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Limitations to the use of arthropods as temperate forests indicators

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Abstract Because arthropods dominate terrestrial ecosystems in species number and biomass, they can potentially play a major role as environmental indicators in applied ecology and nature conservation. We tested the suitability of arthropods as indicators for particular forest types based on a comprehensive standardized sampling of various taxa by different trap types in 93 mature temperate forest sites in three regions of Germany. We tested whether indicator species (1) can be derived for different forest types across regions, (2) are more widespread and more abundant than non-indicator ones, (3) belong to a particular taxon or trophic guild, and (4) are consistent between regions and years. Among 2041 sampled arthropod species, only four were significant indicator species for the same forest type in all region, and no single taxon or guild performed better than other groups. Indicators were generally more abundant and more widespread than non-indicators, but both abundance and distribution varied widely between species. When the analysis was

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repeated using data from the next year, indicator values of species significantly correlated between years, but the identity of more than 50 % of significant indicators changed, suggesting high among-year variability. We conclude that overall, arthropods did not turn out to be reliable indicators, at least at the scale of Germany. If anything, arthropod indicator species should be defined at the regional scale. Furthermore, indicators should be selected across taxa and trophic levels. Future evaluation of indicator species among arthropods should be conducted over several years based on standardized sampling protocols to develop a reliable definition of indicator species despite the high fluctuations in abundance of species among arthropods, which might either mask or overestimate the indicator value of particular species.

Keywords Biodiversity · Environmental indicator · Forest management · Indicator species · Land use · Temporal reliability

Introduction

Arthropods account for the bulk of global organismic diversity, representing almost 60 % of all metazoic species on earth (Whitfield and Purcell III 2012). They are major contributors of the animal biomass in any terrestrial ecosystem and have evolved an astonishing diversity of ecological traits and thus play an important role in ecosystem processes (Weisser and Siemann 2004). Although other taxa, such as mammals and birds, have smaller diversity and contribute less to ecosystem biomass, nature conservation mainly focuses on these taxa. This is also true for approaches where particular species are used as indicators for the value of a particular habitat or overall biodiversity in an area. Despite notable exceptions, such as for specialized butterflies (Brereton et al. 2009), rove and ground beetles (Pohl et al. 2007), spiders (Buchholz 2010), and a few other examples (e.g., Maleque et al. 2009), there is generally little reliable information about how suitable arthropods are as indicators for threat to biodiversity or for particular land-use practices.

In the past two decades, there has been an intensive debate over the best way to define indicator species (Lindenmayer 1999; McGeoch 1998). Indicators for particular land uses differ from other types of indicators such as those indicating high biodiversity. In the latter case, an indicator is a species whose presence and/or abundance correlates well with overall biodiversity. Most studies on biodiversity indicators have focused on indicators of species richness, rather than indicators of other measures of species diversity or of functional richness (Feld et al. 2009). In contrast, indicators of land use are species whose presence, abundance, or absence indicates a particular land use, e.g., a pristine forest habitat or a particular degradation stage. Ground-dwelling spider species, for example, revealed to be good indicators for the degradation of sand ecosystems following a change in land-use practices (Buchholz 2010). Finding such indicators of land use thus implies finding a significant association between a particular land use and the occurrence and abundance of a species and is therefore similar in methodology to finding significant associations between species and particular habitats. For this purpose, a number of approaches have been developed, in particular the species indicator method by Dufrene and Legendre (1997) has been found widespread application (e.g., Kelemen et al. 2013; Kreyling et al. 2008; Lachat et al. 2012). This methodology takes the relative abundance and occupancy of habitats into account and compares the occupancy of a particular species in different habitats with the occupancy predicted by a null model (Dufrene and Legendre 1997). Although it has been shown that for this approach there is a strong positive relationship between abundance, occupancy, and indicator value, relatively rare species are also selected as significant indicators when their association with a particular habitat is strong (e.g., McGeoch et al. 2002; McGeoch and Chown 1998).

While the method of Dufrene and Legendre (1997) was developed more than 15 years ago, it has not been systematically applied for conservation purposes. In the real world of conservation, data-based approaches such as IUCN Red List are still not the norm. Instead, indicators used to select sites for conservation are often species that are considered to be suitable flagship species (i.e., species with an appeal to the general public), umbrella species (i.e., species whose conservation is likely to lead to the conservation of other species as well, i.e., biodiversity indicators), or very rare species, and the selection is mostly not based on data. For example, the species listed in the Appendix II of the European Habitat directive (Council Directive 92/43/EEC of 21 May 1992), the currently most important European-wide legal instrument for conservation, entered this list mostly based on expert opinion rather than data, and present an interesting mix of different types of indicators.

In this study, we used the methodology by Dufrene and Legendre (1997) to test whether canopy and forest-floor living arthropods can be used as indicators for particular forest management types in Europe. The focus habitat are unmanaged beech forests, which would represent the dominant forest ecosystem in Central Europe in the absence of human intervention. Europe has a global responsibility for the protection of the remaining unmodified beech forests. Overall, 93 mature forest sites of three management categories, unmanaged beech forests, managed age-class beech forests, and managed age-class conifer forests, were sampled in three regions in Germany. In particular, we were interested in whether there were indicators for 'unmanaged' beech forests that represent the most pristine forest habitats in Germany. We asked the following questions: (1) Can arthropod indicator species be derived for unmanaged beech forests? (2) Do indicator species exist for any of the other forest management categories? (3) Are indicator species more widespread and more abundant than non-indicator species? (4) Do indicator species belong to a particular taxon or trophic guild? (5) How reliable are those indicator species between regions? and (6) How stable are indicator species between years?

