points (Table 2). Mean species richness was highest in the spruce forests and lowest in the beech forests of the Hainich (Table 2). The highest mean IBP score was reported for the spruce dominated forest stand in the Hainich, while the lowest was observed in the pine stands at Schorfheide (Table 2).

#### 3.1. Estimated relationships between total IBP score and species richness

Estimated relationships between the measured species richness per species group and the respective IBP score were quantified by the increase of n species per increase of 1\*sd of the IBP score (5.28 points). The greatest number of plots (n = 105) was dominated by beech. Within the beech-dominated plots, the strongest estimated relationships with a model probability of > 95% was found for the following species groups: birds (+7.73% or + 0.9 species per increase of 1\*sd of IBP), lichens (+7.49% or + 0.87 species), fungi (+7.09% or 1.08 species), bats (+5.99% or 0.21 species), bryophytes (+5.47% or + 0.77 species), saproxylic beetles (+5.20% or + 0.88 species), and moths (+3.21% or + 2.22 species) (Fig. 1 and Table 4). Positive estimated relationships between species richness and IBP score with a model probability of > 90% were found in the species groups true bugs (+5.68% or + 0.19 species) and plants (+5.28% or + 1.32 species). In the oak-dominated plots, none of the species groups showed an estimated relationship between species richness and IBP with a model probability of > 90% or > 95%. In the pine-dominated plots, species richness of birds (+12.24% or + 0.71 species per increase of 1\*sd of the IBP score) and true bugs (+10.15% or + 0.87 species) were positively correlated with the IBP score (model probability of > 95%). Species richness of fungi (8.57% or + 0.76 species), spiders (+7.57% or + 2.54 species), and moths (+6.10% or + 3.89 species) correlated with the IBP score with a model probability of > 90%. In the pine and beech-dominated plots, species richness of lichens (+9.56%, +0.43 species), true bugs (+9.19% or + 0.63 species), birds (+8.81% or + 0.73 species), and fungi (+8.79% or + 1.18 species), were positively correlated with the IBP score with a model probability of > 90%. In the spruce-dominated stands, we found a positive estimated relationship between species richness and IBP with a model probability of > 95% for the group of moths (+9.17% or + 6.73 species) and with a model probability of > 90% for the groups of lichens (+8.42% or + 0.79 species), fungi (+8.31% or + 0.69 species), birds (+7.79% or + 1.06 species), bryophytes (+7.13 % or + 1.58 species), and necrophagous beetles (+6.35% or + 0.41 species) (Fig. 1 and Table 4).

In summary, we found that 10 of 65 possible estimated relationships (13 species groups \*5 forest types) were positive at a model probability

of > 95%, while in 14 out of 65 cases, estimated relationships were positive with a model probability of > 90%.

### 3.2. Estimated relationships between single IBP factors and species richness

Through a closer look at the different IBP factors, we aimed to identify factors that, together with structural or habitat characteristics, are especially suitable for estimating the potential biodiversity of a forest stand. The identification of structural and habitat characteristics is especially important when it comes to deciding which attributes should be included in monitoring concepts that rely on structural properties. Each of the single factors A-G was tested for estimated relationship with the measured species richness under the same model used for testing the entire IBP score. We did not calculate the effect size per factor, since the precise effect size of a single factor on species richness would be too vague. We only analyzed relationships between species richness and IBP factors.

The score of **factor A**, related to the number of tree species, was not correlated with the species richness of any of the species groups. It was therefore, on its own, not suitable for assessing potential biodiversity (Table A1).

The number of vertical layers, leading to the score of **factor B**, was positively correlated with the measured species richness only in beech, pine, and pine/beech stands. No estimated relationships were found in oak and spruce stands. In beech stands, the species richness of bryophytes, true bugs, lichens, and plants (prob. > 95%), and the species richness of birds, fungi, phytophagous beetles, and saproxylic beetles (prob. > 90%) were correlated with the score of factor B (Table A 2). In pine stands, estimated relationships between the factor's score and species richness were found for spiders, birds, true bugs, moths (95%), and for fungi, lichens, negrophagous beetles, phytophagous beetles, and plants (prob. > 90%). In the pine/beech stands, only the richness of true bugs, lichens, and plants were correlated with the factor's IBP score (prob. > 90%) (Table A2).

