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Faunal surrogates for forest species conservation: A systematic niche-based approach

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ABSTRACT

The accelerating decline of biodiversity paralleled by limited resources available for conservation requires methods for systematically prioritizing conservation efforts. Surrogate species, serving as proxies for the presence or ecological requirements of other species, have thus been proposed in a variety of conceptual approaches, all requiring the selection of representative species on which conservation efforts will be focused. Yet, apart from their inherent ecological limitations, surrogate species approaches often suffer from methodological issues with selection criteria being ill-defined and selection procedures solely expert-based, which makes them irreproducible and prone to bias.

We used a niche-based selection algorithm to identify a set of faunal focal species for promoting biodiversity in temperate forests, using the state of Baden-Württemberg (Southwestern Germany) as example region. Based on a literature-based categorization of each species' resource requirements we identified – from candidate species of five taxonomic groups – species sets that represented all predefined forest structural components with the most sensitive species. In addition, we examined the effect of variance introduced by expert scoring (of bird species' sensitivity) on the stability of set composition.

Candidate species were defined for mammals (N = 24), birds (27), herpetofauna (17), diurnal butterflies (36) and saproxylic beetles (36). The resulting focal-species sets consisted of six (herpetofauna) up to thirteen (diurnal butterflies) species, representing the main forest structural requirements of the faunal forest community at different spatial scales. Non-metric multidimensional scaling showed that the "resource-space" covered by the selected species, both of the multi-taxon and the taxon-specific sets, encompassed the one of the non-selected candidate species, except for mammals. Differences in expert scoring had a major effect on set composition, but dissimilarity between sets decreased with an increasing number of included experts and reached convergence after considering the scoring of 10 and more persons.

Niche-based species selection proved valuable for systematic surrogate selection, as it requires a clear definition of the conservation-targets and environmental components to be represented by the surrogate set. The selected algorithm helps objectifying the selection process according to predefined criteria, which can be flexibly chosen so as to maximize different traits (e.g. sensitivity, flagship-characteristics) in the resulting surrogate set. However, given the high sensitivity, expert scoring (where necessary) should never be based on only one or a few experts. Our proposed sensitivity analysis can help identifying the minimal number of experts required for reaching stability in set composition.

1. Introduction

The worldwide decline of biodiversity under increasing and diversifying pressures calls for substantially strengthening efforts to tackle the extinction of animal and plant populations (Butchart et al., 2010). But conservation efforts are always limited by availability of funding, and setting priorities becomes inevitable. In addition, political decision makers are pressed for time and request prompt solutions how to solve a problem. As a consequence, conservation scientists and practitioners are compelled to take shortcuts in conservation. Surrogate species, serving as proxies for the presence or ecological requirements of other species, have thus been introduced in a variety of approaches (Caro, 2010): Flagship species, for example, are charismatic and therefore expedient to encourage conservation efforts, while promoting

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keystone species should enable preserving ecosystem functions (Caro, 2010). Both, however, did not necessarily result in better biodiversity conservation outcomes than randomly selected species (Andelman and Fagan, 2000). The most frequently employed umbrella species are believed to encapsulate the requirements of an array of other species (Lambeck, 1997) which will profit from conservation measures targeted at the umbrella. However, evidence for the effectiveness of the umbrella concept using single-species proxies is also rare and in particular benefits across taxa have rarely been shown (Roberge and Angelstam, 2004). As a consequence, multi-species or even multi-taxon umbrellas sets are considered more promising (Lambeck, 1997), provided the set-composition is representative of the objects and sensitive towards the objectives of the respective conservation programme. According to Roberge and Angelstam (2004), a "dream team" of surrogate species for conservation (in the following generally termed "focal species") should represent the main ecosystem or landscape types of the focal region, require various resources at various spatial scales, and consist of the species most sensitive towards – and thus indicative of – the environmental aspects (features or functions) the respective conservation programme is targeted on.

Focal species sets are mostly selected based on expert knowledge, e.g. in expert-workshops as often exercised by international conservation organisations (Cowling et al., 2003; Lachat et al., 2012). The result of such expert-based approaches may therefore strongly depend on the choice of incorporated experts and their personal assertiveness (Cowling et al., 2003). Moreover, expert-opinion is often influenced by pragmatic management considerations and may thus lack objectiveness. Finally, it can neither be ensured nor quantified if and to which extent the relevant resources or niches of the targeted species community are encompassed. This, however, is necessary to realistically appraise the extent and limits to which the focal species set can support the aspired conservation goals.

Given these limitations, optimization algorithms are on the raise which execute the selection and prioritization process in a transparent and objective way. They are designed to support conservationists and decision makers to find an optimal solution – among the often innumerable possibilities – for achieving a predefined goal under the given conditions and constraints. Such algorithms are based on the principle of complementarity and have often been applied to spatial prioritization processes, e.g. reserve selection, in conservation management (Ball et al., 2009; Moilanen et al., 2009). Algorithms for selecting surrogate (particularly indicator) species exist as well, but mostly require occurrence data of all potential candidate species (Dufrêne and Legendre, 1997). Selection procedures based on resource or trait classification have rarely been applied to animal species (but see Wade et al. 2014, Butler et al., 2009, 2012), maybe due to the inherently greater difficulty to quantitatively describe and compare the species' resource requirements or traits.

In this study, we used an objective niche-based species selection approach to identify a multi-taxon set of focal species for biodiversity conservation in temperate forests, using the state of Baden-Württemberg, Germany as an example region. We aimed at a set of conservation-relevant species representing the structural and compositional forest features that are subjected to forest management (i.e. features that can be destroyed, depleted, preserved, restored or enhanced by forest management), as focal species for promoting forest structural complexity at various spatial scales. We focused on five faunal groups representing different spatial scales and elements of the forest structural gradient: (i) mammals, associated with various forest structural characteristics from the landscape down to the tree-scale, with especially bats related to three-dimensional forest structures and trees with microhabitats; (ii) birds, with similar spatial requirements, occupying a variety of niches in all forest habitats and successional stages; (iii) herpetofauna, comprising amphibians as "representatives" for wet and reptiles for xeric forest habitats; (iv) diurnal butterflies relying on open forest, gaps and edges, some of them strongly associated to vegetative ecotypes at the stand scale; and (v) saproxylic beetles representing key structural characteristics, especially various deadwood substrates, at the tree-scale (Angelstam et al., 2004; Lawler et al., 2003; Lewandowski et al., 2010; Müller et al., 2005).

As trait-based selection procedures require trait-classifications which are not always available for animal species, we also compared using expert-knowledge to a literature-based input. We examined the effect of variance in expert scoring on the stability of set composition, and determined the number of experts that are required to reach a converging and stable result. Hence, the goal of this study was twofold: first, to identify and evaluate a complementary set of temperate forest species on which forest conservation efforts in the model region shall be focused on in the future, and second, to explore the advantages and limitations of using species selection algorithms for this purpose.

