



## Review

# Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe



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## ABSTRACT

With a growing number of forest biodiversity indicators being applied in forest policy documents and even more being suggested by the scientific community, there is a need to evaluate, review and critically assess the strength of evidence for individual indicators, their interrelationships and potential overlaps and gaps. Biodiversity indicators proposed for forest ecosystems in Europe were reviewed with the overarching aim of providing advice on strategic selection and combination of indicators. The objectives were to (1) establish interrelationships between indicators and their indicandum (i.e. the indicated aspect of biodiversity); (2) assess the strength of scientific evidence for individual indicators; and (3) identify a set of indicators with confirmed validity for further scientific testing and inclusion in long-term reporting and decision-making regarding forest biodiversity. Ten indicator groups and 83 individual indicators were identified with application from stand scale up to landscape scale in 142 eligible scientific papers. In 62 of the 142 studies no statistical correlations between indicator(s) and indicandum were performed and 42 (out of the 62) did not even present a clear indicandum. In the remaining 80 studies, 412 correlations between indicator and indicandum were identified. However, only six correlations were assessed as being supported by strong evidence, i.e. three or more studies found statistical correlation between the indicator and indicandum, and no studies reported contradictory results. For the species richness relationships, there was strong evidence for positive correlations between deadwood volume and wood-living fungal species richness; deadwood volume and saproxylic beetle species richness; deadwood diversity and saproxylic beetle species richness; age of canopy trees and epiphytic lichen species richness. There was strong evidence for a negative correlation between tree canopy cover and spider species richness. Concerning species composition-related correlation, there was strong evidence that the species composition of epiphytic lichens changed with the age of canopy trees. These results imply that the validity of most indicators on which monitoring and conservation planning are based are weakly scientifically supported and that further validation of current biodiversity indicators for forest ecosystems is needed.

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## 1. Introduction

Just 25 years ago, biodiversity was considered a minor issue in environmental policy; too broad and vague a concept to be applied to real-world regulatory and management problems (Noss, 1990). Today, biodiversity conservation has become a key issue in policy and management of all natural resources, not least forest ecosystems which is the focus of this review (Gao et al., 2014; Mace et al., 2012). As foreseen by Noss (1990), the development of measurable biodiversity indicators has been instrumental in this change.

Since the Rio Earth Summit in 1992, a large number of biodiversity indicators for forests and other ecosystems, and changes in these ecosystems over time, have been proposed in individual studies or by large programmes, such as the Convention on Biological Diversity (CBD) (Biodiversity Indicators Partnership, 2010), Forest Europe (2010), the Montréal Process (Process, 2009), Streamlining European Biodiversity Indicators (SEBI) (EEA, 2012), etc. Despite the large number of studies conducted to date, recent policy documents and guidelines have concluded that very few indicators with good Europe-wide coverage are available for assessing trends in these (EEA, 2012). Moreover, several countries have reported efforts to implement biodiversity conservation in working towards sustainable forest management in practice, but none has quantified forest biodiversity targets related directly to specific biodiversity indicators (Barbati et al., 2014). This could be due to the complexity of biodiversity, meaning that there is no easy answer on how to illustrate status, changes and trends in selected components of biological diversity, including loss of biodiversity (EEA, 2012).

Ferris and Humphrey (1999) conducted a review of forest biodiversity indicators and concluded that it is important to understand clearly the interrelationships between indicator species/groups, their habitat requirements and the species groups they are intended to indicate. The dichotomy is that the indicators need to have verified quality, so they do not show or indicate something that is untrue, while at the same time being easy to communicate and understandable to policy makers. As a result, pan-European policy reports on forest biodiversity mention only a few indicators related to biodiversity and forestry. For example, SEBI (EEA, 2012) has only three indicators directly or indirectly connected to biodiversity: forest growing stock, increment and fellings, and the occurrence of deadwood.

Measurable indicators have undoubtedly supported operationalisation of the biodiversity concept. However, we are now at a point where agencies are having difficulties in identifying and choosing between the large number of indicators proposed. This again hinders the same agencies from composing a set of complementary indicators with supplementary properties. A critical

review of the strength of evidence for existing indicators and assessment of their interrelationships (overlaps and gaps) is thus important for continued development and refinement of indicators as policy and management tools for biodiversity conservation. This need is illustrated by the initiative undertaken recently by COST Action E43 to harmonise indicators included in national forest inventories for biodiversity assessment across European countries (e.g. Chirici et al., 2012).

Three primary attributes of biodiversity are widely recognised as providing a framework for research on forest biodiversity (Spanos et al., 2006; Larsson et al., 2001a,b; Noss, 1990; Franklin, 1988). These are: (1) Species/composition; identity and variety of elements, including species lists and measures of species diversity; (2) structure; physiognomy of forest as measured within a stand to variation at forest scale and on to the pattern of forest patches at a landscape scale; and (3) function; ecological and evolutionary processes, including gene flow, disturbances and nutrient cycling. The focus on forest biodiversity indicators in the present review is restricted to species/compositional indicators and structural indicators, because they are more amenable to measurement by forest researchers (Ferris and Humphrey, 1999). In addition, species/compositional and structural elements may act as surrogate functional indicators, e.g. forest stand structures may reflect natural and human disturbance, while deadwood decay stage (a structural indicator) may be a good indicator of decomposition processes.

Simberloff (1997) distinguished two main uses of biodiversity indicators that are still valid today: (i) the presence and fluctuations of the indicator are able to reflect those of other species/taxa in the community; and (ii) the presence and fluctuations of the indicator are able to reflect chemical/physical changes in the environment. Actually, the latter could appropriately be called “environmental indicators” (McGeoch, 1998) or “environmental health indicators” (Caro and O’Doherty, 1999). In the present review, we focused on the first type of biodiversity indicators, i.e. indicators which can be used as a surrogate measure of other components of forest biodiversity (the *indicandum*) and thus provide a short-cut in surveys or monitoring programmes.

The overarching aim of this review was to provide advice on strategic selection and combination of complementary biodiversity indicators, by compiling and assessing species/composition and structural biodiversity indicators suggested for use in European forest ecosystems. Specific objectives were to:

- (1) Establish and review suggested indicators and interrelationships between indicators and their *indicandum* (i.e. the aspect of biodiversity indicated).
- (2) Assess the strength of scientific evidence for individual indicators.

- (3) Suggest a set of indicators with confirmed validity for further scientific testing and eventual inclusion in long-term reporting and decision-making regarding forest biodiversity.

Although the scope was limited to Europe, the variation in forest types in this region is large, where 14 forest types can be distinguished (EEA, 2006). Thus, this review provides a wide view of forest biodiversity indicators in many types of forest ecosystems, the interrelationships between indicators and their indicandum and their contemporary use.

## 2. Method

The search for literature was restricted to peer-reviewed scientific papers reporting indicators for species/taxa in the forest community. Studies reporting data on other types of indirect biodiversity indicator, e.g. environmental indicators, indicators of sustainable forest management, etc., were beyond the scope of this review.

### 2.1. Search strategy

The literature search was conducted from June 2013 to April 2015 in the two major scientific databases Scopus and Web of Science. Aiming for high sensitivity in order to achieve relatively low search specificity, as recommended by Pullin and Stewart (2006), the search was restricted to the following combination of keywords: forest\* AND biodiversity AND indicator\* (\* indicating wild card, i.e. any ending possible). These terms were sought for in terms of topic (in Web of Science), title, keywords and abstract (in Scopus). Titles and abstracts identified by the searches were scrutinised and if they met the inclusion criteria, the entire article was retrieved. The inclusion criteria were that the study had to be:

- Executed in Europe (except reviews and descriptive articles)
- Published in a peer-reviewed scientific journal
- Written in English
- Reporting one or more species/compositional or structural forest biodiversity indicators as surrogate measures of other components of forest biodiversity
- Published before April 2015
- Available via the electronic databases Scopus or Web of Science.

When investigating and summarising a broad and heterogeneous subject, serendipity discoveries (such as finding a relevant paper when searching for something else, or by pursuing references of references) often prove important (Greengalgh and Peacock, 2005). Hence our scope was widened outside the protocol, by examining references cited by the identified papers, so called “snowballing”. Potentially eligible papers were retrieved and included if they met the inclusion criteria. Limiting the search to peer-reviewed scientific papers published in English may have omitted a number of interesting studies published as national reports and papers, but these publications were excluded to assure systematic searches and high data quality.