The score of **factor C**, increasing with the number of standing deadwood items, correlated with species richness in beech stands only for the species groups birds (prob. > 90%), fungi, and lichens (prob. > 95%). In the spruce stands, species richness correlated with the score of factor C in the species groups bats, birds, lichens (prob. > 90%), and fungi and moths (prob. > 95%) (Table A3).

The score of **factor D** (the number of downed deadwood items), in contrast, was correlated with species richness of fungi but only in the beech and spruce stands (prob. > 95%) (Table A4).

The score of **factor E** (the number of large living trees) was correlated with species richness of birds, fungi, and true bugs (prob. > 95%) as well as with bats, bryophytes, and lichens (prob. > 90%) in the beech stands. In oak stands, an estimated relationship was found for birds, fungi (prob. > 95%), and true bugs (prob. > 90%), while in the pine stands only the species richness of bats correlated with the score of factor E (prob. > 95%). In the pine-beech stands the richness of birds, fungi, and true bugs (prob. > 95%), and in the spruce stands the species richness of birds and fungi correlated with the factor's score (prob. > 90%) (Table A5).

The score of **factor F** (the number of tree-related microhabitats) correlated with species richness of different groups in all forest types except the oak stands. In the beech stands, richness of birds, fungi, moths, and saproxylic beetles (prob. > 95%), and bryophytes (prob. > 90%) correlated with the factor's IBP score. In the pine stands, estimated relationships between species richness and the score of factor F were found for birds, fungi, moths, and saproxylic beetles (prob. > 90%). Richness of fungi correlated with the factor's IBP score in the pine-beech stands only (prob. > 90%). In the spruce stands, estimated relationships between species richness and the factor's IBP score were found for all species groups (prob. > 95%) (Table A 6). These estimated relationships were the strongest compared to other stand types.

**Factor G**, scoring the optimal share of gaps, correlated with species richness in the beech stands for spiders, bryophytes, lichens, phytophagous beetles, plants (prob. > 95%), and for birds, carabids, and moths (prob. > 90%). In the oak stands, species richness correlated with the factor's IBP score for spiders, lichens, phytophagous beetles, and plants (prob. > 95%), and for birds, bryophytes, carabids, true bugs, moths, necrophagous beetles (prob. > 90%). In the pine stands, only the species richness of phytophagous beetles and plants (prob. > 95%), and of spiders and lichens (prob. > 90%) were correlated with the factor's IBP score. In the pine-beech stands, species richness of lichens, phytophagous beetles, and plants (prob. > 90%) correlated with the score of factor G, while in the spruce stands only the species richness of plants, saproxylic beetles (prob. > 95%), and lichens (prob. > 90%) were correlated with factor G (Table A7).

Aquatic and rocky habitats were almost completely absent from our plots. The **factors I and J** hence did not yield any extra information. Since the plots were not differently ranked in the **factor H** (historic forest use), this factor also did not provide additional insight. Estimated relationships found in our study are therefore confined to the management-related factors of the IBP.

In summary, factors with the most estimated relationships between the respective IBP score and species richness with a probability of at least 90% were factor G (share of gaps providing flower resources) with 28 positive out of 65 potential estimated relationships (13 species groups\* 5 forest types), factor F (number of TreMs) with 21 positive estimated relationships, factor B (number of layers) with 20 positive estimated relationships, followed by factor E (number of large living trees) with 15 positive estimated relationships, factor C (standing deadwood) with 8 positive estimated relationships, factor D (downed deadwood) with 2 positive estimated relationships and factor A with no estimated relationship. The stand types where most estimated relationships were found over all factors were beech (30), spruce (24), pine (18), oak (13), and pine-beech (9).

## 4. Discussion

Our study offers an approach for testing the IBP's potential as a proxy for estimating biodiversity. For birds, fungi, true bugs, lichens, and moths there were at least 3 of 5 forest types for which our model fitted a positive estimated relationship between IBP and species richness at a model probability of > 90%. The model suggested an increase in species number between 3.21 and 12.24% (between 0.43 and 6.73 species) per increase of 1\*sd of the IBP score, meaning that the effect size was rather low. Still, the estimated relationship between the IBP score and conventionally measured species richness was clear, underscoring the potential of the IBP to depict a forest stand's potential in terms of species richness.