2. Methods

2.1. Study area

The study region encompassed the federal state of Baden-Württemberg which is located in the South-West of Germany with a total area of 35751 km^2. The study focuses on the forested area, which covers 38% of the state. Baden-Württemberg is subdivided into five biogeographic landscape regions (Fig. 1) (slightly modified from Ebert and Rennwald, 1991) and characterized by an altitudinal gradient ranging from 85 m a.s.l. in the Upper Rhine Lowland to 1493 m a.s.l. in the Black Forest. Mean human population density is 306 residents per km^2.

2.2. Focal species selection

Adhering to the ideal focal species set (Roberge and Angelstam, 2004), three basic rules need to be incorporated in species selection algorithms (Wade et al., 2014): First, all predefined resource types used by the wider community must be exploited by at least one species. Second, the resulting set must comprise the most specialized species

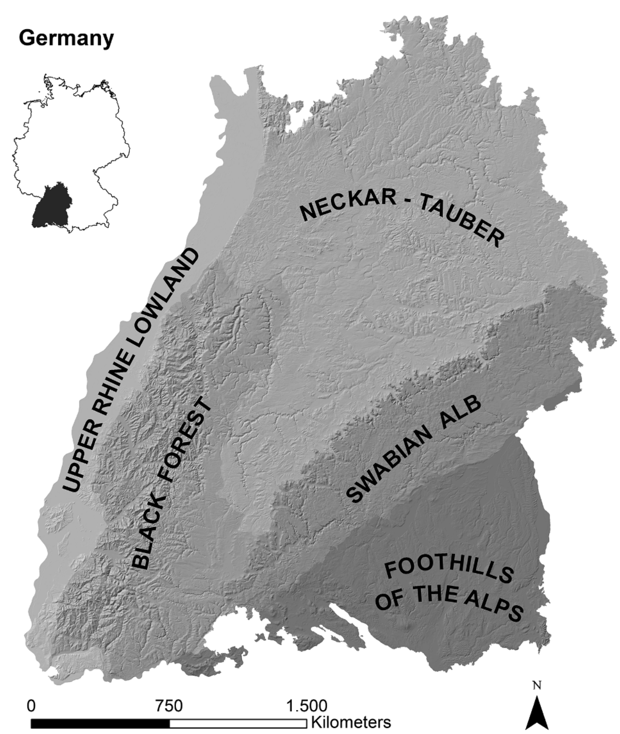

Fig. 1. Study area: The state of Baden-Württemberg, Southwestern Germany, with its five main biogeographic regions.

possible. Third, resources should be represented at all relevant spatial scales.

For the selection procedure we therefore used the species' selection algorithm *SpecSel* (*https://www.uea.ac.uk/computing/specsel)* implemented in a Java program which computes a set of focal species from a pool of candidate species using a niche-based approach. It is based on the concept of minimal dominating sets, i.e. a particular species combination which covers all predefined resources whereby the removal of any species would cause a loss of full resource coverage (Butler et al., 2012; Wade et al., 2014).

As input *SpecSel* requires a matrix of categorized resource requirements for each of the candidate species as well as a score for its "reliance", which estimates the species' dependence on the respective habitat type (Wade et al., 2014), in our case forest. The sensitivity score (or niche breadth) of a species is then defined as the number of used resources multiplied the reliance score, with low values indicating high sensitivity. Both, resource requirements and reliance can be either defined by experts or based on literature (Butler et al., 2009, 2012).

To stepwise approximate the optimal species' combination for a given set size i, *SpecSel* compares the average sensitivity score of all minimal dominating sets containing i species with that of the minimal dominating set(s) containing i-1 species, complemented with the single most sensitive species not included in that set, the minimal dominating set(s) containing i-2 species plus the two most sensitive species not included etc. until the sensitivity score cannot further be reduced (see Wade et al., 2014). Since there is a trade-off between average sensitivity and set size, three alternative set types have been proposed by Butler et al. (2012): (i) the set with the fewest species, (ii) the set with the lowest average sensitivity score and (iii) the set identified by piecewise regression as the optimal breakpoint when relating set size to average sensitivity. For our purpose, we aimed at reaching full resource coverage with the most sensitive species and thus considered the sets with the lowest average sensitivity score. Selection was run for the candidate species of each taxonomic group separately, so as to incorporate different resource requirements and to ascertain the full coverage of structural and spatial requirements across groups. Since more than one combination with the lowest sensitivity score could be identified for a given set size (e.g. when species are interchangeable), we analyzed the five sets with the highest average sensitivity (i.e. lowest sensitivity score) for each taxonomic group. In addition, we pooled the species selected into the most sensitive sets per species group (or the five most sensitive sets per group respectively) to generate a multi-taxon umbrella. The selection procedure and algorithm is described in detail by Butler et al. (2012).

2.3. Candidate species

Candidate species of each of the five taxonomic target groups (mammals, birds, reptiles and amphibians summarized as "herpetofauna", diurnal butterflies and saproxylic beetles) were selected based on forest association and conservation relevance. The latter was defined as being categorized as threatened (i.e. vulnerable (VU), endangered (EN) or critically endangered (CR)) according to the International Union for Conservation of Nature IUCN, listed on the state-specific red list and/or protected by European law in association with Natura2000 (European Commission, 1992, 1979), as specified below. Species for which Baden-Württemberg had a particular responsibility (registered in state-specific red lists) were also considered even if only listed "near threatened NT". Finally, species with extremely low population sizes and/or very restricted spatial occurrence were excluded due to their low and highly stochasticity-dependent survival probability and therefore limited surrogate function. The resulting candidate species are given in Appendix A, the selection details for each taxonomic group are specified below.

Mammals: We considered all forest-associated mammals listed in Annex II and/or IV of the Fauna-Flora-Habitat FFH Directive (European Commission, 1992). The resulting candidate set included all 22 bat species occurring in Baden-Württemberg, as well as the European wild cat (*Felis silvestris*) and the hazel dormouse (*Muscardinus avellanarius*).

Birds: Candidate bird species were preselected based on the red list of breeding birds in Baden-Württemberg (Bauer et al., 2016), as well as Annex 1 and Article 4.2 of the Birds Directive (European Commission, 1979) as stated above. From this species pool we extracted, in a first step, all forest-associated birds based on the habitat classification of (BirdLife International, 2016), i.e. birds with ascertained breeding occurrence in temperate forest habitats. In a second step, we refined the international classification based on regional literature (Bauer et al., 2016) which led to the exclusion of bird species not dependent on forest habitats in Baden-Württemberg and to the inclusion of *Ciconia nigra* due to its dependence on forest habitats in western Europe (Bauer et al., 2016; Jiguet and Villarubias, 2004). We excluded species with less than 10 breeding pairs and a negative population trend in Baden-Württemberg (Bauer et al., 2016).