Methods

Study regions

The study was conducted within the framework of the Biodiversity Exploratory Project in Germany (Fischer et al. 2010) using sites in three regions: Schwäbische Alb (Swabian Jura) in southwest Germany (09°10′49″–09°35′54″ E/48°20′28″–48°32′02″ N), the National Park Hainich and its surrounding areas (Hainich-Dün) in Central Germany (10°10′24″–10°46′45″ E/50°56′14″–51°22′43″ N), and Schorfheide-Chorin in northeast Germany (13°23′27″–14°08′53″ E/52°47′25″–53°13′26″ N) (see Appendix S1 in Supporting Information). Mean annual temperature is 6.0–7.0 °C in the Schwäbische Alb, 6.5–8.0 °C in the Hainich-Dün, and 8.0–8.5 °C in the Schorfheide-Chorin. This corresponds with a decrease in altitude and precipitation from the Schwäbische Alb (460–860 m a.s.l; 700–1,000 mm) to Hainich-Dün (285–550 m a.s.l; 500–800 mm), and to Schorfheide-Chorin (3–140 m a.s.l; 500–600 mm). Details on geology and soil types in the region can be found in Fischer et al. (2010). Forest plots in the three regions were selected using a stratified random sampling design (Fischer et al. 2010). About 500 candidate sites representing major forest types were selected for each region. Survey of soils, vegetation, and management were conducted in all sites. From the candidate points, 50 one-hectare forest plots were selected along a gradient of forest management intensity on the typical soils in the region (Schwäbische Alb: Cambisol/Leptosol; Hainch-Dün: Luvisol/Stagnosol; Schorfheide-Chorin: Cambisol). A number of additional criteria were employed for plot selection, e.g., a distance of at least 200 m between the borders of each plot (Fischer et al. 2010). The stratified random selection of plots was also used to reduce spatial autocorrelation problems.

Land-use categories and study plots

In all regions, unmanaged and differently managed beech (*Fagus sylvatica*) forests occur. In addition, there are stands of conifers, spruce *Picea abies* age-class forests in the Schwäbische Alb and Hainich-Dün, and pine *Pinus sylvestris* age-class forests in the Schorfheide-Chorin, all planted on former beech forest sites for timber production. For the present study, we were particularly concerned with the arthropod indicators associated with unmanaged beech forests (UB) and how they may differ from indicator species of managed beech (MB) and managed conifer forests (MC). The order of forest types from UB to MB to MC corresponds well with an increase in management intensity (Fig. S1-2). For this study, we selected 93 stands of the timber stage with tree age > 60 years, all located within large forest patches (see Appendix S1).

The unmanaged beech forests (19 stands) differ due to differences in past land use. In the Schwäbische Alb, today's unmanaged forests (five plots, see Appendix S1) were used formerly as pasture woodland resulting in very old beech trees (>200 years) with big crowns and low branching. The structural importance of these trees for biodiversity led to the protection of these stands. To achieve the aims of protecting the old beech trees, spruce trees are removed when necessary. Besides these minor management activities, three stands have not been managed for 70–80 years; the other two studied stands since 20–30 years. In the Hainich-Dün, unmanaged forests (seven plots) occur within the National Park Hainich that covers an area of 7,600 ha and was founded in 1997. The current area of the national park was a protection zone for a military training range from 1945 until 1990 and is characterized by uneven-aged (up to 250 years) beech forests today. In the Schorfheide-Chorin, unmanaged forests (seven plots) occur inside core areas scattered within the biosphere reserve. They are free of forest management since 1990, and maximum tree age is 180 years.

The managed beech forests (40 stands) are characterized by even-aged stands of different developmental stages (age classes). Rotation time for beech age-class forests is around 160 (±30) years. We selected even-aged beech-dominated (>70 % beech of tree basal area) stands of the timber stage (>80 years). Both, the unmanaged and the managed beech forests are characterized by an almost closed canopy structure without gaps. These shady conditions result in a nearly complete absence of a shrub layer. We studied 18 stands of this intensity class in the Schwäbische Alb, eight in the Hainich-Dün and 14 in the Schorfheide-Chorin.

For the conifer stands studied (28 stands), rotation time is around 100 years, shorter than in beech which leads to more frequent harvesting events. We thus considered this forest type to be the most intensively managed one. We selected twelve spruce stands in the Schwäbische Alb, four spruce stands in the Hainich-Dün region where this forest type is very rare, and twelve pine stands in the Schorfheide-Chorin. All stands were between 60 and 80 years old.

Arthropod sampling

Arthropods were sampled in 2008 using two methods. First, three funnel (pitfall) traps of 15 cm diameter (Lange et al. 2011) were buried in the forest floor in three corners of the 1-ha forest plots. Second, flight-interception traps were placed in the understory (1.5 m height) and in the mid-canopy (Kowalski et al. 2011) in the same corners. Flight-interception traps consisted of two crossed transparent plastic shields (40 cm × 60 cm) with a smooth plastic funnel attached to the bottom and to the top. At the end of both funnels, sampling jars were mounted.

For both trap types, a 3 % copper sulfate solution was used. A drop of detergent was added to reduce surface tension. Sampling was continuous from mid of April to mid of October (185 days each year) during the entire season. Traps were emptied monthly. Total sampling effort per plot was 370 trap-days for each of the three trap types. Samples were transferred to 70 % ethanol in the field. For the analysis of temporal reliability, we resampled 23 stands (Schwäbische Alb: 8, Hainch-Dün: 8, Schorfheide-Chorin: 7) including all forest types (UB: 8, MB: 6, MC: 9) with the same methodology in 2009 (see Appendix S1).

In the laboratory, samples were sorted to order level and the following taxa were identified to species level by taxonomic specialists: Araneae (pitfall traps only), Coleoptera (all traps), Hemiptera: Auchenorrhyncha, Heteroptera (all traps), Hymenoptera: Symphyta (all traps), Neuroptera (all traps), Mecoptera (all traps), Opiliones and Pseudoscorpiones (pitfall traps only), and Rhaphidioptera (all traps). For 2009, only data on Araneae (pitfall traps only), Coleoptera, Hemiptera: Auchenorrhyncha, Heteroptera, and Hymenoptera: Symphyta (all traps) was used.