The IBP factors B (vertical layers), E (large living trees), F (number of TreMs), and G (share of gaps providing flower resources) in particular were positively correlated with the measured species richness of a large number of species groups and forest types. However, even if the IBP can provide a rough estimate of potential biodiversity or can evaluate important habitat characteristics, it should not be over-interpreted. A given score of the IPB in a stand does not mean that the number of species of a given taxonomic group yields a certain IBP number. Nonetheless, we consider the results as relevant for demonstrating the potential of the IBP as a structure-based biodiversity assessment tool, considering the temporally efficient and easy assessment of the IBP and the temporal duration of species richness recording years in our study.

### 4.1. Positive estimated relationships between IBP score and species richness

Only positive estimated relationships between the IBP and species richness were found. This shows that the IBP reflects the measured species richness by increasing with increasing number of present

species. Especially since measuring biodiversity is often based on species composition data (Yao et al., 2019), considering structural attributes in addition might have a great potential for a more comprehensive biodiversity monitoring and conservation management (Angiolini et al., 2021). For birds, fungi, true bugs, lichens, and moths, the IBP and conventionally measured species richness were positively correlated. We assume this was due to the selection of factors contained in the IBP. In particular, tree species diversity (Ammer and Schubert, 1999; Ampoorter et al., 2020; Poulsen, 2002), old and large trees (Moning and Müller, 2009), gaps (Gosselin et al., 2006), deadwood (Burrascano et al., 2008; Mag and Ódor, 2015; Müller et al., 2015; Seibold et al., 2014), and structural heterogeneity in general (Heidrich et al., 2020; Larrieu et al., 2015; Márialigetű et al., 2009; Tews et al., 2004) correlated with one or another of the above-mentioned species groups. These factors are contained in the IBP, and may therefore account well for the habitat needs of those species groups, even though dominant tree species was not a decisive factor in our analysis. In our study, few or no estimated relationships were found between the IBP and species richness of spiders, carabids, necrophagous beetles, phytophagous beetles, saproxylic beetles, and plants. For saproxylic beetles, the range of the amount of deadwood recorded in our study might not be suitable to get the full beetle community. It may be that substantial canopy opening, which are key drivers for saproxylic beetles (Bouget et al., 2013), were less frequent in the forests studied here; the forest management intensity gradient of our study may have therefore been too small to cover the full range of environmental conditions (Neff et al., 2021). It is well known that spiders, carabids, and phytophagous beetles benefit directly or indirectly from canopy openings, since these increase plant diversity and plant cover (Junker et al., 2000; Seibold et al., 2016; Winter et al., 2015).

#### 4.2. Differences between forest types

Differences in the estimated relationships between IBP score and species richness in the model outcomes may also have resulted from different sample sizes. Most plots were dominated by beech; our results are therefore most representative of beech forests. For beech forests, the IBP score indicates key stand structures: large trees, vertical layers, and gaps seem to promote species richness. Since far fewer phytophagous insect and mite species feed on beech than on other hardwood or softwood species (Brändle and Brandl, 2001), gaps enable the establishment of additional plant tissue fostering species richness (Dormann et al., 2020). Against this background, the results from oak and pine-beech forests should be interpreted carefully.

#### 4.3. Estimated relationship between single IBP factors and species richness

The number of vertical layers was especially clearly correlated with species richness per species group (Table A 2). This result is in accord with the literature, which has found that a larger number of vertical layers provides habitats for and increases the species richness of arthropods (Müller et al., 2018) and lichens (Penone et al., 2019). Additionally, a higher number of large living trees and the resulting tree-related microhabitats can foster species richness according to the habitat heterogeneity theory (Tews et al., 2004). Understorey plant composition, e.g., is strongly dependent on the overstorey (Yilmaz et al., 2018), which confirms the importance of including vertical layers, large trees, and gaps in the IBP. The number and diversity of TreMs formed the score of IBP's factor F, for which an estimated relationship with species richness was found. This finding was not expected, since a recent analysis of the relationship between TreM density and diversity and biodiversity yielded weak results (Bouget and Larrieu, 2017; Paillet et al., 2018). Paillet et al. (2018) concluded that "tree microhabitats may serve as indicators for bats and birds, but they are not a universal biodiversity indicator". However, the timeframe of that study was relatively small, covering only one sampling season. Other reasons for weak estimated