Herpetofauna: Candidate species of forest-associated herpetofauna were either red-listed as threatened (Laufer et al., 2007) or listed in Annex II or IV of the Flora-Fauna-Habitat Directive (European Commission, 1992). We did not include *Salamadra atra* due to its marginal occurrence in Baden-Württemberg restricted to the alpine region on the border to Bavaria and since there is no particular responsibility of the state for this species (Laufer et al., 2007).

Diurnal butterflies: Candidate species were defined by means of the Red List of Butterflies Baden-Württemberg (Ebert et al., 2008). We selected threatened diurnal butterflies (*Papilionidae, Pieridae, Nymphalidae, Satyrida, Lycaenidae, Hesperiidae*) and burnet moths (*Zygaenidae*) with forest association in accordance to the habitat classification of Ebert (1994) and Ebert and Rennwald (1991). From the resulting set, three species (*Hipparchia fagi, Clossiana thore, Hypodryas maturna*) were excluded due to very restricted occurrence (unpublished data).

Saproxylic beetles: We restricted the candidate species pool to relict species of primeval forest ("Urwaldreliktarten"), i.e. saproxylic beetles reliant on structural qualities and forest habitat tradition as defined by Müller et al. (2005), which were classified as threatened in Baden-Württemberg (Bense, 2002). We excluded all species with deficient data or lacking proof of occurrence after 2000.

2.4. Resource requirements and reliance on forest

The "resources categories" used for constructing the resource requirement matrices were defined at three levels: The first level represented the forest structural features and resources a species required for foraging and reproduction; the second the forest type(s) a species used, and the third the biogeographic region(s) in which a species occurred (Table 1). The resource categories were defined specifically per taxon-group, thereby particularly focusing on species-relevant forest structural features that are prone to modification by forest management or habitat restoration (Table 1). Species were assigned a score of 1 if the respective resource or feature was obligatorily needed for foraging or reproduction and a zero otherwise. The forest communities in the study region were aggregated to five main forest habitat types, namely deciduous, coniferous, riparian and xerophytic forest as well as bog woodland according to Ebert and Rennwald (1991) (Appendix B). Species' occurrence (i.e. literature stating the species' use of the specific forest type as habitat), was indicated by either 1 (occurrence) or 0 (non-occurrence). Finally, occurrence was also documented within each of the five main biogeographic landscape regions of Baden-Württemberg, according to Ebert and Rennwald (1991): (1) Upper Rhine Lowland, (2) Black Forest, (3) Neckar-Tauber, (4) Swabian Alb and (5) Foothills of the Alps (Fig. 1).

Each species' requirements and its reliance on forest habitat were categorized based on literature as specified below.

Mammals: Resource requirement matrices (Table 1; Appendix C1) were constructed based on Braun and Dieterlen (2003), Dietz et al.

Table 1
Forest structures and forest types included in the resource requirement matrices of the different taxonomic groups. For the requirements of each species see Appendix C.

Species group	Resource requirements	Categories defined
Mammals	Foraging habitat	
	Diet	*Invertebrates on the ground; above-ground invertebrates; fruits & nuts; vertebrates*
	Habitat structure	*Tree/crown; shrub; herb; litter; water body*
	Forest denseness	*Dense forest (Canopy cover > 70%); gappy forest (70–30%); clearing (< 30%)*
	Nesting/Reproduction habitat	
	Habitat structure	*Tree hole; tree crack or bark scab; living tree/crown; dead tree/crown; other (building/bunker/rock)*
	Forest denseness	*Dense forest (Canopy cover > 70%); gappy forest (70–30%); clearing (< 30%)*
	Forest type	*deciduous forest; xerophytic forest; coniferous forest; riparian forest; bog woodland*
Birds	Foraging habitat	
	Diet	*Below-ground invertebrates; above-ground invertebrates; plant material; seeds; vertebrates*
	Habitat structure	*Living tree/crown; dead tree/crown; shrub layer; ground vegetation/litter; bare ground; lying deadwood; water body*
	Forest denseness	*Dense forest (Canopy cover > 70%); gappy forest (70–30%); clearing (< 30%)*
	Nesting habitat	
	Nest type	*Self-made hole; existing hole; external*
	Habitat structure	*Living tree/crown; dead tree/crown; shrub; ground vegetation/litter; bare ground*
	Forest denseness	*Dense forest (Canopy cover > 70%); gappy forest (70–30%); clearing (< 30%)*
	Forest type	*deciduous forest; xerophytic forest; coniferous forest; riparian forest; bog woodland*
Herpetofauna	Foraging and reproduction habitat	
	Diet	*Plant material; aquatic invertebrates or carrion; below-ground invertebrates; above-ground invertebrates; vertebrates*
	Habitat structure	*Living tree/crown; shrub; ground vegetation/litter; lying dead wood; bare ground; rocky ground; dry ground; wet ground; sunny locations*
	Water body type	*Riparian; sunny standing water; shady standing water; small temporary pool; pond; slowly flowing water*
	Forest denseness	*Dense forest (Canopy cover > 70%); gappy forest (70–30%); clearing (< 30%)*
	Forest type	*deciduous forest; xerophytic forest; coniferous forest; riparian forest; bog woodland*
Diurnal butterflies	Adult habitat	
	Diet	*Grass; herbs/tall forbs/ferns; dwarf shrub; woody plants (excl. dwarf shrub); lichen/mosses/algae; mineral substances*
	Habitat structure	*Tree/crown; shrub; clearance herb vegetation; subalpine tall forb meadow; ground vegetation; bare ground*
	Shrubbery type	*Wet coppice/margin; mesophilic coppice/margin; dry coppice/margin*
	Forest type	*deciduous forest; coniferous forest; riparian forest; xerophytic forest; bog woodland*
	Larval habitat	
	Diet	*Grass; herbs/tall forbs/ferns; dwarf shrub; woody plants (excl. dwarf shrub); lichen/mosses/algae; mineral substances*
	Habitat structure	*Tree/crown; shrub; clearance herb vegetation; subalpine tall forb meadow; ground vegetation; bare ground*
	Shrubbery type	*Wet coppice/margin; mesophilic coppice/margin; dry coppice/margin*
	Forest type	*deciduous forest; xerophytic forest; coniferous forest; riparian forest; bog woodland*
Saproxylic beetles	Substrate guild	*Old rotten dead wood in a variety of conditions; fresh deadwood; rot-holes; fungi on deadwood or fungi-infested deadwood*
	Forest/tree type	*Deciduous forest; coniferous forest; riparian forest; oak in particular (Quercus spec)*

(2007), Meschede and Heller (2000), Tress et al. (2012), Von Helversen et al. (2001). In bats we assigned a major reliance on forest (score: 1) to species with obligatory forest habitat use during both roosting and foraging, bats obligatorily bound to forest habitats during either roosting or foraging were assigned moderate reliance (score: 2), while bats with optional forest habitat use regarding both activities were allotted a minor reliance (score: 3). Reliance scores of wildcat and hazel dormouse were based on habitat use according to Braun and Dieterlen (2005).