Species were divided into trophic guilds using the following main categories: herbivores (parts of Coleoptera, Hemiptera: Auchenorrhyncha, Heteroptera, Symphyta), predators (Araneae, Opiliones, Pseudoscorpiones, Neuroptera, Rhaphidioptera, and parts of Coleoptera and Heteroptera), decomposers (parts of Coleoptera), and omnivores (parts of Hemiptera: Heteroptera, Mecoptera). Within these guilds, subgroups were distinguished (see Appendix S2). We defined herbivores as all species feeding by chewing or sucking predominantly on living plant tissue, predators as species feeding mainly on other arthropods (sucking or chewing), and decomposers as species feeding on fungi (mycetophagous), species decomposing wood (xylophages), other plant material (saprophagous), carrion (necrophagous), or feces (coprophagous). Finally, omnivores were defined as species in which several other guilds are a significant part of their diet (for details on classification see Appendix S2).

Data analysis

We used individual-based rarefaction curves and abundance-based species richness estimation (Chao 1987) to test for sampling completeness of the three forest types in the three regions.

For identifying indicator species, the approach by Dufrene and Legendre (1997) was applied. We used the enhancement of the method described by De Caceres and Legendre (2009) and De Caceres et al. (2010) which is provided by the R package 'indicspecies' (De Caceres and Jansen 2010). We used the group-based approach within the function *signassoc* to test the null hypothesis that the preference of a particular species for one of the forest types is due to chance only, using 9999 permutations to calculate p values for each forest type. Indicator values (IndVal.g), ranging from 0 (no association) to 1 (complete association), were calculated using the function *strassoc* (De Caceres and Jansen 2010) that are identical to the values returned by the original function of Dufrene and Legendre (1997). To correct for multiple testing, Sidak's p value correction was applied, implemented in *signassoc*. It was preferred to the more common Bonferroni correction due to its better statistical performance (Abdi 2007).

We calculated the indicator value, and its significance, for every species, separately for each of the three forest types and for each region. After identifying the indicator species, we analyzed how they were distributed among taxonomic orders and trophic guilds. Replicated goodness-of-fit tests were used, first, to test for heterogeneity in the proportion of indicator species among taxa and trophic guilds and, second, to test whether the proportion of indicator species in each taxon differs from the total observed proportion. For the heterogeneity test, the five taxa (Auchenorrhyncha, Mecoptera, Pseudoscorpiones, Raphidioptera, Symphyta) with a low number of species were lumped together (see Appendix S3 and S2). We tested whether indicator species differed from non-indicator species with respect to frequency of occurrence and overall abundance using Wilcoxon rank sum tests with continuity correction.

In a final analysis, we compared indicator species among regions. To analyze whether communities of all species, or of indicator species only, differed among regions and forest type, a non-metric multidimensional scaling based on Bray-Curtis distance matrices was applied, using the *vegdist* and *metaMDS* functions within the R package 'vegan' (Oksanen et al. 2010).

To analyze temporal reliability, we use the Pearson product moment correlation between the indicator values of species sampled in both 2008 and 2009.

All calculations were performed within the R software R 2.14.0 (RDevelopmentCoreTeam 2011).

Results

Overall, we found 233,234 specimens of 2,041 arthropod species in the 93 plots of the three regions (Schwäbische Alb: 1,018; Hainich-Dün: 943; Schorfheide-Chorin: 1,521). Sampling completeness of the three forest types in the three regions ranged from 63 % (unmanaged beech forests in the Schorfheide-Chorin) to 78 % (managed beech forests in the Hainich-Dün) (see Appendix S4). Three hundred and eighty-two species (25 %) were calculated to be indicator species at least in one of the three regions (Fig. 1): 114 in the Schwäbische Alb (11 % of all species sampled in the region), 112 (12 %) in the Hainich-Dün, and 241 (16 %) in the Schorfheide-Chorin. Most (57 %) of these 382 indicator species were indicators for conifer forests. In the Schwäbische Alb, 10.4 % of all species sampled in conifer forests were indicators for this forest type in the Hainich-Dün and Schorfheide-Chorin, and the proportion were 11.1 and 13.2 %, respectively. Overall, 20 % of indicator species were indicators for managed beech (3.8, 5.9, 5.4 %) and 15 % were indicators for unmanaged beech forests (3.8, 3.4, 6.3 %). Only in the Schorfheide-Chorin,