### 2.2. Data extraction, synthesis and analysis

For each study that met the inclusion criteria, bibliographical information was extracted on: (a) the country/countries in which the study was conducted, (b) the type of indicators or the identity description of indicators, (c) the indicandum, (d) the scale at which the indicator was tested or suggested and (e) results of any tests on correlations between indicator and indicandum in the articles.

Quantitative synthesis and meta-analysis were not deemed suitable due to the combined effects of (1) low number of studies on

each indicator and indicandum relationship (<8), (2) heterogeneity of studies concerning indicator, indicandum, and (3) difference in scale, forest type, methodology and the reporting of data. Instead, qualitative synthesis and assessments were applied, as also used in other reviews of biodiversity (e.g. Farinha-Marques et al., 2011; McKinney, 2002) and reviews focusing on particular species groups (e.g. Heink and Kowarik, 2010; Ferris and Humphrey, 1999).

The scale at which the indicator was tested and/or suggested was extracted in terms of the author/s' direct description. When the scale was not described directly by the author/s of a study, we defined it based on the sample size applied in the study, distinguishing between stand, forest and landscape scale. The stand scale refers to sample sizes up to 1 ha (Hannon, 2005). Obeysekera and Rutchey (1997) found that in areas larger than 1 km<sup>2</sup>, the differences between sub-areas in a given region in terms of most landscape metrics of everglade landscape tend to disappear. Many forest sites of special scientific interest (SSSI) in the UK, which are mostly about 100 ha or less, are now well managed. However, the wider landscape in which these sites are located continues to be of variable quality, affecting the status of these forest sites (Natural England, 2011). Therefore in the present review, forest scale was defined as sample size between 1 ha and 1 km<sup>2</sup> (Hannon, 2005). Sample size larger than 1 km<sup>2</sup> was considered landscape scale.

A mind mapping method was applied to analyse the interrelationships between indicators and their indicandum and identify overlaps and gaps visually and holistically. Mind mapping is a technique in which analytical processes are visually represented by connecting concepts and ideas related to a central issue or problem (Buzan, 1995). Mind maps provide insights into the manner in which people organise knowledge by capturing concepts deemed relevant to a particular problem (Kern et al., 2006). The process begins by placing a single concept in the centre of the map. In the present case, each indicator group in turn was set as the single concept, i.e. the key issue to be addressed. Branching from the indicator group in question were related sub-concepts, i.e. individual indicators. These sub-concepts were further linked with their respective indicandum by different patterns of arrow lines in terms of strength of evidence and scales at which the indicators were tested.

### 2.3. Strong, moderate and weak evidence

The strength of evidence for the relationship between indicator and indicandum was classified into one of five levels: (1) Untested; i.e. none of the studies reviewed conducted statistical testing of correlations between indicator and indicandum; (2) no indicator value; i.e. one or more studies identified no correlation between indicator and its indicandum(s) based on statistical testing of empirical data; (3) weak evidence; i.e. only one study had found a correlation, or two or more studies reported divergent correlations between indicator and its indicandum(s); (4) moderate evidence; i.e. two studies confirmed a correlation (positive or negative) between indicator and indicandum(s) and no other studies reported contradictory results; and (5) strong evidence; i.e. if three or more studies confirmed a correlation (positive or negative) between indicator and indicandum(s) and no studies reported contradictory results.

## 3. Results

The search generated 857 hits in Scopus and 1140 hits in Web of Science. After screening of titles and abstracts, 129 potentially eligible papers were retrieved from Scopus and 134 from Web of Science, many of which overlapped between the two databases. The remaining papers were excluded because the indicator(s) studied was not related to forest biodiversity or the study was conducted

outside Europe. Finally 142 papers were included in the review (eight identified through the Scopus search, 13 through the search in Web of Science and 121 in both). The snowballing did not supply additional studies.

### 3.1. Bibliographical overview of studies

Within the 142 papers, 10 groups of forest biodiversity indicator and 83 individual indicators were presented on various scales (Table 1). Reviews and conceptual studies (e.g. not based on own data collection) made up 39 (27.5%) of the 142 papers, while empirical studies based on data collection in 21 different European countries comprised 103 (72.5%). Of these 103 empirical studies, 18 were conducted in Sweden, involving nine indicator groups with 36 individual indicators; 11 were conducted in Italy, involving all 10 indicator groups and 29 individual indicators, 10 were conducted in Finland and France respectively, eight studies each in Spain and Germany. In the remaining countries, less than five studies met the inclusion criteria and only seven studies were based on data collected in more than one European country (Fig. 1a).

According to the types of European forest ecosystems (EEA, 2006), studies were primarily carried out in hemiboreal, and nemoral coniferous and mixed broadleaved-coniferous forest ( $n=28$  with nine indicator groups), mesophytic deciduous forest ( $n=27$  with eight indicator groups), boreal forest ( $n=22$  with nine indicator groups), mountainous beech forest ( $n=19$  with seven indicator groups), lowland to sub-mountainous beech forest ( $n=13$  with six indicator groups), coniferous forests of the Mediterranean, Anatolian and Macaronesian regions ( $n=12$  with five indicator groups), alpine coniferous forest ( $n=8$  with six indicator groups), thermophilous deciduous forest ( $n=8$  with nine indicator groups) (Fig. 1b). In the remaining types, only sporadic studies ( $n=6$ ) met the inclusion criteria (Fig. 1b).

In 52 of the studies only one indicator was presented, while the other 90 studies involved more than one indicator and up to 33 indicators (Chirici et al., 2012) (Fig. 2). There were only 3 studies that tested a large number ( $n \geq 10$ ) of indicators statistically, and all of which included a number of indicators concerning individual species and species groups, e.g. birds, vascular plants and bryophytes (Smith et al., 2008; Zerbe et al., 2007; Berglund and Jonsson, 2001). The common results demonstrated that none of the species/species groups could act as indicator for all of the other species groups, and only certain species/species groups could act as surrogates for each other.

As shown in Fig. 3, structural indicators, i.e. deadwood ( $n=58$ ), vegetation structural indicators ( $n=49$ ) and other structural indicators ( $n=53$ ), were the most studied indicator groups. Among species/composition indicators, vascular plants ( $n=45$ ) and birds ( $n=33$ ) were most commonly studied. Beetles was the most taxa studied among invertebrate indicators (15/23 studies). Mammals and reptiles ( $n=12$ ), fungi ( $n=15$ ) and bryophytes ( $n=17$ ) were the least studied indicator groups (Fig. 3).

Among the individual indicators, deadwood volume, age of canopy trees, vascular plant species richness, tree canopy cover, decay class and deadwood diversity were the most frequently and widely used indicators in Europe, reflecting 24, 20, 19, 18, 14 and 9 indicandums respectively (Table 2). Among the 52 indicandums cited, three (species richness of overall birds, bryophytes, vascular plants) were intensively tested at different scales relating to 44, 52 and 53 individual indicators, respectively (see Appendices 1 and 2).