Birds: The resource requirement matrix (Table 1; Appendix C2) was based on Hölzinger (1999, 1997), Hölzinger and Boschert (2001), Hölzinger and Mahler (2002), Korňan and Adamík (2008) and OGBW (2016). Reliance on forest was assigned using the international classification of forest dependency of BirdLife International (2016), whereby high dependency was defined as major reliance on forest, medium dependency as moderate and low dependency as minor reliance. For *Ciconia nigra,* which is not included in the BirdLife-classification, we referred to the score of Wade et al. (2014).

Herpetofauna: For herpetofauna the resource requirement matrix (Table 1; Appendix C3) was constructed based on Glandt (2008), Hofer et al. (2001) and Laufer et al. (2007). We scored reliance on forest according to the categorization of Laufer et al. (2007): assigning to species with strong preference for forest habitats a major reliance on forest, species with only local occurrence in forests a moderate reliance on forest, and species that occur in forests only occasionally on special sites a minor reliance on forest.

Diurnal butterflies: Resource requirement matrices were constructed following the habitat classification of Ebert (1994) and Ebert and Rennwald (1991) by translating it into binary data. We reclassified "resource utilization" or "resource reliance" to *1*, "questionable" or "none utilization" to *0* (Appendix C4). Adhering to Butler et al. (2009), we scored reliance on forest based on the number of non-forest habitats (i.e. dry grassland, fertile meadow, marshland, peat bog, sand and stream gravel vegetation, intensively or extensively cultivated land and orchards according to Ebert (1994) and Ebert and Rennwald (1991) used by a species. Species occurring solely in forests or utilize one additional habitat type were scored as having major reliance on forest, those that utilize two or three additional habitat types were scored as having a moderate reliance on forest and those that utilize four or more additional habitat types were scored as having a minor reliance on forest.

Saproxylic beetles: Resource requirements (Table 1; Appendix C5) were extracted based on Moeller (2009), Müller et al. (2005) and Schmidl and Bußler (2004). Since all candidate species by definition have a major reliance on forest, we did not assign reliance scores. Instead, we focused on beetle body size as a proxy for flagship characteristics and suitability for monitoring. Analogously to the three categories of reliance on forest requested by the algorithm (Wade et al., 2014), we scored body sizes (Köhler, 2000) with > 20 mm as *1*, body sizes between 10 and 20 mm as *2* and body sizes < 10 mm as *3*. We verified our classification with the species' suitability for monitoring purposes according to Schmidl and Bußler (2004) to ensure that all species hard to identify got a score of 3 in our classification.

Table 2
Resulting focal species sets per taxonomic group. The species selected into the set with the lowest average sensitivity (a), the species present in all of the five most sensitive sets (b), and the species selected in only some of the 5 most sensitive sets (c) are indicated.

Species group	(a) Set with lowest average sensitivity	(b) Obligatory in five most sensitive sets	(c) Optional in set (in some but not all of the five most sensitive sets)
Mammals	*Barbastellus barbastellus* *Felis silvestris* *Muscardinus avellanarius* *Myothis alcathoe* *Myotis myotis* *Nyctalus noctula* *Pipistrellus nathusii*	*Felis silvestris* *Muscardinus avellanarius* *Myotis alcathoe* *Myotis myotis* *Pipistrellus nathusii*	*Barbastellus barbastellus* *Myotis bechsteinii* *Nyctalus leisleri* *Nyctalus noctula*
Birds (Literature-based)	*Aegolius funereus* *Ciconia nigra* *Oriolus oriolus* *Dryocopus martius* *Leiopicus medius* *Lullula arborea* *Picoides tridactylus* *Tetrao urogallus* *Turdus torquatus*	*Aegolius funereus* *Ciconia nigra* *Oriolus oriolus* *Dryocopus martius* *Lullula arborea* *Tetrao urogallus* *Turdus torquatus*	*Carduelis citrinella* *Leiopicus medius*
Birds (Expert-based)	*Carduelis citrinella* *Ciconia nigra* *Dryocopus martius* *Glaucidium passerinum* *Lullula arborea* *Phylloscopus bonelli* *Picoides tridactylus* *Tetrao urogallus* *Turdus torquatus*	*Carduelis citrinella* *Ciconia nigra* *Dryocopus martius* *Picoides tridactylus* *Tetrao urogallus* *Turdus torquatus*	*Phylloscopus bonelli* *Phylloscopus sibilatrix* *Scolopax rusticola*
Herpetofauna	*Hyla arborea* *Lacerta agilis* *Rana dalmatina* *Salamandra salamandra* *Vipera aspis* *Vipera berus*	*Hyla arborea* *Salamandra salamandra* *Vipera aspis* *Vipera berus*	*Bombina variegata* *Lacerta agilis* *Lacerta bilineata* *Rana arvalis* *Rana dalmatina*
Diurnal butterflies	*Apatura ilia* *Coenonympha hero* *Colias palaeno* *Limenitis reducta* *Lopinga achine* *Nymphalis antiopa* *Parnassius mnemosyne* *Plebejus idas* *Satyrium ilicis* *Zygaena angelicae* *Zygaena fausta*	*Apatura ilia* *Coenonympha hero* *Colias palaeno* *Limenitis reducta* *Lopinga achine* *Nymphalis antiopa* *Parnassius mnemosyne* *Plebejus idas* *Zygaena angelicae* *Zygaena fausta*	*Boloria aquilonaris* *Limenitis populi* *Satyrium ilicis*
Saproxylic beetles	*Cerambyx cerdo* *Dicerca alni* *Megopis scabricornis* *Mycetoma suturale* *Osmoderma eremita* *Rosalia alpina*	*Cerambyx cerdo* *Megopis scabricornis* *Osmoderma eremita* *Rosalia alpina*	*Ceruchus chrysomelinus* *Dicerca alni* *Dicerca berolinensis* *Eurythyrea quercus* *Mycetoma suturale* *Triplax collaris*

2.5. Effects of variance in expert-scoring

Species' reliance on a particular habitat type can either be based on a literature key, as described above, or based on expert opinion (Wade et al., 2014). In order to examine the consistency of the latter, we compared both approaches using the birds as an example group. We asked 13 ornithological experts from the study region – without prior knowledge of the study – to independently score each of the candidate bird species' reliance on forests (Appendix D). To analyze the effect of differences in expert scoring on the composition of the resulting focal species sets and to identify the number of experts necessary to obtain a stable result we ran the SpecSel algorithm, stepwise including the estimates of one up to 13 experts (i.e. drawing the respective number of experts without replacement), each time generating 100 random samples. For each run, we used the modal value (function *modal* (Hijmans, 2015) with argument *ties* set to highest) of the expert scores per species. In case an expert did not specify a score for a specific bird species, we inserted the modal value of all scores given to that specific species across all experts in the respective sample. To analyze the stability of set composition (i.e. the dissimilarity between the resulting sets) in relation to the number of included experts, we built a community data matrix using the species selected into the most sensitive set of each run. The dissimilarity between the 100 resulting sets for each number of experts was then calculated using the *Sørensen index of dissimilarity* (Oksanen et al., 2015).