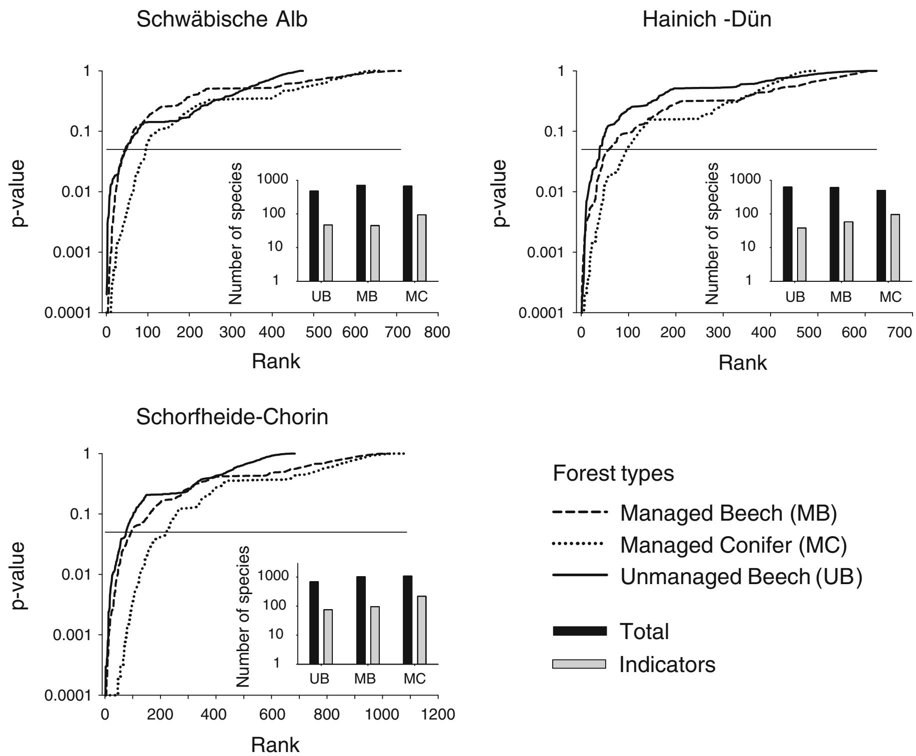

Fig. 1 Indicator-value analysis for arthropods in three regions of Germany. Graphs show, for each species sampled, the significance of its Indicator value. Species are ranked according to the *p* value of the analysis. The *solid line* in each figure indicates the border for significant indicator species at $p \leq 0.05$. The *inset* shows the number of total species and indicator species for each of the three forest types. A total of 2041 arthropod species were analyzed

the percentage of indicators for unmanaged beech were higher than those for managed beech forests (Fig. 1).

Indicators in different arthropod orders

Indicator species were found in almost all taxa investigated (Fig. 2). The distribution of indicator species among taxonomic grouping often deviated from a random distribution, but there was no taxon that consistently had a higher proportion of indicator species (Fig. 2). For Opiliones, Neuroptera, Araneae, and Heteroptera, relatively high indicator values were found in all three regions (Fig. 2, Table S1-1), mainly for conifer forests. The percentage of indicators for unmanaged beech were generally low, and often these indicator species were true bugs, Heteroptera (Fig. 2, Table S1-1).

Indicator species frequency and abundance

The proportion of forest stands occupied and average abundances were generally higher in indicator species than in non-indicator species (Fig. 3). However, indicator species included both rare and abundant species as well as frequently occurring and not so

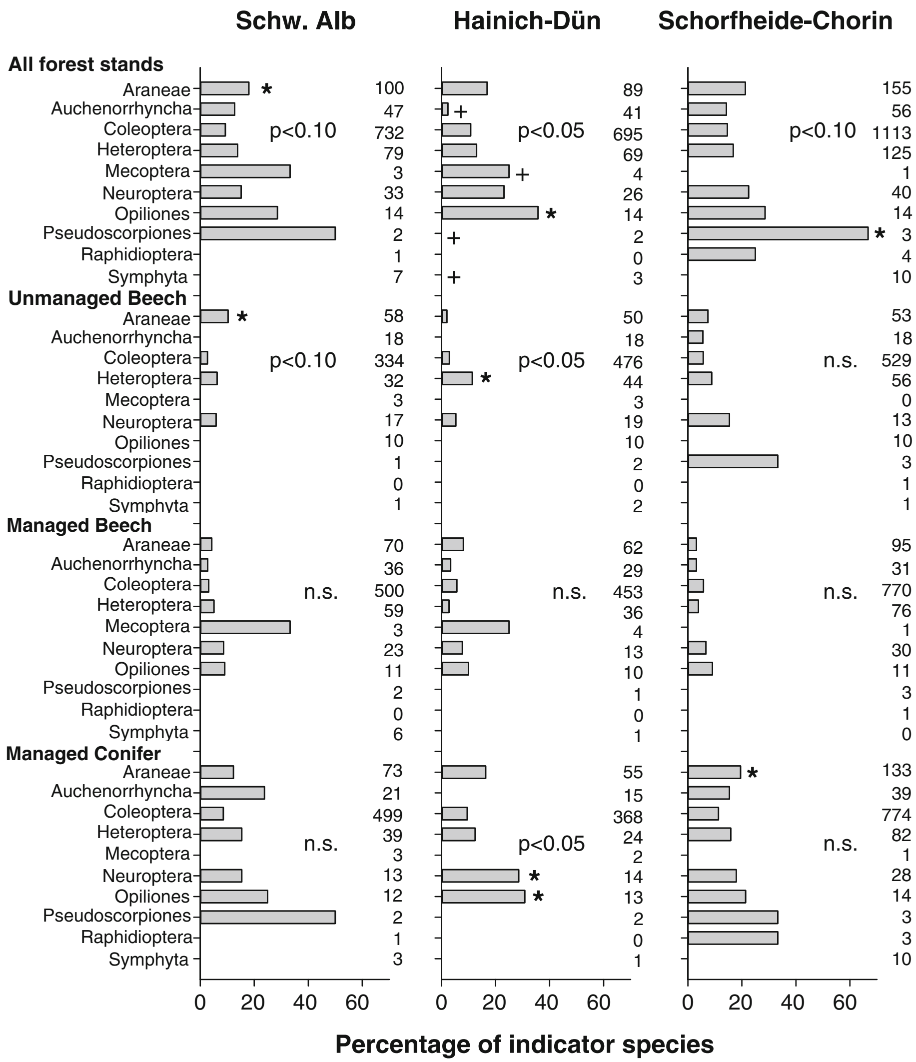

Fig. 2 Differences in the percentage of species within each taxonomic group that were found to be significant indicators (*bars*). The G statistic was used (i) to test for heterogeneity in the percentage of indicator species among taxa (*p* values in figure) and (ii) to test whether the percentage of indicator species in each taxon differs from the total percentage of indicator species found for one particular forest type (*, taxa significantly higher at 0.05; + pooled taxa with IS ≤ 1 significantly smaller at 0.05). For the heterogeneity test, taxa with IS ≤ 1 were lumped together. The numbers right of the *bars* indicate total number of sampled species within each taxon. Details and statistics are given in the Appendix S3

frequently occurring species (Fig. 3). Abundance ranks of indicator species based on mean species abundances per occupied plot ranged between 1 and 1,355 (mean rank 434). In the Schwäbische Alb, regional abundance ranks of indicators ranged from 5 to 583 (mean rank 195), in the Hainich-Dün from 2 to 748 (203), and in the Schorfheide-Chorin from 1 to 1,093 (326).