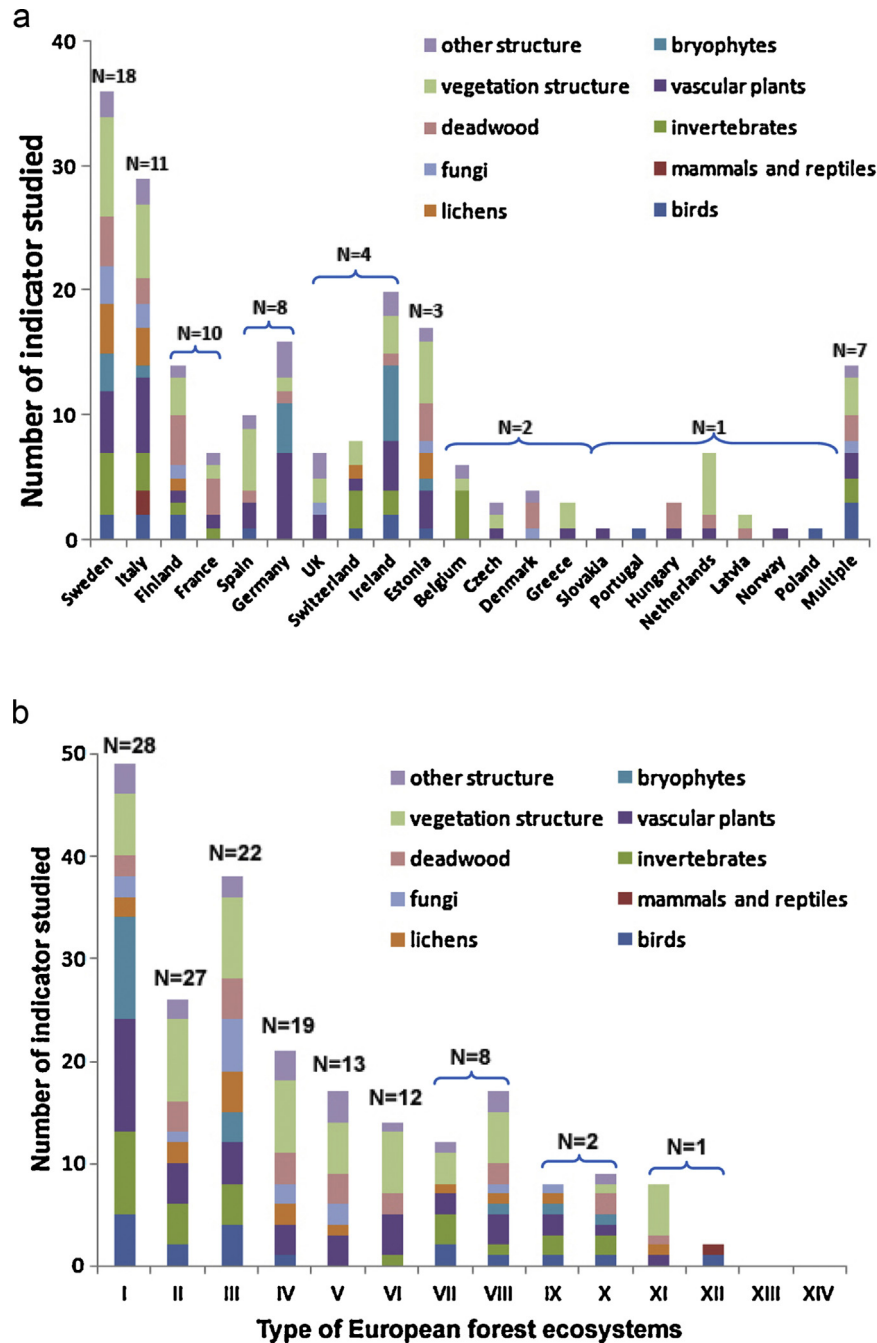
All the studies applied the indicators in tests of “present” connections between indicator and indicandum, rather than temporal trends in biodiversity. As the only exception, Gil-Tena et al. (2009) compared the change in richness of Mediterranean specialist and generalist forest bird species in two different periods over the last 20 years of the 20th century, based on forest maturation and spread.

**Table 1**

Indicator group and individual indicators identified in the 133 studies included in this review. “S”, “F” and “L” denote stand, forest and landscape scale, respectively, on which the indicators were tested or applied.

	Indicator group	Individual indicators
Species/compositional indicator	Bird (S/F/L)	Selection of bird species (S/F/L), Woodpecker family (L), Overall birds (S/F), <i>Tetrao urogallus</i> (F), <i>Dendrocopos leucotos</i> (L), <i>Dendrocopos medius/minor</i> (L), <i>Picooides tridactylus</i> (L), <i>Parus caeruleus</i> (F), <i>Prunella modularis</i> (S), <i>Troglodytes troglodytes</i> (S), <i>Turdus merula</i> (S), <i>Regulus regulus</i> (S)
	Mammal/reptile (F)	<i>Clethrionomys glareolus</i> , <i>Podarcis muralis</i>
	Invertebrate (S)	Overall beetles, Single saproxylic beetle species, Beetle family/genera richness, Rove beetles, Ground beetles, Saproxylic beetles, Red-listed saproxylic beetles, Worms, Centipedes, Millipedes, Butterflies, Spiders
	Vascular plant (S)	Short-lived trees, Understory of upper tree canopy, Woody vascular plants, Tree species/genus richness, Selection of vascular plant species, Overall vascular plants, <i>Fraxinus excelsior</i> , <i>Picea sitchensis</i> , <i>Agrimonia eupatoria</i> , <i>Euphorbia cyparissias</i> , <i>Polygonatum odoratum</i> , <i>Rubus</i> spp., <i>Vaccinium vitis-idaea</i> , <i>Corylus avellana</i>
	Bryophyte (S)	Mosses, Liverworts, Overall bryophytes, <i>Dicranum polysetum</i> , <i>Leucobryum glaucum</i> , <i>Pohlia nutans</i> , <i>Ptilidium ciliare</i> , <i>Thuidium tamariscinum</i> , <i>Hypnum jutlandicum</i> , <i>Dicranum scoparium</i> , <i>Kindbergia praelonga</i> , <i>Plagiothecium undulatum</i>
	Lichen (S)	Overall lichens, Epiphytic lichens, Macrolichens, Crustose lichens, <i>Lobaria pulmonaria</i>
	Fungus (S/F)	Overall fungus (S), Wood-living fungus (S), Corticioid fungus (S), Polypore (S), Selection of polypore species (S), Macrofungus genus richness (F)
Structural indicator	Deadwood (S)	Deadwood volume, Deadwood diversity, Decay class, DBH of CWD
	Vegetation structure (S/F/L)	Tree canopy cover (S/F/L), Shrub cover (S), Field layer cover (S), Vertical stratification (S/F), Forest shape (F), Basal area of trees (S), Tree DBH (S), No. of DBH class (S), Stem density (S), Tree height (S/F), Forest area (F/L), Forest fragmentation (L), Volume of living trees (S)
	Temporal and other structural indicator (S/F/L)	Age of canopy trees (S/F/L), Forest continuity (F), Microhabitat (S)

Note: The categorisation concerning indicator groups of vegetation structure and temporal and other structural indicators was based on a study by Zehm et al. (2003). Selection of bird/vascular plant/polypore species means that the species selected for birds, vascular plants and polypores were randomly chosen and belonged to different families. Microhabitat refers to any combination of the following elements: cavities, fruiting bodies of saproxylic fungi, ivy, sap runs, dead branches/crowns, missing/loose bark, etc. (Smith et al., 2008; Winter and Möller, 2008; Bouget et al., 2013; Regnery et al., 2013).



**Fig. 1.** (a) Categorisation of studies of forest biodiversity indicators according to indicator group and country in which the study was conducted. “N” refers to the number of articles from each country or multiple countries. (b) Categorisation of studies of forest biodiversity indicators according to indicator group and forest type in which the study was conducted. “N” refers to the number of articles from each forest type. I: hemiboreal, and nemoral coniferous and mixed broadleaved-coniferous forest; II: mesophytic deciduous forest; III: boreal forest; IV: mountainous beech forest; V: lowland to sub-mountainous beech forest; VI: coniferous forests of the Mediterranean, Anatolian and Macaronesian regions; VII: alpine coniferous forest; VIII: thermophilous deciduous forest; IX: broadleaved evergreen forest; X: acidophilous oak wood and oak-birch forest; XI: plantations and self-sown exotic forest; XII: floodplain forest; XIII: non-riverine alder, birch or aspen forest; XIV: mire and swamp forest (EEA, 2006).

The results demonstrated that species richness of both specialist and generalist forest birds increased with the forest age and size.

### 3.2. Scale of test/application of indicators

The group of bird indicators and the group of temporal and other structural indicators were studied from stand scale up to landscape scale. Only five correlations between species richness of birds and any specific indicandum were studied across different scales. Eglington et al. (2012) found that bird species richness very weakly reflected species richness of vascular plants, reptiles,

beetles and butterflies on all scales and only moderately reflected mammal species richness at larger spatial scales. However, other studies showed that bird species richness is positively correlated with species richness of vascular plants (Blasi et al., 2010; Santi et al., 2010) and butterflies (Santi et al., 2010) on stand scale.