2.6. Expert vs. literature-based scoring

To compare the expert-based and the literature-based approach, we also calculated the dissimilarity between each of the 100 replicate sets and the species set using reliance scores based on literature (BirdLife International, 2016). We finally tested whether the scoring of experts differed from literature-based scoring (i.e. if experts tended to allocate higher or lower scores) using a Wilcoxon Test. All statistical analyses were conducted using R software Version 3.2.3 (R Core Team, 2015).

2.7. Resource coverage

To evaluate the coverage of the "resource space" and the sensitivity of the selected compared to the non-selected candidate species, both for each species group separately and for a multi-taxon focal species set consisting of the selected species of all groups, to we used non-metric multidimensional scaling (Minchin, 1987). This way, the multiple resources used by a species, as given in the resource matrices (Appendices C1-C5), were condensed into two dimensions using the function metaMDS in the package "vegan" (Oksanen et al., 2015). Similarities between species were calculated using the Jaccard-distance, as preferable for binary data.

For evaluating the resource-coverage of the multi-taxon focal species set, we merged the resource matrices of all species-groups (Appendix C1-C5) into one single matrix, but without discriminating between reproduction, foraging, larval or adult habitat (i.e. each structure was only listed once, and a species was assigned a one when it required that particular structure in at least one of its live stages and a zero otherwise). Based on this matrix multi-taxon sensitivity scores were calculated on as described in 2.2.

We first tested for differences in multivariate dispersion between selected and non-selected species (function "betadisper" (Anderson et al., 2006)) as a prerequisite for correctly assessing differences in means using a PERMANOVA (function "adonis" (Anderson, 2001), both package "vegan" (Oksanen et al., 2015)).

3. Results

3.1. Focal species selection

In accordance with the selection criteria, the candidate species sets comprised 24 species in the mammals-group, 27 species of birds, 17 species in the herpetofauna group, 36 species of diurnal butterflies and 36 species of saproxylic beetles (Appendix A).

For mammals, the focal species-set with the lowest average sensitivity score (i.e. the most sensitive set) consisted of seven species (Table 2). Across the five most sensitive sets of mammals, the average sensitivity score per set ranged between 17.86 and 18.00 and the number of species per set between six and eight species (Fig. 2a). *Nyctalus noctula* and *Barbastellus barbastellus* were interchangeable without loss of total resource coverage or change in average set sensitivity. The same applied to *Myotis bechsteinii* and *Nyctalus leisleri.*

For birds the most sensitive set consisted of nine species (Table 2). Within the five most sensitive sets, the average sensitivity score per set ranged between 17.78 and 18.75 and set size from eight to 10 species (Fig. 2b). None of the bird species were interchangeable.

In the herpetofauna group, the species set with the lowest average sensitivity score comprised six species (Table 2). Average sensitivity scores in the five most sensitive sets ranged between 23.50 and 24.50 and the number of species per set from five to seven (Fig. 2d). *Lacerta agilis* was interchangeable with *Lacerta bilineata* without loss of total resource coverage but causing a slight increase of average set sensitivity score (from 23.50 to 24.33). *Rana arvalis* and *Bombina variegata* were interchangeable within the five most sensitive sets without loss of total resource coverage or change in average set sensitivity.

The most sensitive set in the diurnal butterfly group consisted of eleven species (Table 2). The five most sensitive sets ranged between eleven and thirteen species and average sensitivity scores between 17.83 and 17.92 (Fig. 2e). *Limenitis populi* and *Satyrium ilicis* were interchangeable without loss of total resource coverage or change in set sensitivity.

In saproxylic beetles the set with the lowest average sensitivity score consisted of six species (Table 2), with an average set sensitivity score of the five most sensitive sets between 5.00 and 5.33. Set sizes ranged from six to eight species (Fig. 2f). *Dicerca berolinensis* and *Eurythyrea quercus* were interchangeable without change in total resource coverage or set sensitivity. The combination of *Dicerca alni* and *Mycetoma suturale* was interchangeable with the combination of *Ceruchus chrysomelinus* and *Triplax collaris*, with an increase in average set sensitivity from 5.00 to 5.33.

The multi-taxon set, consisting of the most sensitive sets per group, comprised 39 species. Set size increased to 52 when using all species selected into the five most sensitive sets per group.

3.2. Effects of variance in expert-scoring

For eight bird species expert scores for reliance on forest were consistent among all experts. For 15 species, scores differed between major and moderate or between moderate and minor, respectively. For four species, scores even differed between major and minor reliance on forest (Appendix D). Differences in expert scores had a major effect on the composition of the most sensitive forest bird sets, with the sets of some experts or expert-combinations showing very low overlap with regard to the selected species (Fig. 3a).

The highest dissimilarity among focal species sets was observed when considering the scores of two experts: The mean and maximum dissimilarity among 100 random samples was 0.31 and 0.68, respectively, meaning that on average 31% and maximally 68% of the species did not overlap between sets (Fig. 3a). Naturally, dissimilarity among sets decreased with increasing the number of experts included (Fig. 3) and maximum dissimilarity seemed to reach convergence at 0.176 when considering the scores of 10 and more experts.

3.3. Expert vs. literature-based scoring

Expert-based reliance-scores (modal value across all 13 experts) differed significantly from literature-based scores (Wilcoxon Test, $p = 0.04743$), with experts generally attributing higher reliance (lower scores) to the species than given by literature (Appendix D). Expert- and literature-based scores agreed for 13 species. For 13 species, scores differed between major and moderate or between moderate and minor, respectively. For one species (*Phylloscopus bonelli*), scores even differed between major and minor reliance on forest (Appendix C2). The most sensitive sets resulting from the two approaches both comprised nine species (Table 2), with an overlap of six species while three species were exclusive. Among the five most sensitive bird-sets obtained using expert-based reliance, the average sensitivity score per set ranged between 14.67 and 14.80 (Fig. 2c; compared to 17.78 and 18.75 in the literature-based approach), with seven species shared between both approaches, four species exclusive for the expert-based and three for the literature-based approach. Mean dissimilarity between the most sensitive sets of the two approaches was not related to the number of included experts, the maximum dissimilarity, however, reached convergence with 9 and more included experts (Fig. 3b).