relationships may be the overall low number of TreMs in managed forests, the sampling design, or the focus on biodiversity in general, rather than a focus on TreM-related species (Bouget and Larrieu, 2017). In any case, the estimated relationship between TreMs and species richness found in our study and elsewhere (Bouget et al., 2013), suggests the need for more detailed analysis. It would be valuable to identify which TreMs are particularly important for different species groups (Larrieu et al., 2019) and should therefore be included in monitoring concepts. The share of gaps did correlate with the species richness of most species groups. This effect can result from a changed microclimate or an increase in resources (e. g., flowering plants) and confirms other studies that have identified estimated relationships with the richness of lichens and arthropods (Bonari et al., 2017; Horak et al., 2014), plants and beetles (Leidinger et al., 2020), bryophytes (Bardat and Aubert, 2007), and birds (Przepióra et al., 2020). The IBP factors for standing and fallen deadwood were correlated with species richness of birds, fungi, lichens, and moths only, but not in all forest types. Even though this result was expected for fungi (Blaser et al., 2013) and lichens (Dittrich et al., 2014), and less so for birds (Mag and Ódor, 2015) and moths (Heidrich et al., 2020), the temporal difference between species monitoring and recording of the IBP and of the changing decay states of deadwood items may have influenced our results. The amount of deadwood between the first and second forest inventories on the plots of the Biodiversity Exploratories had substantially decreased due to reduced management activities (e.g., leaving harvesting residues, actively increasing the share of deadwood). In contrast, the number of tree species did correlate with the species richness of the different groups, possibly because nearly all examined forest stands reached the highest score of 5 points and nearly no differentiation between the examined plots could be provided for the model. When examining the estimated relationship between individual factors and the species richness of the different species groups, weaker estimated relationships were found compared to the total IBP score. Correlating an individual factor with species richness does have a smaller range of IBP points (1–5 points). A weaker estimated relationship effect was therefore expected.

#### 4.4. Time difference between species monitoring and IBP recording

Since species richness on the experimental plots was monitored only once between 2007 and 2018, we expected some variation between the year of monitoring and the year 2020, when the IBP was recorded. Three plots that had been affected by storms during that time period were excluded from the analysis. However, very few of the IBP factors are likely to have changed dramatically over a short time. Still, the data on species richness was unique and was the best available for a comparison with the IBP on the same plots. We therefore considered the time difference acceptable and assumed that in those cases where a relationship between species richness and IBP was found, this relationship would have been even stronger if the time difference between recording species and assessing the IBP had been smaller.

#### 4.5. Critical aspects of the IBP and our results

Differently managed stands and thus a range of different stand structures were included in our study. The IBP covers a large range of resulting scores. Different combinations of structural characteristics can lead to similar final scores, however, some plots could have achieved similar scores due to different factors. Nonetheless, certain species groups need a combination of certain structural characteristics (Larrieu et al., 2019), which is why we examined the estimated relationship between different IBP factors and species richness of the different species groups. For such detailed analyses, the sample size was, however, considerably smaller and the model outcome may have been less reliable. For some forest types (oak, pine-beech forests) sample sizes may have been too small to draw general conclusions. Additional factors such as adjacent habitats, microclimate, or soil characteristics are not covered