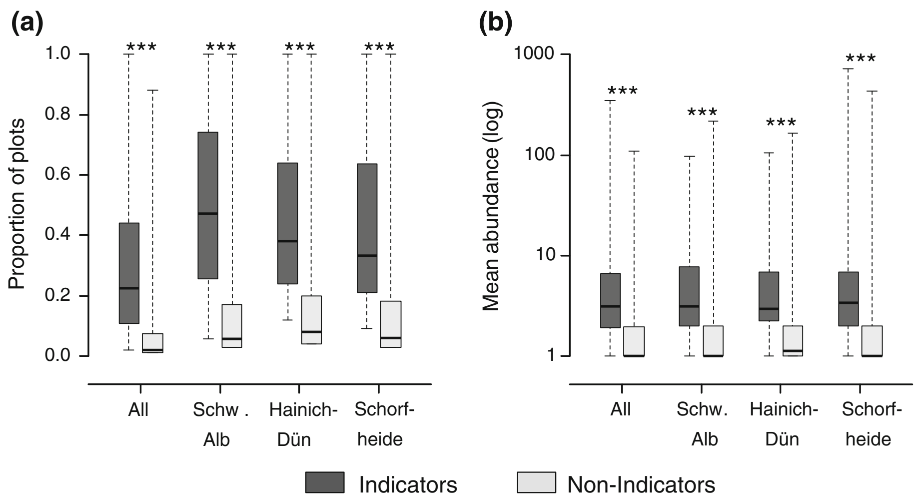

Fig. 3 Frequency (**a**) and local abundance (**b**) of indicator and non-indicator species. Frequency was defined as the proportion of plots where a particular species occurred (all plots or plots of a particular region); local abundance was defined as mean abundance per plot in which a particular species occurred. *Boxes* indicate 25 and 75 % quantiles and whisker the Min–Max values. In all three regions, frequency and mean abundance of indicator species were significantly higher than those of non-indicator species (Wilcoxon rank sum test with continuity correction; *** $p < 0.001$)

Indicators in different trophic guilds

Indicators occurred in all trophic guilds, and generally no guild had a higher than expected number of indicator species (Fig. 4). Although in all three regions the highest fraction of indicators were observed in omnivores and predators, differences among trophic guilds were only significant in the Schwäbische Alb and the Hainich-Dün (Fig. 4, Appendix S2). Herbivores were significant indicators less often than expected, but only in the Hainich-Dün and the Schorfheide-Chorin. While omnivores and xylophagous species showed the highest percentage of indicators for unmanaged beech, these were necrophagous and omnivorous for managed beech and predators, mycetophagous, and xylophagous for conifer forests (see Appendix S2).

National versus regional indicators

In total, there was a considerable degree of overlap of species occurrence between the different regions in Germany; 23.8 % of all species occurred in all regions and 46.8 % of all species in at least two regions (Fig. 5). The highest number of region-specific species was found in the Schorfheide-Chorin. Despite this overlap in regional species occurrence, the regional overlap in indicator species was low. Approx. 80 % of all indicator species were found to be indicator in one region only, and only 19 % were indicators in two regions. Interestingly, species were sometimes indicators for different forest types in different regions (22 = 6 % of all indicator species). In total, only seven species were indicators in all regions (Fig. 5), and only four of those were indicators for the same forest type in each region. Among these, *Phytocoris tiliae* (Heteroptera: Miridae) was the sole indicator of unmanaged beech forest in Germany. This species is omnivorous: Both larvae and adults feed on both leaves and other arthropods on deciduous trees. Similarly, a very

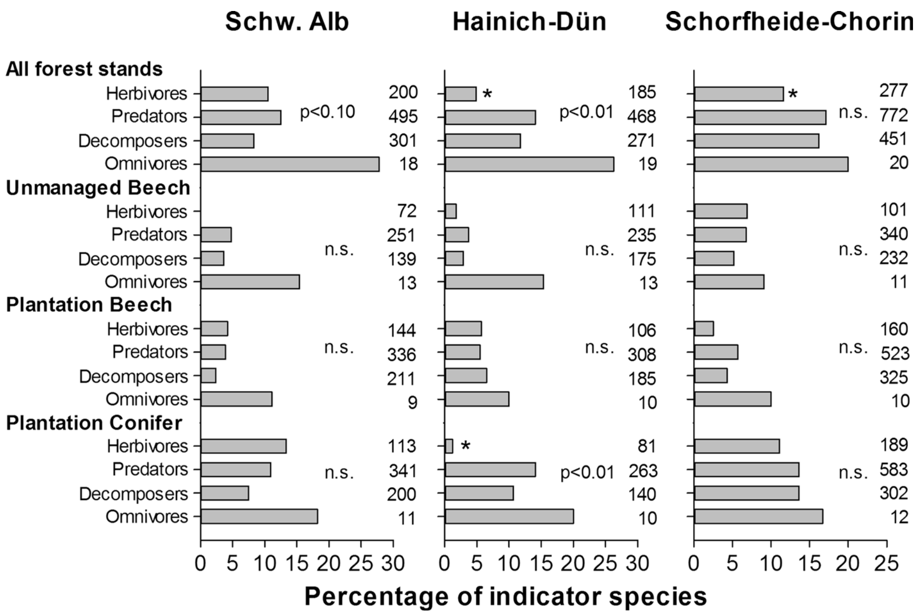

Fig. 4 Differences in the percentage of indicator species among trophic guilds. The G statistic was used (i) to test for heterogeneity in the proportion of indicator species among trophic guilds (*p* values in figure) and (ii) to test whether the proportion of indicator species in each trophic guild differs from the total observed proportion (*, significantly smaller at 0.05). The numbers right of the *bars* indicate species numbers. Details and statistics are given in the Appendix S2