3.4. Resource coverage

The NMDS-plots indicated that the "resource-space" covered by the selected focal species largely encompassed the resources required by the non-selected candidate species, which were additionally less sensitive (i.e. had higher sensitivity scores) than the former. This applied to both the group-specific sets (Appendix E) and the multi-taxon set (Fig. 4). Only for the mammals significant (i.e. not dispersion-related) differences between the two groups were found (Appendix F). When considering all species that were selected in one of the five most sensitive sets, the resource-coverage was slightly higher than when only considering only the species selected in the set with the lowest sensitivity score, which was reflected by the smaller number of non-selected species (one versus two species) located outside polygon encompassing the focal species (Appendix E, Fig. 4). Moreover, for birds, the focal

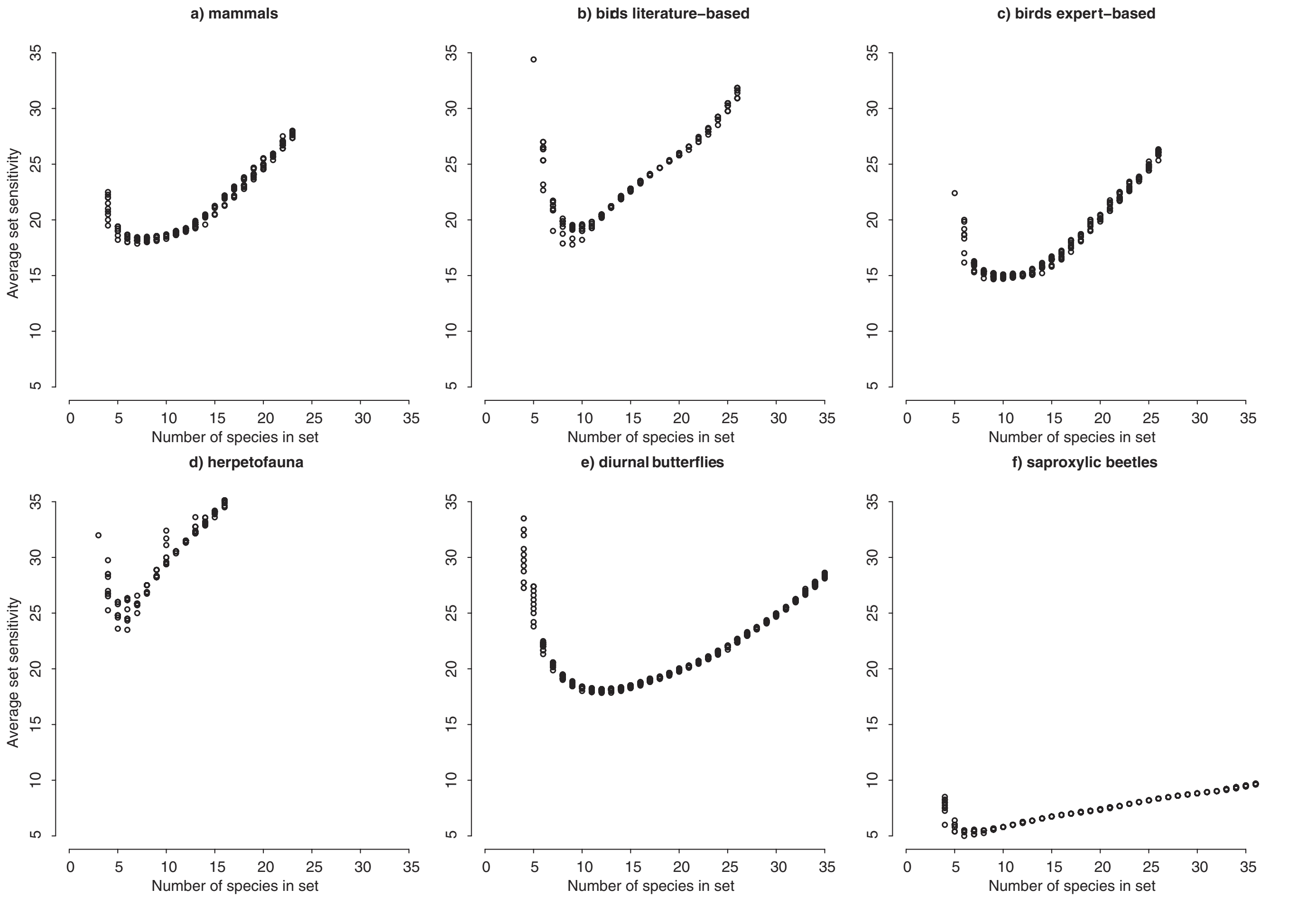

Fig. 2. Trade-off between species set size and average sensitivity of the species selected into the set, shown for each taxonomic group. For birds, sensitivity was either calculated using literature-based (b) or expert-based (c) reliance scores.

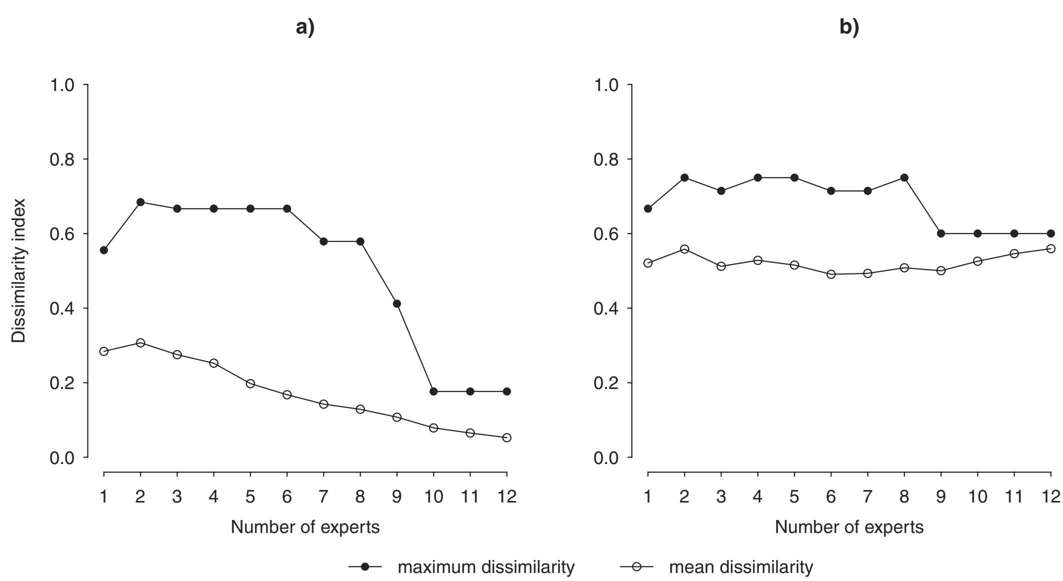

Fig. 3. Dissimilarity between focal species sets generated using reliance-scores (reliance on forest) obtained from an increasing number of experts, in comparison with a literature-based set. Mean and maximum dissimilarity are shown (a) among focal species sets obtained with the reliance-scores of 1 up to 12 experts (100 random replicates for each expert-group size) and (b) between the each of the 100 replicate sets and the species set generated using literature-based reliance scores. Dissimilarity was calculated using the Sørensen index ranging from 0 (when two sets share all species) to 1 (no common species in both sets).