by the IBP, as its goal is rapid and easy assessment. Adjacent habitat types and the connectivity of habitats can dramatically influence species richness (Tilman et al., 1994). Moreover, once species disappear due to habitat destruction, they will not be found in a forest stand even though the stand offers the needed structural characteristics (Jackson and Sax, 2010). Since the experimental plots of the Biodiversity Exploratories were set up for directly comparing biodiversity in differently managed and differently composed stands, the external variation can be considered as low and differences in species richness are most likely the result of plot-related (structural) characteristics. Another limitation of our results is that species richness was not differentiated among rare, red-listed, or introduced species for the respective regions. The IBP assumes that the more species there are, the more likely it is that all functions will be performed properly. Species richness alone does not, therefore, account for conservation-relevant species. This would be worth including in monitoring concepts, even if it increased the effort due to the required taxonomic knowledge (Lelli et al., 2019). The IBP further rates high tree species richness as superior to monospecific stands even though, e.g., in beech forests, high tree species richness would naturally not be expected. Whether or not the currently present species only occasionally occur in a forest is often difficult to determine due to rapid climatic changes, land use, habitat fragmentation (Kriebitzsch et al., 2013), and lack of comparable, undisturbed pristine forests. Further limitations of the IBP result from the fact that it does not include soil biodiversity or physico-chemical characteristics of the water in aquatic environments to identify pollution effects, but these are also not covered in most types of biodiversity monitoring (Guerra et al., 2020). When it comes to deadwood, the IBP considers only large deadwood items, which are important, e.g., for saproxylic beetles (Bouget et al., 2013) and cannot be substituted by the same volume of smaller pieces (Lachat et al., 2013). Still, small pieces of deadwood are equally important for certain species (Brin et al., 2011) and especially for the diversity of fungi (Heilmann-Clausen and Christensen, 2004). The diversity of deadwood is also not accounted for, but would be worth recording due to estimated relationships with bryophyte diversity (Müller et al., 2015), saproxylic beetle diversity (Bouget et al., 2013; Johansson et al., 2007), lichen diversity (Nascimbene et al., 2013), and fungal diversity (Norden et al., 2018).

#### 4.6. Applicability of the IBP at landscape scale

The IBP is a stand-based index that refers to alpha diversity. Most comparisons of managed and unmanaged stands rely on  $\alpha$ -diversity only. However, forest management systems are characterized by different stages; these must be accounted for by comparisons at the landscape level and thus also by addressing  $\gamma$ -diversity (Schall et al., 2018a). In age-class forests, each forest patch may provide completely different habitats, whereas in continuous cover forests, the stands are expected to be more similar (Schall et al., 2018a). To estimate the potential biodiversity at the landscape level, a grid or other system of multiple sampling points throughout the forest landscape would be necessary, including the need to aggregate stand-level IBP scores in a meaningful way. Nonetheless, the total IBP score would not show the differences between grid points and similar scores could result from different structural characteristics. Since environmental heterogeneity is pivotal to biodiversity, it may be more useful to focus on high variation in scores of specific IBP factors. For example, the final score for a landscape should be higher if the factors A (tree species richness), B (vertical structure) and G (gaps) show high variation. Here, compositional variation could be of greater interest than a simple comparison of scores that count the number of, e.g., tree species. If the different stands varied in habitat supply, this could therefore be measured not only by

scoring the different structural attributes but also by considering the type of structures, tree species, etc. resulting in a certain score. In fact, recent studies have shown that some species require pure stands (Heinrichs et al., 2019) and many benefit from early successional stages (Hilmers et al., 2018). Landscapes composed of stands that differ strongly in composition and structure may therefore promote biodiversity (Schall et al., 2020). This should be reflected in a landscape related version of the IBP, if such an index were to be developed. Compared to remote sensing (Bae et al., 2019), however, the IBP may not be as cost and time efficient unless some of the structural attributes that are currently part of the IBP were recorded during the forest inventory routine.

#### 4.7. Conclusions

The IBP can provide only a rough estimate of the potentially present biodiversity in a forest. It is, however, easy to apply and can indicate a forest's capacity to host forest-dwelling taxa according to stand structure, composition, and habitat attributes. It seems to be especially effective in doing so for birds, true bugs, lichens, and moths. Due to its time and cost efficiency, it has great potential for application in science and in forest management. In scientifically-motivated or commercial forest inventories it might be possible to record the index additionally to the existing parameters in order to get an idea on the biodiversity potential of a forest stand. It can therefore be of help when developing monitoring concepts. Forest managers would thus get feedback on the impact of their chosen management regimes on biodiversity when recording the index regularly. Also a comparison between differently managed stands might be possible to compare the ecological impact of different management interventions. Since the IBP does not provide information on species identity and diversity, it is not a substitute for conventional species-based monitoring and must be interpreted with care. Single components of the IBP; presence of canopy gaps, which provide different microclimate and resources (e.g., flowering plants), as well as the number of vertical layers, large living trees, and microhabitats, were clearly correlated with species richness in our study. These structural attributes should be explored in more detail for their potential as surrogate measures of species diversity.