low number of species were nation-wide indicators for the other forest types in all regions: For managed beech, it was only *Hemerobius micans* (Neuroptera: Hemerobiidae), a predator which prefers monodominant beech forests. For conifer forests, two species were indicators in all regions, the xylophagous bark beetle *Hylastes cunicularius* (Coleoptera: Scolytidae) which is known to attack different conifer species and the beetle *Anisotoma humeralis* (Coleoptera: Leiodidae) which feeds on fungi growing on deadwood. One more indicator species for unmanaged beech (Araneae: *Microneta viaria*), two more for managed beech (Coleoptera: *Anoplotrupes stercorosus*, *Nargus wilkinii*), and four more for conifer forests (Araneae: *Tenuiphantes tenebricola*; Coleoptera: *Agathidium atrum*, *Crypturgus cinereus*, *Xantholinus tricolor*) were observed when a Sidak-corrected *p* value between 0.05 and 0.10 was accepted for one or two regions. The Schwäbische Alb and the Hainich-Dün showed a much higher similarity in indicators than both of these regions to the Schorfheide-Chorin (Fig. 5). When, for the overall analysis, only those regions were considered for a particular species where at least one individual of the species occurred, nine additional indicator species for unmanaged beech, ten for managed beech, and 74 for conifer forests were observed (Appendix S5).

The differences in species composition among the different regions were confirmed in a non-metric multidimensional scaling analysis based on abundances (Fig. 6). Independent of whether the ordination was based on the abundances of all species or only of indicator species, the three regions were clearly separated, with communities in the Schwäbische Alb and Hainich-Dün being more similar to one another than to those of the Schorfheide-Chorin. Differences between forest types were also conspicuous, in particular between conifer forests and the two beech forest types (Fig. 6).

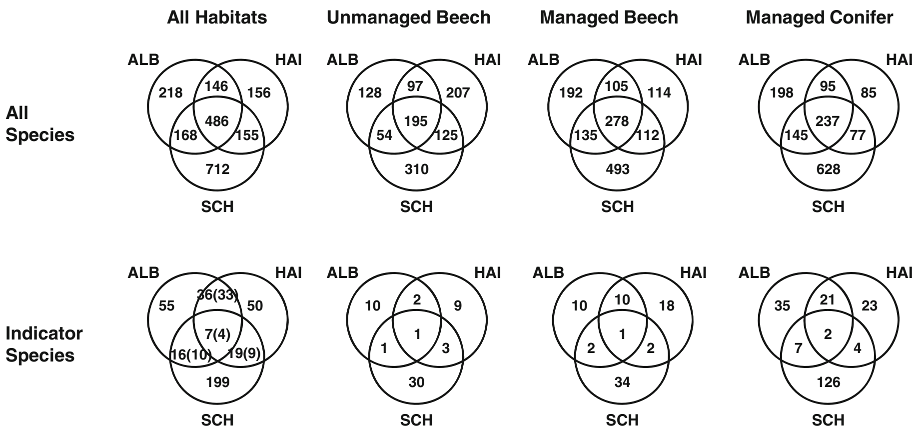

Fig. 5 Venn diagrams showing species overlap regarding all species (*top row*) and indicator species (*bottom*) among regions (ALB = Schwäbische Alb, HAI = Hainich-Dün, SCH = Schorfheide-Chorin). In the Venn diagram showing indicator species of 'All Habitats,' the number of species that revealed to be indicators for the same habitat in two and three regions, respectively, is given in brackets

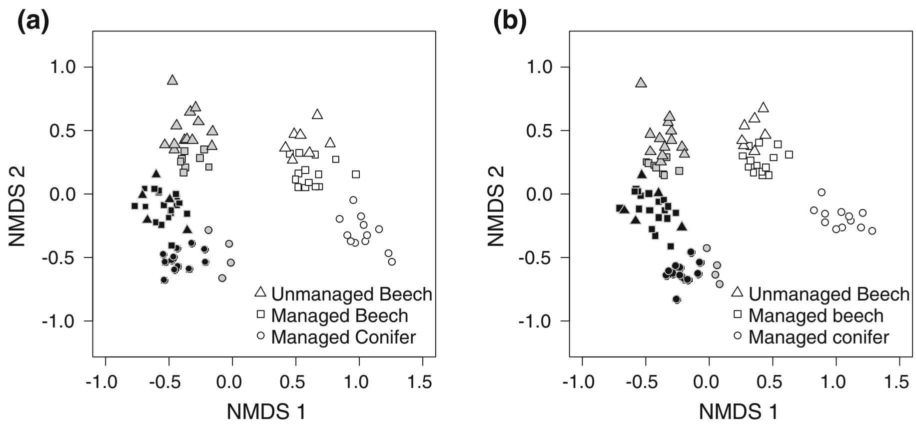

Fig. 6 Non-metric multidimensional scaling of arthropod community composition in the different forest plots based on the abundances of **a** all species and **b** indicator species. Stress values are **a** 0.115 and **b** 0.111. *Open symbols* Schorfheide-Chorin, *black symbols* Hainich-Dün, and *gray symbols* Schwäbische Alb

Temporal reliability

In total, 51,562 and 37,227 specimens were collected in the subset of 23 timber plots in 2008 and 2009, respectively, including 1,563 species of Araneae, Coleoptera, and Hemiptera (Heteroptera, Auchenorrhyncha). Of these, 819 species occurred in both years (mean abundance: total: 105 ± 18SE, 2008: 61 ± 12; 2009: 44 ± 7), while 407 species (mean abundance: 5 ± 1) and 336 (3 ± 1) were only trapped in 2008 and 2009, respectively. Indicator values of species encountered in both years correlated between years, for all three forest types (Pearson product moment correlation; unmanaged beech: $df = 817$, $r = 0.585$, $p < 0.001$; managed beech: $df = 817$, $r = 0.529$, $p < 0.001$, managed conifer: $df = 817$, $r = 0.643$, $p < 0.001$). For 494 (60 %) of these species, the highest indicator values were found for the same forest type in both years and their indicator values were also highly correlated between years (unmanaged beech: $df = 71$, Correlation Coefficient $r = 0.635$, $p < 0.001$; managed beech: $df = 150$, $r = 0.515$, $p < 0.001$, managed conifer: $df = 267$, $r = 0.632$, $p < 0.001$) (see Appendix S6).