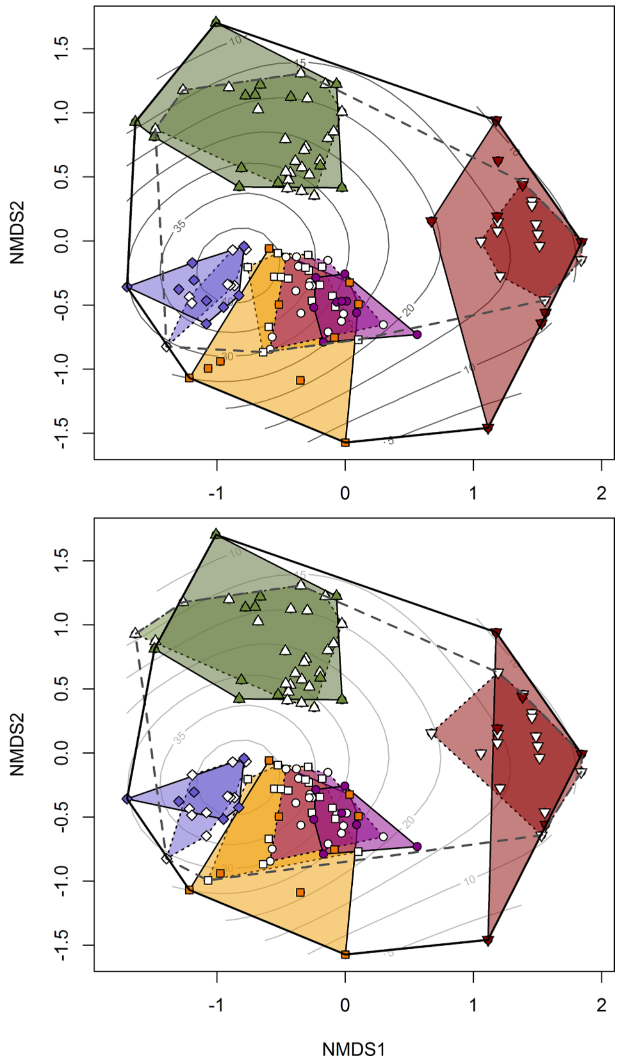

Fig. 4. Coverage of the "resource space" and sensitivity of the species selected in the multi-taxon focal species set (coloured symbols) compared to the non-selected candidate species (white symbols). Each colour and symbol represents a taxonomic group (mammals: lilac points; birds: orange squares; herpetofauna: blue diamonds; diurnal butterflies: green triangles; saproxylic beetles: brown triangles). Resource requirements were summarized by non-metric multi-dimensional scaling (NMDS) with dissimilarity between species calculated using the Jaccard-index. a: species selected in the five most sensitive sets, b: species selected into the most sensitive set. Sensitivity values are shown as isolines with low values indicating high sensitivity.

species sets generated using literature-based reliance scores performed better than the sets based on expert scores.

4. Discussion

The worldwide decline of biodiversity requires shortcuts in species conservation, and surrogate species may help to focus conservation actions, but only if selected in an appropriate way. We show that niche-based species selection is a valuable tool for systematic and reproducible surrogate selection, as the defined "resource space" was covered by the selected focal species, thus encompassing the requirements of the entire candidate species pool.

4.1. Systematic focal species selection

Given the inherent limitations of surrogate species approaches, focal species sets need to be best possible tailored to the underlying conservation objective, the target region and the relevant spatial scales. This requires a clear a-priori definition of the conservation aim and the environmental components to be covered, an inherent prerequisite when using algorithm-based approaches. As a tool for promoting forest biodiversity, our focal species set was designed to represent the main forest types of the respective region and the embedded forest structural elements from stand-scale down to tree-scale microhabitat structures.

Within each taxonomic group, we concentrated on the species with low ecological resilience, a narrow niche breadth and a strong reliance on forest. In contrast to Wade et al. (2014), we therefore only examined the sets with lowest average sensitivity score instead of considering the smallest possible sets which still ensure total resource coverage. Given the trade-off between sets size and average sensitivity (Fig. 2), we preferred larger sets with more specialized species over small sets including generalists, since specialists have narrower niche requirements and are thus more demanding with regards to habitat quality. While generalists show greater ecological resilience to human-induced environmental changes, specialist species face a disproportionally higher risk of extinction (Gallagher et al., 2015) and consequently require more conservation effort. Andelman and Fagan (2000) evaluated various surrogate schemes and found the scheme consisting of habitat specialists most promising, covering more than 60% of the other threatened species.

Hunter et al. (2016) proposed a clear distinction between indicator surrogates to get information about the state of an ecological system and management surrogates which facilitate to achieve management goals. Even though the niche-based species selection framework was originally developed for monitoring the state of biodiversity by selecting indicator species (Wade et al., 2014), we used it to identify management surrogates on which conservation actions should be focused. Our candidate species pool was therefore selected considering a species' regional and international conservation status. In a study of Lawler et al. (2003), at-risk species performed well as a focal species group as their site-selection included 84% of all other species.

In our study, the coverage of the requirements of the entire candidate species pool was given by the selected focal species, within the group-specific sets as well as for the multi-taxon set. Our approach to consider the five most sensitive sets slightly enhanced coverage compared to considering only the most sensitive set. Moreover, combining the species specific sets to a multi-taxon set provided better overall resource coverage than the species-specific sets, as the requirements of some "outlier"-species, which were not covered by the selected species of their own group, were encompassed by the focal species of another, related taxonomic group. This was especially evident for mammals (mainly bats) whose requirement were largely encompassed by the birds' set.

Due to calculation constraints (the memory space limits the number of species and resources that can be included) it was not possible to run a focal species selection on the multi-taxon resource matrix and to compare the resulting set with the set based on pooling the group specific sets. We expect though that the resulting set would have been smaller, as exchangeable species across taxonomic groups would have been excluded.

4.2. Alternative approaches

Algorithm-based approaches to systematically select surrogate species rely on the availability of comprehensive data of species distributions or classifications of their environmental requirements (Dufrêne and Legendre, 1997). Such data are usually available for floral, less so for faunal taxonomic groups. Given the huge effort to compile the necessary data, selection procedures are often conducted under involvement of experts but are then not necessarily systematic (Halme et al., 2009), although they can be carried out in a systematic way, e.g. using the Delphi survey method (Beazley and Cardinal, 2004). Selection based on expert opinion is prone to bias depending on the experts' personal experiences and uneven knowledge. On the other hand, expert knowledge allows for consideration of details which cannot be incorporated in a framework as used in this study. Consequently, systematic, algorithm-based approaches and expert opinion should be used complementary instead of alternatively (Cowling et al., 2003).