#### CRediT authorship contribution statement

**Laura Zeller:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Charlotte Baumann:** Data curation, Investigation. **Pierre Gonin:** Writing – review & editing. **Lea Heidrich:** Data curation, Writing – review & editing. **Constanze Keye:** Writing – review & editing. **Felix Konrad:** Data curation, Investigation. **Laurent Larrieu:** Conceptualization, Data curation, Writing – review & editing. **Peter Meyer:** Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Holger Sennhenn-Reulen:** Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Jörg Müller:** Writing – review & editing. **Peter Schall:** Data curation, Writing – review & editing. **Christian Ammer:** Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

#### 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 A1**

Factor A - estimated relationship between the score for the number of tree species and species richness.

A	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders										
Bats										
Birds										
Bryophytes										
Carabids										
Fungi										
True bugs					n.s.					
Lichens										
Moths										
Necrophagous beetles										
Phytophagous beetles										
Plants										
Saproxyllic beetles										
1*sd of IBP score (5.28 points)										

**Table A2**

Factor B - estimated relationship between the score for the number of layers and species richness.

B	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders					x					
Bats										
Birds		x			x					
Bryophytes	x									
Carabids										
Fungi		x				x				
True bugs	x				x		x			
Lichens	x					x		x		
Moths					x					
Necrophagous beetles								x		
Phytophagous beetles		x						x		
Plants	x					x			x	
Saproxyllic beetles				x						
1*sd of IBP score (5.28 points)										

**Table A3**  
Factor C - estimated relationship between the score for standing deadwood and species richness.

C	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders										
Bats										x
Birds		x								x
Bryophytes										
Carabids										
Fungi	x							x		
True bugs										
Lichens	x									x
Moths									x	
Necrophagous beetles										
Phytophagous beetles										
Plants										
Saproxylic beetles										
1*sd of IBP score (5.28 points)										

**Table A4**  
Factor D - estimated relationship between the score for downed deadwood and species richness.

D	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders										
Bats										
Birds										
Bryophytes										
Carabids										
Fungi	x								x	
True bugs										
Lichens										
Moths										
Necrophagous beetles										
Phytophagous beetles										
Plants										
Saproxylic beetles										
1*sd of IBP score (5.28 points)										

**Table A5**  
Factor E - estimated relationship between the score for large living trees and species richness.

E	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders										
Bats		x			x					
Birds	x		x				x			x
Bryophytes		x								
Carabids										
Fungi	x		x				x			x
True bugs	x						x			
Lichens		x								
Moths										
Necrophagous beetles										
Phytophagous beetles										
Plants										
Saproxylic beetles										
1*sd of IBP score (5.28 points)										

**Table A6**  
Factor F - estimated relationship between the score for microhabitats and species richness.

F	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders									x	
Bats									x	
Birds	x					x			x	
Bryophytes		x							x	
Carabids									x	
Fungi	x					x		x	x	
True bugs									x	
Lichens									x	
Moths	x					x			x	
Necrophagous beetles									x	
Phytophagous beetles									x	
Plants									x	
Saproxylic beetles	x					x			x	
1*sd of IBP score (5.28 points)										

**Table A7**  
Factor G - estimated relationship between the score for the share of gaps providing resources (e.g. flowering plants) and species richness.

G	effect size (increase of n species per increase of 1*sd IBP score)									
	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%	>95%	>90%
<b>Species group / forest type</b>	<b>Beech</b>		<b>Oak</b>		<b>Pine</b>		<b>Pine/Beech</b>		<b>Spruce</b>	
Spiders	x		x			x				
Bats										
Birds		x		x						
Bryophytes	x			x						
Carabids		x		x						
Fungi										
True bugs				x						
Lichens	x		x			x		x		x
Moths		x		x						
Necrophagous beetles				x						
Phytophagous beetles	x		x		x			x	x	
Plants	x		x		x			x	x	
Saproxylic beetles										
1*sd of IBP score (5.28 points)										

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