Of the 123 species that showed significant indicator values in 2008 (without Sidak-correction), 49 species (40 %) showed also significant indicator values in 2009, however three of these species for a different forest type. Of the four indicator species identified for the entire sampling area (2008), three species were also indicators for the same forest type in 2009 (*P. tiliae* for unmanaged beech, *H. cunicularius*, and *A. humeralis* for managed conifer), at least at the $p < 0.10$ level. The fourth belong to the order Neuroptera, which was not analyzed in 2009. Details on indicator species in 2008 and 2009 including indicator values and p values are given in Table S6-2 of the supplementary material.

Discussion

We tested the suitability of arthropods as indicators for forest management types in Central Europe, using the improved method of Dufrene and Legendre (1997). Using intensive sampling in a large number of study sites, we found that only a small fraction of the species were significant indicators for a particular forest management type. Only one species turned out to be an indicator for unmanaged beech forests at the national level. At the regional level, more species were found to be indicators for the different forest types. Indicator species were on average abundant and frequent, but also less abundant and less frequent species were found to be significantly associated with a particular forest type, illustrating the advantages of the Dufrêne and Legendre approach. While there was significant temporal turnover in the arthropod communities, the indicator values of species were strongly correlated between years. Nevertheless, for fewer than half of the indicator species of the first year showed the analysis a significant indicator value for the 2 years. Overall, our results suggest that the similarities in the arthropod communities between the different forest types and dynamic nature of the communities themselves do not allow for the development of arthropod forest land-use indicators, at least not at the national level.

Central Europe and especially Germany have a high responsibility for protecting beech forests including its naturally evolved arthropod communities (Knapp et al. 2007). For beech forests, it has been recently shown that mapping of structural and microhabitat variables only is not suitable to predict species occurrences and diversities and hence predict a high conservation value (Batary et al. 2012; Gossner et al. 2013). Hence, it would be very useful to define indicator species that help to identify forests with high conservation value. Ideally, such indicators should be the same over large areas, at least at the national scale. We tested for the existence of indicator species for unmanaged beech forests that have been selected as conservation sites based on a number of other variables. Our results show that from a total of 2041 analyzed arthropod species found in the differently managed forests investigated, only one was a significant indicator for unmanaged beech forests at the national scale. Below, we discuss the factors that contribute to the low suitability of forest arthropods for indication purposes.

Limitations to species distribution due to regional differences

Although all forests in our study were classified as lowland to submontane beech forests (Bohn and Neuhäusl 2000/2003), abiotic parameters differ between regions. In particular, the Schorfheide-Chorin region is different from the other two regions and characterized by dryer and warmer conditions, and by soils developed from glacial till and not from limestone as in the other regions. Due to the soil properties, pine rather than spruce is planted in this region. These specificities resulted in the highest proportion of unique species among the regions. Several indicator species are known to occur exclusively on calcareous sites (e.g., *Carabus irregularis* as indicator for managed beech) and therefore are restricted to the Schwäbische Alb and the Hainich-Dün regions. Additionally, historical constraints, i.e., past histories in the distribution of species due to changes in climate in the recent geological past, might be responsible for the regional species turnover that we observe today. Continued cycles of local extinction and re-invasion of species have shaped species distributions in the highly fragmented landscape of Central Europe, but drivers might differ between regions depending on historical land use and forest patch–matrix dynamics (Banks-Leite et al. 2012). Excluding regions where a species is absent from the analysis resulted in a much higher number of 'national' indicators, i.e., 93 species (cf. Table S6-1).

Differences between forest types

Many of the species (739 = 36 %) were found in all forest types and thus did not appear to distinguish between the three management regimes despite some known differences in forest structure and the composition of the plant communities. All currently unmanaged beech forests in Germany were managed at some time in the past or at least affected by some form of human land use, for example, extensive royal hunting in the Schorfheide-Chorin. Although they do not represent 'pristine' forests, they are considered to be of high nature conservation value due to the occurrence of old trees, plant species diversity, etc. Thus, the similarity in arthropod species composition with the much more intensively managed age-class beech forests is surprising. The results are likely to indicate that the currently protected unmanaged forests are in fact not that different from managed beech forests, at least as far as the arthropod community is concerned. This is supported by recent studies on saproxylic beetles that found that protection status was not a good variable explaining the diversity of these deadwood-depending species (Gossner et al. 2013).

There was a clearer contrast between conifer versus broad-leaved forests. It is well known that beech forests differ from spruce or pine forests in the identity of herbivores as these are often specific to a particular tree species (Strong et al. 1984; Gossner 2008). Similar results have been found for soil communities (e.g., Salamon et al. 2008). As a consequence, the highest number of indicator species was derived for conifer forests. On the other hand, the fact that there were different tree species dominating the conifer forests in the Schwäbische Alb/Hainich-Dün versus Schorfheide-Chorin resulted in relatively few indicators for conifer forests at the national scale.