Mammal/reptile indicators were studied on forest scale. Invertebrate, vascular plant, bryophyte, lichen, fungus, deadwood and vegetation structural indicators were mostly studied on stand scale, except for three studies testing the correlation between macrofungal genus richness and macrofungal species richness at forest scale (Balmford et al., 2000), vertical stratification and woodpecker and

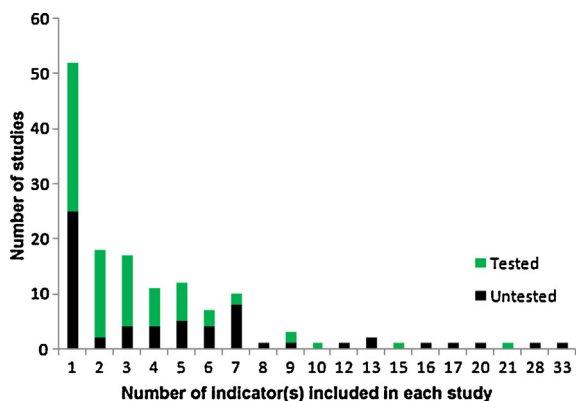


Fig. 2. Number of indicator(s) included in statistically tested and untested studies.

passerine species richness at forest scale (Kati et al., 2009), and age of canopy trees and forest bird species richness at landscape scale (Gil-Tena et al., 2009).

### 3.3. Strength of evidence for individual indicators

Surprisingly perhaps, 62 (43.7%) of the 142 studies did not test for statistical correlations between indicator(s) and indicandum. Of these 62 studies, 42 did not even present a clear indicandum. In more than 50% of all studies about birds, vascular plants, deadwood indicators and temporal and other structural indicators no statistical test of correlations were performed. The proportion was even less for mammals and reptiles, where only one study out of 12 tested the validity of the indicators (Fig. 3).

In total, 412 correlations between indicator and indicandum were identified, of which 388 were in relation to species richness/diversity and 24 included both species richness/diversity and species composition. Most of these correlations ( $n=380$ ) were tested only by one or two studies, leaving only 32 correlations with repeated tests in more than two studies. All these 32 correlations were tested at stand scale, the only exception being the correlation between species richness/diversity of bird and vascular plants, which was also tested at both forest and landscape scale (Eglington et al., 2012) (see Appendix 1).

Accordingly, correlations between indicator and indicandum were mostly assessed as having no indicator value ( $n=200$ , at

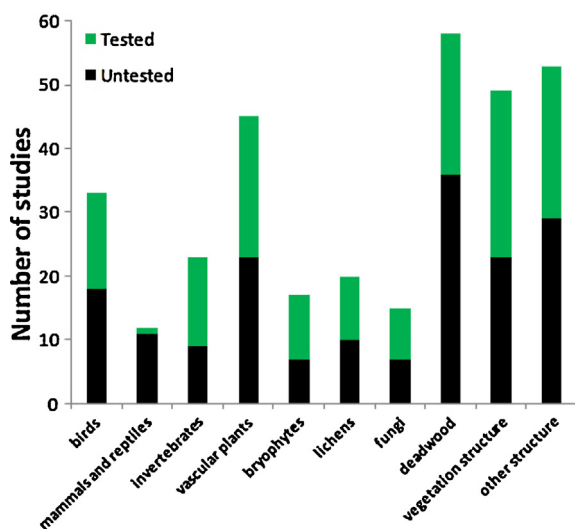


Fig. 3. Number of statistically tested and statistically untested studies for each of the indicator groups.

various scales) or weak evidence ( $n=215$ , at various scales). It is noteworthy that, 11 correlations, which were tested in more than two studies with no divergent result, were assessed as having no indicator value at stand scale (Fig. 4). 16 correlations were assessed as having moderate evidence (Fig. 4), which were mostly tested at stand scale except for two studies on forest scale (Dumortier et al., 2002; Berglund and Jonsson, 2001) and two on landscape scale (Gil-Tena et al., 2009; Jansson and Andrén, 2003). Only six correlations (five in terms of species richness/diversity and one in terms of species composition) were assessed as having strong evidence and all of these tests were conducted at stand scale (Table 2, Fig. 4).

For the species richness relationships, there was strong evidence of positive correlation in four cases, between: (1) deadwood volume and wood-living fungal species richness (four studies, conducted in both northern and southern Europe); (2) deadwood volume and saproxylic beetle species richness (one study each in Italy, Finland and Germany, three in France and two conducted across countries); (3) deadwood diversity and saproxylic beetle species richness (two studies in France and another two in Finland and Sweden); and (4) age of canopy trees and epiphytic lichen species richness (two studies each in Italy and Sweden) (Tables 2 and 3, Fig. 4). There was strong evidence of a negative correlation between tree canopy cover and spider species richness (three studies, all in Ireland; Tables 2 and 3, Fig. 4). Concerning the species composition-related correlation, there was strong evidence that the species composition of epiphytic lichens changed with the age of canopy trees (two studies each in Italy and Sweden; Tables 2 and 3, Fig. 4).

## 4. Discussion

A total of 142 research papers from Europe concerning indicators of forest biodiversity were investigated in this review. The studies were chosen from 857 hits in Scopus and 1140 hits in Web of Science by a number of criteria. The fact that the snowballing did not identify further eligible studies would suggest that the search strategy used was successful in identifying most relevant papers concerning indicators of forest biodiversity in Europe. By limiting the scope to Europe, we were able to compare the indicators against policies and also to limit the forest types to certain extent (e.g. excluding tropical forests, although there are up to 14 different forest types in Europe; EEA, 2006). We identified 83 indicators, representing 52 aspects of biodiversity (indicandum). In the studies reviewed, 412 correlations between indicator and indicandum could be distinguished. Sometimes the role of these was two-fold, i.e. an indicandum was also an indicator. Surprisingly, many studies did not test statistical correlation between indicator(s) and indicandum to validate whether the indicator truly indicated biodiversity. Despite this, there seems to be more or less consensus on existing indicators in EU policies, national environmental objectives and certification standards (FSC, PEFC). The number of studies on individual indicator and indicandum correlation was too low to provide a sound basis for meta-analysis or other statistical testing. Accordingly, qualitative synthesis and assessments were applied in the assessment of strength of evidence. Thus many results of this review are only as important as the recommendations for further research prompted by them.

### 4.1. Status of species/compositional indicators

Our review demonstrated that no species/compositional indicator had strong evidence of a correlation with its indicandum. Because so few studies tested correlations between a particular indicator and indicandum, only a low number of studies confirmed possible correlations. However, previous studies have found that

**Table 2**

The most tested correlations concerning species richness/abundance/composition between indicator (x-axis) and indicandum (y-axis). “S”, “M”, “W” and “N” denote Strong, Moderate, Weak evidence and No indicator value, respectively. Superscript letters “S”, “F” and “L” denote Stand, Forest and Landscape scale, respectively. Asterisk (\*) means that species composition of indicandum changes with species composition of species indicators or with configuration of structural indicators. Underlining, i.e. “\_” and “~”, indicates that the correlation was tested by ≥ 3 studies and by two studies, respectively.

	Age of canopy trees	Tree canopy cover	Decay class	Deadwood diversity	Deadwood volume	Overall vascular plant
Overall bird						<u>M<sup>S</sup></u>
Red-list bird						
Forest bird						
Old forest bird						
Woodpecker						
Passerine						
Mammal						
Herpfile						
Bat						
Overall beetle			<u>N<sup>S</sup></u>	<u>N<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>N<sup>S</sup></u>
Red-list beetle	<u>W<sup>S</sup></u>			<u>S<sup>S</sup></u>	<u>S<sup>S</sup></u>	<u>N<sup>S</sup></u>
Saproxyltic beetle		<u>W<sup>S</sup></u>	<u>M<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	
Red-list saproxyltic beetle		<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	
Conifer specialist saproxyltic beetle		<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	
Broadleaf specialist saproxyltic beetle		<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	
Generalist saproxyltic beetle		<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>	
Rove beetle	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>				<u>W<sup>S</sup></u>
Click beetle	<u>W<sup>S</sup></u>	<u>W<sup>S</sup></u>				<u>W<sup>S</sup></u>
Ground beetle						
Forest ground beetle	<u>W<sup>S</sup></u>					
Non-forest ground beetle	<u>W<sup>S</sup></u>					
Ant						
Ground-dwelling spider						
Butterfly						
Snail						
Centipede						
Hoverfly						
Millipede						
Oligochaete						<u>N<sup>S</sup></u>
Overall vascular plant						
Forest vascular plant						
Understory vascular plant						
Overall lichen						<u>N<sup>S</sup></u>
Red-list lichen						<u>W<sup>S</sup></u>
Epiphytic lichen						<u>N<sup>S</sup></u>
Crustose lichen						<u>W<sup>S</sup></u>
Cyanolichen						<u>N<sup>S</sup></u>
Macrolichen						<u>W<sup>S</sup></u>
Epiphytic microlichen						<u>N<sup>S</sup></u>
Overall fungus						
Red-list fungus						<u>W<sup>S</sup></u>
Polypore						<u>W<sup>S</sup></u>
Corticioid fungus						<u>N<sup>S</sup></u>
Macrofungus						<u>W<sup>S</sup></u>
Red-list macrofungus						<u>W<sup>S</sup></u>
Wood-living fungus						<u>N<sup>S</sup></u>
Red-list wood-living fungus						<u>W<sup>S</sup></u>
Overall bryophyte						<u>W<sup>S</sup></u>
Red-list bryophyte						<u>W<sup>S</sup></u>
Forest bryophyte						<u>W<sup>S</sup></u>
Mass						<u>W<sup>S</sup></u>
Liverwort						<u>W<sup>S</sup></u>
<b>Sum of indicandum</b>						<b>19</b>
						<b>24</b>
						<b>9</b>
						<b>14</b>
						<b>18</b>
						<b>20</b>