Hence we did not focus one single, optimal (in our case most sensitive) species set but extracted the five most sensitive species-combinations, which would allow for an expert-based decision which of the interchangeable species might be the better choice, or if species that do not further contribute to resource coverage but are only included to increase the average set sensitivity should be included. Criteria for decision could include species-specific, target-specific or regional details, e.g. the responsibility of the target region for a species in a nationwide or European context, depending on the species' geographic range and the importance of a region for its conservation with respect to irreplaceability (Brooks et al., 2006). In our study, this would be the case for the two bat species *Myotis bechsteinii* and *Barbastellus barbastellus,* species of national responsibility (BfN, 2016), which makes these them the preferred choice over their respective counterparts.

4.3. Resource requirements

The construction of the resource requirement matrices, i.e. the definition of the species-specific requirements, demanded a trade-off between precision, limiting the ability to categorize, and coarseness, limiting the differentiation between species-specific requirements. In addition, literature sometimes provides contradicting information which can make the decision how to score the resource use a discretionary decision. The use of existing databases (in our case diurnal butterflies and saproxylic beetles) proved to be very valuable in this context. However, the availability of such detailed and structured information is limited. Handing the resource matrices to regional species experts may help to consolidate the niche categorizations in such cases.

We see another shortcoming with the construction of the resource requirements following the method of Wade et al. (2014). The sum of used resources is used to calculate the sensitivity score: Generalist species, using a variety of different resources, obtain a higher sensitivity scores (i.e. being less specific). However, as focal species are supposed to represent a specific resource, species should preferentially be selected that are specialized on the resource, instead of only using the resource once in a while or among many others. Defining only strong dependence on a resource use as "use", however, would lower the total amount of resources used by generalist species – and along with it their sensitivity score – which suggests them being more specific as they actually are. This problem may be solved by adapting the algorithm so as to allow scoring the reliance on a resource instead of using an overall reliance score.

4.4. Scoring reliance

Another difficulty in defining the reliance, in our case on forest, is to which space and time is being referred, and to which degree adaptation and behavioral plasticity is considered. While the first aspect can easily be solved by clearly defining the target region, the point in time to which is being referred is more problematic: A species' reliance on a specific habitat type can be strongly altered by changes in land use. Changes in forestry may have forced forest-dwelling species to retreat to secondary habitats such as vineyards, orchards or parks. Such species might originally have had a strong reliance on forest and would have been scored accordingly by experts at that time, but considering their current key habitats, they would not be assigned a high level of reliance, and consequently not be incorporated in our resulting sets.

One example is the collared flycatcher *Ficedula albicollis*, a genuine forest species (Walankiewicz et al., 2007) that today in the European temperate zone is breeding in orchards as secondary habitat (Grüebler et al., 2013). In Baden-Württemberg, orchards are even the main breeding habitat, probably as a result of a lack of suitable tree holes in deciduous forests, with the few remaining being already occupied by other species when this late migrant returns in spring (Hölzinger, 1997).

Northwestern European forests have considerably changed since the industrialization and the recent sharp differentiation and spatial segregation between forest and farmland is solely anthropogenic (Vos and Meekes, 1999) – inevitably causing species depending on ecotones between forest and farmland to decline. The contemporary view, defining the reliance on forest without consideration of ecotone species is thus an artificial categorization.

4.5. Effects of expert-based input

Given the difficulties of literature-based scoring in some groups, we explored the effect of variance in expert input on the set-composition, by using expert-scores for the most sensitive metric, the reliance score, in the most well-known group, the birds. Since the number of resources used by a species is multiplied by this score, it strongly influences a species' sensitivity-score and thus its probability to be included in the most sensitive focal species set. The estimated reliance on forest of all candidate bird species differed considerably between experts and showed a strong effect on the results, i.e. the most sensitive set derived from the input of one expert could be very different to the set based on another expert. For some species, experts agreed upon the reliance score, e.g. for *Tetrao urogallus*, *Glaucidium passerinum*, *Phylloscopus sibilatrix*, for others, the scores even diverged between major and minor reliance, e.g. *Phylloscopus trochilus* or *Caprimulgus europaeus.*

However, the dissimilarity between sets decreased with the number of included experts, until it converged with 10 or more experts. Our results suggest that any expert opinion should not be based on one single person only, but requires the inclusion of as many experts as possible. A sensitivity analysis, as proposed in this study, can help to determine the sufficient number.

Basing reliance on a literature key, depending on the habitats used besides forest (Butler et al., 2009), may be the more constructive approach if appropriate literature, i.e. specific literature for the region for which species are selected, is available. The use of international classification for a regional assessment, however, may be misleading as reliance scores may differ regionally. In our comparison, the literature-based international classification and the expert-based regional scores differed significantly (more than 50% of the reliance scores did not match), which was also reflected in the differing resulting sets. The dissimilarity between the resulting sets of the two approaches did not decrease with an increasing number of experts included. Nevertheless, with regard to resource coverage, the focal species set using literature-based reliance scores still performed better than the sets based on expert scores.

4.6. Other surrogate types

Despite explicitly designed for indicator species selection, or identifying management surrogates as in our case, species selection algorithms can also be used to derive other types of surrogate species, by maximizing other criteria than sensitivity. We modified the common approach with regard to the saproxylic beetles, by replacing the reliance on forest with body size as a proxy for flagship characteristics and a species' suitability for monitoring purposes. We solely concentrated on relict species of primeval forest, which are per definition all highly reliant on and therefore indicative of primeval forest structures and features (Müller et al., 2005). Since the resource requirement matrix for this group was based on the substrate guilds, with all species being assigned to only one guild, the algorithm aims at achieving full resource coverage by highly specialized species, while additionally maximizing their flagship characteristics. This approach of algorithm-based selection of flagship species is new, although favoritism of large and eye-catching species obviously played already a role when saproxylic beetles for Natura2000 (European Commission, 1992) were selected based on expert opinion (Lachat et al., 2012) and also Sebek et al. (2012) concentrate on “easy to identify” saproxylic beetle species in their surrogate approach.

5. Conclusion

The presented approach of using systematic, niche-based focal species selection considering multiple taxonomic groups resulted in a surrogate species set that provided full coverage of the predefined resources with the most sensitive species. Its additional advantage lies in the clear definition of the conservation-targets and environmental components to be represented by the focal species set, while the algorithm helps objectifying the selection process and guarantees its reproducibility. Predefined criteria can be flexibly chosen so as to maximize different traits (e.g. sensitivity, flagship-characteristics) in the resulting surrogate set. Scoring can be based on literature or expert-opinion, however, since the applied algorithm is very sensitive to small changes in scoring, we recommend a sensitivity analysis to identify the number of experts necessary to achieve stable set compositions. Finally, systematic, algorithm-based approaches and expert opinion should be used complementary instead of alternatively.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.01.084.

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