Differences in species in preferences for different forest types in different regions

While a quarter of all species occurred in all three regions, for 22 species their preference for forest types shifted between regions. For example, the carabid *Notiophilus biguttatus* and the staphylinid *Xantholinus bicolor* showed a preference for spruce forests in the Schwäbische Alb and Hainich-Dün, but for unmanaged beech and managed beech, respectively, in the Schorfheide-Chorin. Other species showed a change in preference from managed to unmanaged forests between regions, e.g., the spider *Diplocephalus picinus* from unmanaged beech in the Schwäbische Alb and Hainich-Dün to managed beech in the

Schorfheide-Chorin and the true bugs *Pentatoma rufipes* and *Psallus varians* from unmanaged beech in the Hainich-Dün to managed beech in the Schwäbische Alb and Schorfheide-Chorin. Reason for this change in preference may be related to the differing abiotic conditions in different regions. A change in habitat preference along altitudinal and latitudinal gradients is, for example, a well-known phenomenon in Central European Carabidae (Müller-Motzfeld 2001). The authors pointed to close association of the carabid beetles with particular microclimatic conditions (temperature, precipitation) in Carabidae. These differ along the gradients such that particular species always occur under the same microclimatic conditions but in other habitats along the gradients. Such regional changes in abiotic conditions might explain the observed change in preference of the carabid *Notiophilus biguttatus* among regions. For other species, historical management may affect current distribution, for example, by influencing the availability of deadwood in the different forest types studied. In Schorfheide-Chorin, the amount of deadwood is significantly higher in unmanaged beech than in managed, beech and conifer, forests. In the Schwäbische Alb, there is no difference among forest types in the amount of deadwood, while in Hainich-Dün, deadwood was more abundant in managed spruce forests compared to unmanaged beech forests (Kahl, unpubl. data). This may underlie the preference of the xylophagous *Dryocoetes autographus* for unmanaged beech in the Schorheide-Chorin, but for managed spruce in the Hainch-Dün region. More studies are needed to reveal mechanisms underlying habitat preference change among regions in other species.

Indicators in different taxonomic groups and trophic guilds

In our study, there were no systematic differences between different taxa or functional groups with respect to their suitability as indicator species. This is in contrast to previous suggestions that particular taxa might be more suitable than others as indicator group for habitat quality or local species diversity (Duelli and Obrist 1998; McGeoch 1998). In Germany, beetles, butterflies, grasshoppers, dragonflies, and partly spiders are generally considered to be the most relevant arthropods for landscape planning (e.g., Chauvat et al. 2011) or for the monitoring within the habitat directive (Gesellschaft für Angewandte Carabidologie eV 2009). It has also been suggested that xylophagous or other species associated with deadwood are suitable indicators of unmanaged beech forests, at least for most Central European forests (Grove 2002; Brunet et al. 2010). Our results do not support this assumption and also suggest that trophic guilds are not generally different in their suitability for being indicators. One caveat is that several deadwood-associated species are very rare and are unlikely to be caught in our funnel or flight-interception traps, e.g., the hermit beetle *Osmoderma eremita* (Ranius and Hedin 2001).

Temporal reliability

Most indicator studies focusing on various taxa were conducted during a period of 1 year only (Schmidt et al. 2013; Schulze et al. 2004; Chen et al. 2011). Our study suggests that it is useful to study the indicator value of species over several years before making final decisions as to their suitability as indicators. On the one hand, the indicator values of species found in both years were generally well correlated, and of the four nation-wide indicator species for a particular forest type, three could be confirmed as nation-wide indicators for the same forest type 1 year later. On the other hand, however, more than 50 % of the indicators of the first year were not significant indicators in the second, or were even indicators for a different forest type. Some of them apparently had such low abundances that they were not trapped in the subsequent year. All this suggests that the dynamics of arthropod species do require indicator studies to be carried out over several years. It may turn out that of the indicator species identified in our study, none will be a significant indicator over a longer period of, e.g., 10 years, but this needs to be tested.

Abundance and frequency of occurrence

The indicator species in our study were significantly more abundant and widespread than non-indicator species, but exhibited high variation. Thus, even species with lower abundances were found to be significant indicator species for a forest type. Obviously, however, for a quantitative association to be significant, a species has to have some minimum abundance, not the least because only a fraction of all individuals will be sampled. Current conservation strategies are often based on rare species (e.g., 'Urwald relect species' such as the hermit beetle *Osmoderma eremita* or the Rosalia longicorn *Rosalia alpina*; Müller et al. 2005), but their temporal or absolute rarity makes them unsuitable for quantitative estimates, and also because of practical consideration such as cost-efficiency and effectiveness (McGeoch 1998). In our study, we only found three 'Urwald relict species' with $\leq$5 individuals each; all of these only occurred in the Schorfheide-Chorin, but were sampled in different forest management types. It may well be the case that such species that may have been indicators of pristine (beech) forests in Europe in historical times are nowadays absent from these forests or extremely rare. For example, Bußler and Müller (2005) illustrated in a comparison of different broad-leaved forests of Central Europe that such species are rare in forest of southern Germany. In fact, *Osmoderma eremita* that can be locally common but shows low dispersal (e.g., Ranius and Hedin 2001) nowadays often occurs in parks or churchyards where old trees with sufficiently large tree hollows exist, rather than in forests where such old trees are rare. This makes such a species rather unsuitable as indicators for forests to be preserved.

Conclusions

It would be desirable to give arthropods, which represent a major part of biodiversity in all terrestrial ecosystems, a greater role in the selection of sites for conservation. Given the high diversity of arthropods in our study system, with more than 2,000 species captured within a year, we a priori expected that some of these species would make suitable indicators for unmanaged beech forests. Our results show that to select unmanaged beech forest sites for conservation, arthropods—at least those that were studied here—have some limitations, mostly because the differences between different forest management practices are not great enough to allow for significant associations of species with unmanaged beech forests only.

Overall, the following implications can be derived from our study: (1) indicator species should be tested and ideally defined at the regional scale as their occurrence and indicator value may differ among regions; (2) there is no need to concentrate on a particular taxon and trophic guild in the search for indicators; (3) future evaluation of indicator species among arthropods should be conducted over several years based on standardized sampling protocols and by including also other important forest taxa such as Lepidoptera and Diptera that were not studied here due to methodological or taxonomical limitations; (4) future studies should additionally focus on alternative measures of the conservation value of forests, i.e., trait-based functional composition of arthropod communities. The results of our study also include the possibility that there may be no reliable arthropod indicator species for the forest types studied.

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