**Table 3**

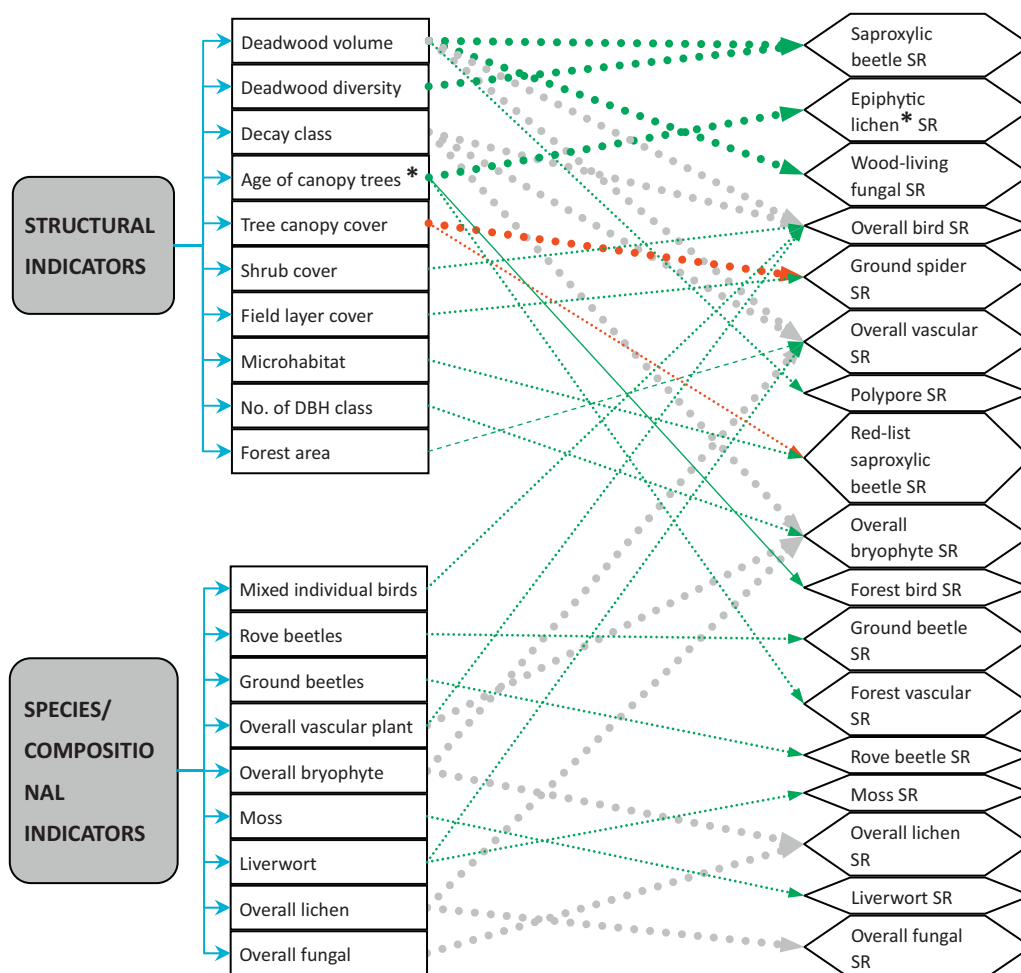
Details of studies reporting correlations with strong evidence, i.e. correlations between (1) deadwood volume–wood-living fungi; (2) deadwood volume–saproxylic beetles; (3) deadwood diversity–saproxylic beetles; (4) age of canopy trees–epiphytic lichens; (5) tree canopy cover–ground spiders. Asterisk (\*) means that species composition of indicandum changes with configuration of structural indicators.

Author	Country	Indicator	Indicandum	Scale	Approach	Result
Blasi et al. (2010)	Italy	Deadwood volume Deadwood volume	Wood-living fungi <sup>1</sup> Saproxylic beetles <sup>2</sup>	Stand	Forest structure, vascular plants, lichens, bryophytes, wood-living fungi, saproxylic beetles and birds were sampled in mature and old-growth stands in southern Italy. Spearman's correlation coefficients between species richness data and structural attributes were calculated.	Deadwood volume was positively correlated with species richness of wood-living fungi ( $p < 0.05$ ) and saproxylic beetles ( $p < 0.001$ ).
Bouget et al. (2013)	France	Deadwood volume Deadwood diversity	Saproxylic beetles <sup>2</sup> Saproxylic beetles <sup>3</sup>	Stand	Data on saproxylic beetles in 104 oak and 49 beech stands in seven French lowland forests was collected. Deadwood, microhabitat and stand features (large trees, openness) were used as predictor variables to describe local forest conditions.	Deadwood diversity was a consistent key habitat feature for saproxylic beetle species richness and composition in deciduous forests. Large downed deadwood volume was a significant predictor of beetle species richness in oak forests.
Brin et al. (2009)	France	Deadwood volume Deadwood diversity	Saproxylic beetles <sup>2</sup> Saproxylic beetles <sup>3</sup>	Stand	Species richness of saproxylic beetles was used as a case study to test the "species" and "environmental" indicator approaches. Single species abundance or occurrence and deadwood volume or diversity was compared as predictor variables.	Deadwood variables appeared to be good predictors of saproxylic beetle richness at the stand scale, with at least 75% of variance explained. Deadwood diversity variables consistently provided better predictive models than volume variables.
Brin et al. (2011)	France	Deadwood volume	Saproxylic beetles <sup>2</sup>	Stand	The differences in saproxylic beetle assemblages were investigated among four different diameter classes of downed woody oak and maritime pine debris in France. Beetles were sampled using in situ emergence traps. The diameter of deadwood pieces ranged from 1 to 40 cm.	More saproxylic species were observed in large logs and branches than in small logs. This study confirms that not only large deadwood pieces are relevant for saproxylic biodiversity conservation but also the smallest pieces. Therefore, forest managers would be well advised to maintain a high diversity of deadwood to maintain saproxylic biodiversity.
Djupström et al. (2010)	Sweden	Deadwood diversity	Saproxylic beetles <sup>3</sup>	Stand	The surrogate capacity of dead wood was tested. A species and dead wood inventory was conducted in forest sites in a boreal forest region in central Sweden.	Dead wood diversity represented saproxylic beetles and bryophytes better than random selection and might therefore function as a conservation surrogate for those taxa.
Juutinen et al. (2006)	Finland	Deadwood volume Deadwood volume Deadwood diversity	Wood-living fungi <sup>1</sup> Saproxylic beetles <sup>2</sup> Saproxylic beetles <sup>3</sup>	Stand	How well reserve selection was tested based on the amount and quality of decaying wood results in a representation of four ecologically different taxa (beetles, birds, wood-inhabiting fungi and vascular plants).	Deadwood volume and diversity were relatively good indicators of saproxylic beetle species but not overall species richness. Also good for wood-inhabiting fungi species, but not good for birds and vascular plants.
Lachat et al. (2012)	Multiple	Deadwood volume	Saproxylic beetles <sup>2</sup>	Stand	The effect of the amount of dead wood and temperature on saproxylic beetle species presence was studied. Data from 988 trap catches from 209 sites in 7 European countries was analysed.	Generally, we found more saproxylic beetle species at sites with larger amounts of dead wood.
Lassauce et al. (2011)	Multiple	Deadwood volume Deadwood volume	Wood-living fungus <sup>1</sup> Saproxylic beetles <sup>2</sup>	Stand	A meta-analysis was used to study the correlation between deadwood volume and the species richness of saproxylic beetles and wood-living fungi relative to several predictors at the forest stand level: biome, type of deadwood (log, snag, and stump) and decay class (fresh vs. decayed).	The correlation between deadwood volume and species richness of saproxylic beetles and fungi was significant but moderate, and was more correlated in boreal forests than in temperate forests.
Müller et al. (2010)	Germany	Deadwood volume	Saproxylic beetles <sup>2</sup>	Stand	The effects of dead wood due to bark beetle infestation and tree senility on abundance and richness of saproxylic species of beetles were investigated.	Increasing amounts of dead wood had positive effects on the abundance of host-generalist, broadleaf-specialist, conifer-specialist, and red-listed saproxylic beetles.



Table 3 (Continued)

Author	Country	Indicator	Indicandum	Scale	Approach	Result
Ylläsjärvi et al. (2011)	Finland	Deadwood volume	Wood-living fungi <sup>1</sup>	Stand	The relationships between 86 wood-inhabiting fungal species richness and 35 habitat variables in 81 northern boreal old-growth forest stands in Finland were analysed using generalised linear models.	The species richness increased with the volume of coarse woody debris (CWD), the mean DBH of CWD and the basal area of living trees.
Brunialti et al. (2010)	Italy	Age of canopy trees	Epiphytic lichens <sup>4*</sup>	Stand	Plots representing two forest types ( <i>Fagus sylvatica</i> and <i>Quercus cerris</i> forests) and two forest categories (old-growth (OG) and non-OG forests) were selected in the Cilento and Vallo di Diano National Park (Italy). The presence and the abundance of bryophytes and epiphytic lichens were recorded. Structural variables of the forests and vascular plant species richness were used as predictors.	Higher species richness of epiphytic lichen was related to OG stands, while a qualitative (species composition) rather than a quantitative (species richness) difference between the two forest types was observed. The results suggest that old trees are a main structural feature affecting cryptogam communities.
Fritz et al. (2008)	Sweden	Age of canopy trees	Epiphytic lichens <sup>4*</sup>	Stand	The effects of forest continuity at local scale for red-listed and indicator species of epiphytic lichens and bryophytes were investigated in 150 <i>Fagus sylvatica</i> stands in southern Sweden.	Stand age was significantly positively correlated to the different epiphytic lichen groups. The quantity of substrates, stand age and forest continuity were the three most important factors explaining species richness and composition of the studied epiphytes.
Johansson et al. (2007)	Sweden	Age of canopy trees	Epiphytic lichens <sup>4*</sup>	Stand	The influence of tree- and stand-level conditions on lichen diversity on 143 ash trees varying in age from 11 to 140+y was examined in 5 deciduous stands in southern Sweden.	Lichen species richness increased with tree age until 65 years and lichen species composition changed along with tree age. Species richness over time depended more on species turnover.
Nascimbene et al. (2009)	Italy	Age of canopy trees	Epiphytic lichens <sup>4*</sup>	Stand	The influence of tree age and age-related parameters on tree-level richness and community composition of lichens on spruce was evaluated in an Alpine forest. Survey of lichen community in the Paneveggio spruce forest.	Lichen species richness increased with tree age, and several lichens were associated with over-mature trees. Lichen species composition changed from young to old trees too.
Smith et al. (2008)	Ireland	Tree canopy cover	Ground spiders <sup>5</sup>	Stand	Compositional, structural and functional indicators of biodiversity were developed for five taxonomic groups—bryophytes, vascular plants, spiders, hoverflies and birds—using data from 44 Sitka spruce ( <i>Picea sitchensis</i> ) and ash ( <i>Fraxinus excelsior</i> ) plantation forests in Ireland.	Spider species richness decreased with tree canopy coverage.
Coote et al. (2013)	Ireland	Tree canopy cover	Ground spiders <sup>5</sup>	Stand	Candidate biodiversity indicators had been identified in a previous study using data from Irish Sitka spruce ( <i>Picea sitchensis</i> ) and ash ( <i>Fraxinus excelsior</i> ) plantations but had yet to be tested on independent data. In this study, the provisional indicators for vascular plant, bryophyte, spider and bird diversity were tested on data from Irish Scots pine ( <i>Pinus sylvestris</i> ), oak ( <i>Quercus petraea/Quercus robur</i> ), Sitka spruce and lodgepole pine ( <i>Pinus contorta</i> ) plantations.	Ground spider species richness decreased with tree canopy cover, especially in coniferous forest. The same applied to forest-associated spider species richness.
Oxbrough et al. (2006)	Ireland	Tree canopy cover	Ground spiders <sup>5</sup>	Stand	Ground-dwelling spider assemblages in glades, rides and forest roads of various sizes were investigated in 12 mature Sitka spruce ( <i>Picea sitchensis</i> ) plantations across Ireland. Spiders were sampled along a transect from the open space into the forest using pitfall traps.	Ground spider species richness and abundance decreased with tree canopy coverage. Open space in forest was an important determinant of spider assemblage structure, which supported a unique spider fauna, absent within the highly closed forests.



**Fig. 4.** Correlations with strong evidence (bold green/red arrow lines,  $n = 5$ ), moderate evidence (fine green/red arrow lines,  $n = 16$ ) and no indicator value (tested by  $\geq 3$  studies without divergent results, bold grey arrow lines,  $n = 11$ ) between indicators (rectangles) and their indicandum (hexagons). Green arrow represents positive correlation, red arrow represents negative correlation, grey arrow represents no correlation. Dotted lines represent stand scale, dashed lines forest scale and solid lines landscape scale. Asterisk (\*) indicates that species composition of indicandum changes with configuration of structural indicator. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

correlations in species richness between taxa vary with habitat, scale and landscape context (e.g. [Ekroos et al., 2013](#)). [Vessby et al. \(2002\)](#) studied the extent of covariation between species richness of six different taxa (plants, birds, butterflies, bumblebees, ground beetles and dung beetles) in non-forested ecosystems (31 Swedish semi-natural grasslands) and found few correlations between taxa. Identification of indicator species which can provide information on the presence and status of a range of species groups sounds plausible and if such indicator relationships can be shown to exist, sampling for just the selected species might greatly reduce the workload and the costs of field surveys. However, these indicator relationships are poorly understood and rarely substantiated across habitats, scales etc. Some correlations were found in the results, none of them with strong evidence. The species/compositional indicators could be studied repeatedly by unifying forest types, scales and landscape contexts. Future studies should initially focus on those indicators with moderate evidence, e.g. shrub cover, tree diameter class, microhabitat etc. ([Fig. 4](#)).

#### 4.2. Importance of structural indicators

Of the 412 correlations, strong evidence that the indicators in question accurately indicated specific aspects of biodiversity were

found for only six, and all of these were related to four structural indicators (i.e. dead wood volume, dead wood diversity, tree canopy cover and age of canopy trees). The indicandums of the indicators with strong evidence of a correlation were relatively narrow within the biodiversity spectrum. For example, saproxylic beetle species comprised 37% of the total number of beetle species studied in European forests ([Juutinen et al., 2006](#)), making it relatively easy to find an indicator indicating the status of saproxylic beetles rather than the status of total beetles. An indicator for the wider biodiversity spectrum was not identified. There is probably a dichotomy here, since an indicator of wider spectrum of biodiversity could be better by indicating “more biodiversity”, but at the same time could lose precision because the correlation between indicator and indicandum could be more susceptible to influences from variation of habitat, scale and landscape context ([Ekroos et al., 2013](#)). For example, the results showed that species richness/diversity of overall vascular plants and overall bryophytes were the most studied indicandums, but no correlation with strong evidence was found between them and their indicators. Therefore, future studies should re-test any correlations with moderate and weak evidence, rather than choosing new indicators to test. Furthermore, the identified indicators could be used together to indicate a wider spectrum of biodiversity.

#### 4.3. Methodological strengths and weaknesses of biodiversity indicator research

Many of the studies reviewed (62/142) did not test the statistical validity of indicators, but used a selection of indicators referred to in other studies (e.g. [Brin et al., 2008](#)) or by logical inference (e.g. [Virkkala, 2006](#)). Furthermore, 42 out of these 62 studies did not present a clear indicandum, but merely stated “biodiversity”. For example, [Torrás and Saura \(2008\)](#) studied the effects of silvicultural treatments on biodiversity maintenance in Mediterranean forests. They chose six forest biodiversity indicators (snags, mature trees, shrub abundance, shrub species richness, tree species richness and tree species diversity) cited in other studies as representing biodiversity. However, the study described only how silvicultural treatments impacted on the six indicators, without reporting which aspect of biodiversity was affected by the treatments. Failing to define an indicandum of biodiversity and confusing indicandum and indicator seemed to be the main faults in many of the studies concerning biodiversity indicators. The indicandum of biodiversity is the ‘endpoint’ or the ‘fundamental objective’, whereas the indicator is the method or strategy used to achieve the ‘fundamental objective’ ([Failing and Gregory, 2003](#)). [Gao et al. \(2014\)](#) pointed out that although methods may be devised for measuring biodiversity in forests, these are useless unless the specific goals of forest management for biodiversity are known. Biodiversity indicators should thus correlate well with biodiversity end points of interest (e.g. [Duelli and Obrist, 2003](#); [Olsgard et al., 2003](#)). In a previous overview of forestry policies in Europe, [Kraus and Krumm \(2013\)](#) emphasised the problem of continuous debate between specialists and decision makers concerning the relevance of some indicators (e.g. landscape patterns), identification of critical threshold values for indicators (e.g. minimum amount of deadwood left in the forest), and the development of new combined indicators to describe forest biodiversity. [Larsson et al. \(2001a\)](#) also noted that use of structural indicators based on supposition, e.g. a more complex habitat will support a greater variety of species, need to be further validated.

#### 4.4. Lack of large-scale studies

As for the scales applied in the tests, most correlations were studied on stand scale, except for some bird indicator studies, and all correlations with strong evidence were identified on stand scale. This finding is interesting and probably says more about study methods (easier to study stand scale than landscapes) and the forester’s view of forests (stand scale is the most commonly entity in management of forests) than the actual importance of landscape. Individual indicators provide very specific perspectives on changes in components of biodiversity at the level of ecosystems, species and genes ([EEA, 2012](#)). The total species diversity in a landscape (gamma diversity) depends on alpha diversity (the number of species in a distinct forest stand, forest patch, or forest type) and beta diversity (the degree of variation of alpha measures across different stands, forest patches, or forest types) ([Kraus and Krumm, 2013](#)). Therefore only sampling on stand scale could be problematic, since e.g. the areas surrounding the stand are important refuges when management practices such as clearcutting are conducted in the landscape. Taking the long-term perspective, only extremely large stands can be successfully managed alone ([Larsson et al., 2001b](#)). A number of the papers reviewed (e.g. [Lassaue et al., 2011](#); [Gunnarsson et al., 2004](#)) extrapolated the results to larger landscapes and even national areas, but this could be misleading since diversity can vary within patches. Problems always arise when research results are generalised. For example, [Brin et al. \(2009, Section 4.3\)](#) suggested that the deadwood variable provides a suitable sustainable forest management indicator allowing evaluation of new management options. Such a conclusion is probably

true with regard to saproxylic beetles, but extrapolation to cover other taxa is risky. Nevertheless, SEBI has called for sub-regional scales of indicators (e.g. Mediterranean or Scandinavian scale) and also European scale ([EEA, 2012](#)). However, SEBI emphasises that very few indicators are available with good Europe-wide coverage for assessing trends ([EEA, 2012](#)). Thus, there is a need for scientifically tested indicators on landscape scale in order to create reliable pan-European indicators, although there are strong methodological and budget constraints on performing such large-scale studies.

#### 4.5. Long-term studies

The most important limitation in determining biodiversity trends is the general lack of long-term monitoring data ([Normander et al., 2012](#); [Collen et al., 2009](#)). [Normander et al. \(2012\)](#) concluded that if the purpose is to evaluate the 2020 targets for the EU, further efforts in monitoring programmes to obtain reliable, high quality data on biodiversity at acceptable spatial and temporal resolution are required. In the present review we found a number of long-term datasets (e.g. [Beck et al., 2013](#); [Sebek et al., 2012](#)), but only one revealing changes in species richness in relation to structure ([Gil-Tena et al., 2009](#)). However, we did not primarily search for and emphasise long-term data, but rather “present data”.

#### 4.6. Implications for policy and future practice

We found that indicators were unevenly studied according to the 14 European forest types, which was consistent with the number of studies across countries. This finding implies that most indicator–indicandum correlations have only been tested in one or few forest types, even including some correlations with strong evidence e.g. the correlation between tree canopy cover and spider species richness tested in hemiboreal, and nemoral coniferous and mixed broadleaved-coniferous forest ([Coote et al., 2013](#); [Smith et al., 2008](#); [Oxbrough et al., 2006](#)). Only the correlation between deadwood volume and saproxylic beetle species richness has been tested in various forest types ( $n=9$ ). This more or less reflects the outcome of existing pan-European indicators such as SEBI ([EEA, 2012](#)), where deadwood is the only indicator directly related to forest biodiversity. Deadwood seems to have become an important indicator in general, e.g. it is integrated as an indicator in the Swedish Environmental Quality Objectives (Sustainable forests), and thus it is worthwhile obtaining deeper knowledge about this indicator. [Rondeux and Sanchez \(2010\)](#) found that deadwood seems to be more complex than other forest variables (such as stand structure, vegetation and stand age) and thus difficult to harmonise between National Forest Inventories (NFIs) in Europe. Our review confirmed that a large number of studies have used deadwood as an indicator, but new regional or national inventories (or revisions of existing ones) to streamline deadwood are needed ([Rondeux and Sanchez, 2010](#)). For other indicators, particularly those with moderate and strong evidence, further studies should preferably focus on expanding the scope to forest types where the individual indicators validity have not yet been tested. Before such tests have been done, harmonisation of biodiversity indicators included in NFIs across Europe would not be valid, at least not from a scientific point of view.

Moreover, in a number of countries only a few indicators have been studied ([Fig. 1a](#)) and some countries use only one indicator (e.g. Slovakia, Portugal, Norway and Poland). Due to the complexity of biodiversity of forest ecosystems, with local preconditions for biodiversity, local areas could be neglected if indicators based on conditions in other countries are implemented. Therefore further investigation of more indicators in each country, locally and nationally, is recommended. Alternatively, future studies on biodiversity indicators could either prioritise those indicators with

moderate evidence, or continue testing for new indicandums for those indicators that already have strong evidence for one indicandum. Meanwhile, indicators with strong evidence of no correlation to the intended indicandum should be avoided.

The collection of data on threatened species is time-consuming and expensive, especially in conditions of high biological diversity and large forest areas (Kraus and Krumm, 2013). Our review found that some indicators have stronger evidence than others, which might be of use in future data collection work when there is a need to prioritise among indicators. Deadwood has been used as an indicator in scientific research and policy-related projects. Our results revealed that there was strong evidence only for deadwood volume and diversity as indicators of saproxylic beetle and fungal species, and extrapolating this relationship to other elements of biodiversity could be, as most projects did, misleading. Our results also revealed that individual biodiversity indicators normally only indicate a narrow spectrum of biodiversity. Multiple indicators need to be applied if a wider spectrum of biodiversity is to be described. However, it may be impossible to cover “overall” biodiversity, because the diversity of different taxa often appears idiosyncratic. Moreover, we found that the most frequently used indicators were

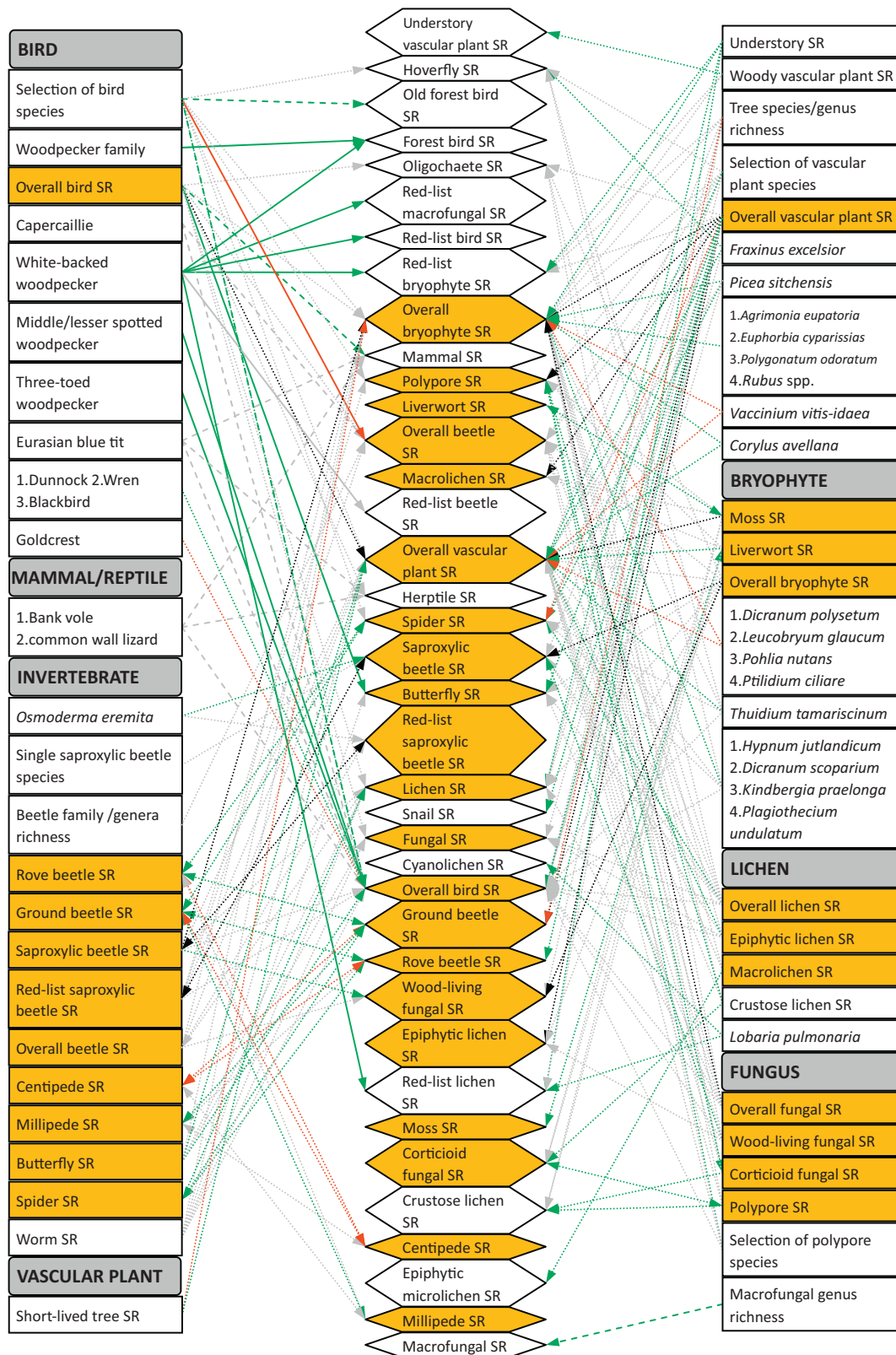
structure-based types that are easier for foresters and landscape managers to use than species/composition-based indicators. Going from science to implications and policies is not easy, so further validation is needed for the most frequently used indicators for which there is moderate and weak evidence and for other complementary indicators, e.g. for birds, mammals etc. Besides, future studies ought to find out the mechanisms driving correlations between indicators and indicandums, in order to choose and apply more robust indicators.

This review examined existing indicators and what they truly indicate in terms of European forest diversity. Due to the wide range of European forest ecosystems covered, the results might also be applicable beyond Europe and hopefully can be used in the next step of finding indicators for biodiversity functions.

### **Acknowledgements**

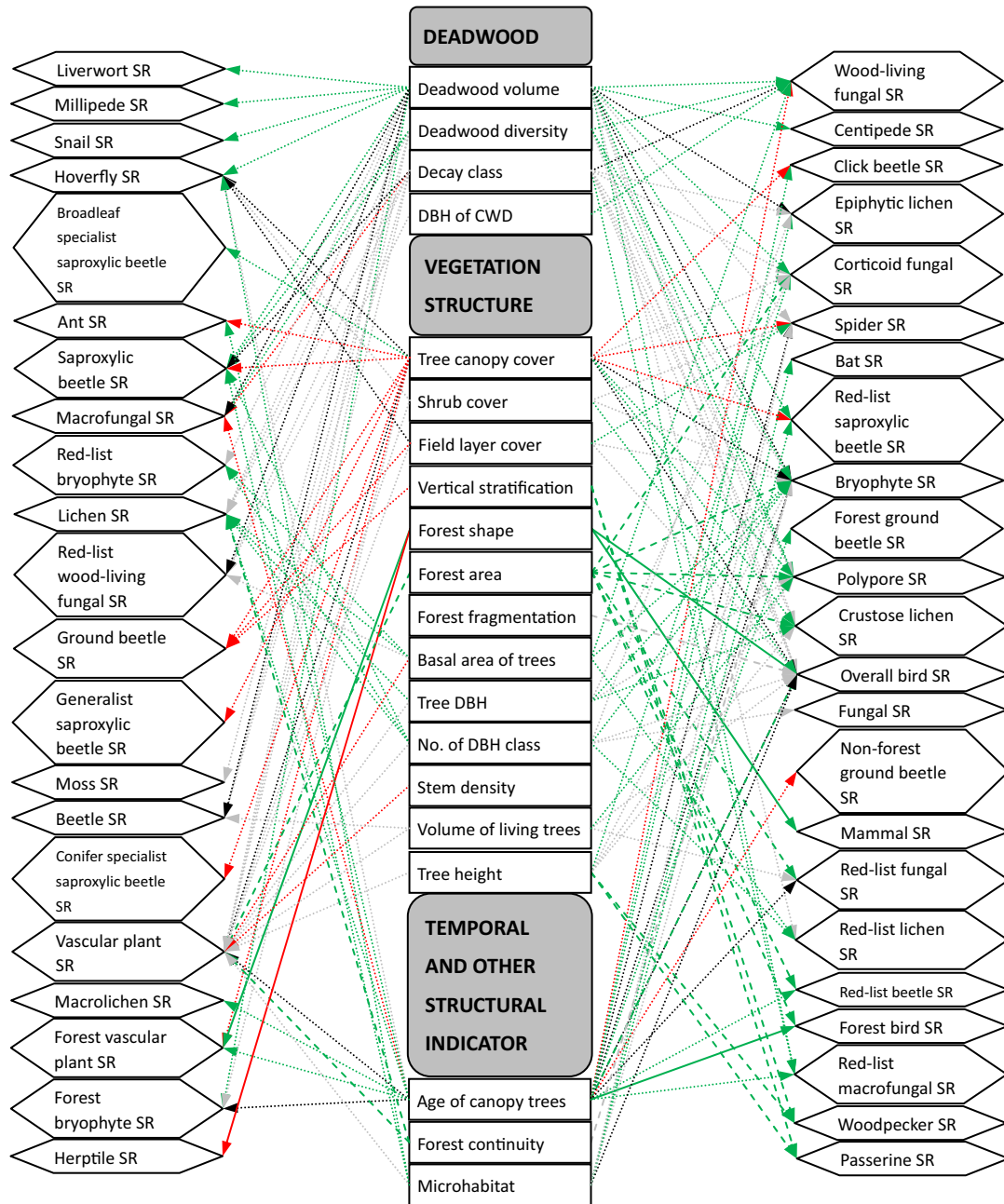
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Appendix 1.



**Fig. A1.** Correlation between species/composition indicators and their indicandum. Green arrow represents positive correlation, red arrow represents negative correlation, grey arrow represents no correlation, and black arrow represents uncertain correlation. Dotted line represents stand scale, dashed line forest scale and solid line landscape scale. Orange highlight means the element stands for both indicator and indicandum. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

Appendix 2.



**Fig. A2.** Correlation between structural indicators and their indicandum. Green arrow represents positive correlation, red arrow represents negative correlation, grey arrow represents no correlation, and black arrow represents uncertain correlation. Dotted line represents stand scale, dashed line forest scale and solid line landscape scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

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