



“Primeval forest relict beetles” of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants

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Received: 24 February 2017 / Accepted: 23 October 2017 / Published online: 30 November 2017
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Abstract

Identification of forest stands with priority for the conservation of biodiversity is of particular importance in landscapes with a long cultural and agricultural history, such as Central Europe. A group of species with a high indicator value for the naturalness of forest ecosystems are saproxylic insects. Some of these species, especially within the order Coleoptera, have been described as primeval forests relicts. Here, we compiled a list of 168 “primeval forest relict species” of saproxylic beetles based on expert knowledge. These species can serve as focal and umbrella species for forest conservation in Central Europe. They were selected because of their dependence on the continuous presence of primeval forest habitat features, such as over-mature trees, high amounts of dead wood, and dead wood diversity, as well as their absence in managed Central European forests. These primeval forest relict species showed a moderately strong clumping pattern within the phylogeny of beetles, as indicated by phylogenetic signal testing using the *D*-statistic. When we controlled for phylogenetic relatedness, an ordinal linear model revealed that large body size and preference for dead wood and trees of large diameter are the main characteristics of these species. This list of species can be used to identify forest stands of conservation value throughout Central Europe, to prioritize conservation and to raise public awareness for conservation issues related to primeval forests.

Keywords Saproxylic beetles · Old growth · Primeval forest relicts · Habitat continuity · Megatree continuity · Forest conservation · Flagship species · Umbrella species

Introduction

The anthropogenic pressure on forests in Central Europe has a continuous history of more than a millennium (Grove 2002). After centuries of heavy deforestation, the growing stock of forests has been steadily restored since the establishment of modern forestry in the late eighteenth century (Whitehouse 2006). However, this increase in growing stock was accompanied by forest management strategies that structurally homogenized forests and led to dramatic alterations in species composition. Naturally broadleaf-dominated

forests were turned into conifer-dominated plantations (Dirkx 1998; Radkau 2007), and closed forests replaced most natural dynamic open and semi-open woodlands (Miklin and Cizek 2014). Over-mature trees, which had often survived as pollards or in wood pastures, and other open wooded habitats, were compromised by increased canopy closure or their deliberate removal (Buse et al. 2008; Sebek et al. 2016). These alterations of forests selectively affected those wood-inhabiting species with life history and specific habitat traits that make them susceptible to specific structural changes (Seibold et al. 2015). In particular, saproxylic beetle species of lowland forests, species living on broadleaf trees, species of large body size, species living in dead wood of large diameter and species living in sunny dead-wood habitats have suffered from human-induced forest changes and are thus today considered as threatened in the Red Lists.

Today, only a few forest stands that have continuously possessed primeval habitat features remain in Central

Electronic supplementary material The online version of this article (doi:10.1007/s10841-017-0028-6) contains supplementary material, which is available to authorized users.

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Europe. These features include high amounts of dead wood, dead wood of large diameter, a high abundance and diversity of tree microhabitats, large and hollow trees as result of natural senescence, and dead wood created by natural disturbances. Here, we call this type of forest “primeval forest” *sensu* Whitehead (1997), which refers to the continuity in supply of primeval habitat features as “continuous habitat availability”. This expands on the term “megatree continuity” (i.e. continuous persistence of a species in a single old tree; Nilsson and Baranowski 1993, 1994) by considering the continuous persistence of a species in a forest stand instead of in an individual tree. Some saproxylic species survive only in primeval forest stands and disappeared from managed forests, because they require continuous habitat availability. This pattern is best documented for saproxylic beetles and was already observed during the first half of the twentieth century (Freude et al. 1964–1983; Horion 1941–1974; Saalas 1917; Palm 1950, 1959; Iablokoff 1951). These species are referred to as “primeval forest relicts”.

Despite high conservation value, some forest stands with primeval forest attributes are still threatened today because their importance has gone unrecognized, because adequate conservation management measures are lacking (Sebek et al. 2015), or because of competing interests, such as economically motivated salvage logging in the unique lowland forests of Białowieża (Chylarecki and Selva 2016). To assure the survival of primeval faunal elements, it is thus crucial to identify the most valuable forest stands across Central Europe and ensure their protection and adequate management. The occurrence of primeval forest relict species can be used to identify forests with high conservation value. Moreover, their unique association with primeval forests makes these species charismatic despite their relatively small size and therefore suitable for raising public awareness and for policy making. The rediscovery of the cerambycid *Tragosoma depsarium* in the mountains of the Bavarian Forest National Park in Germany, for instance, was reported by several national newspapers and a television station and inspired a storybook for children. Similar to classic surrogate species concepts for conservation (Favreau et al. 2006), primeval forest relict species as a group can thus be used as target species for the conservation of stands with primeval forest characteristics and continuous habitat availability. By protecting and managing forest habitats for these species, a range of taxa, including many wood and forest-inhabiting birds, fungi, mosses and lichens, might benefit from an umbrella effect (e.g. Ranius 2002; Foit et al. 2016).

The first list of saproxylic primeval forest relict species was presented by Müller et al. (2005), but its range was limited to Germany. As this list was frequently applied in Germany and other countries (Brustel 2004; Nieto and Alexander 2010; Müller et al. 2016; Sanchez et al. 2016), we decided to extend this list to Central Europe, accounting

for biogeographical differences in habitat preferences of species. Here we present a new Central European list compiled by beetle experts. To evaluate which properties characterize primeval forest relict species, we determined the distribution of these species across the evolutionary lineages of beetles and modelled the primeval forest relict status relative to life-history and habitat-related traits.

Materials and methods

Definitions and assessment of primeval forest relict species

The scope of this work was to expand the primeval forest relict species list for Germany (Müller et al. 2005) to Central Europe, which is defined for our purpose as encompassing Austria, Switzerland, Czechia, Germany, Hungary, Poland and Slovakia. The applicability of the list includes as well the non-Mediterranean parts of Slovenia and France.

We here use the term primeval, but terms such as old-growth, virgin or urwald can be considered synonyms. Based on various definitions of primeval forest (Johnson et al. 1995; Whitehead 1997; Hilbert and Wiensczyk 2007; Bauhus et al. 2009; Cateau et al. 2015) and considering the ecology of saproxylic beetles, we consider primeval forest habitat features as follows: high number of large and old trees and/or large dead trees created by natural disturbances; presence of veteran trees (also called habitat trees), living cavity-bearing trees and trees with stem or root rot; high variation in tree size; heterogeneous spatial distribution of trees of different age creating a range in canopy openness from closed to open; high amounts of fallen and standing dead wood, including dead wood of large diameter; wide distribution of diameter and decay stages of dead wood; presence of broken and deformed tops; and presence of rare wood-dwelling fungi. The occurrence of primeval habitat features might not be restricted exclusively to primeval forest stands; one to several of these features can also occur in forests managed for timber production, although usually to a lesser extent or without continuous habitat availability (Christensen et al. 2005).

Following the classification of Müller et al. (2005) and within the biogeographical scope of this study (Central Europe), we define saproxylic primeval forest relict beetles as species that (1) require primeval habitat features and continuous habitat availability, (2) have high requirements with regard to dead wood quality and quantity and (3) became extinct or were severely diminished in forests managed for timber production. Within this group, we distinguish primeval forest relict species *sensu stricto* (=category 1) and *sensu lato* (=category 2). Species of category 1 are today restricted to a few remnants of natural forests. Species of

category 2 follow the definition criteria but might also occur in production forests if their specific habitat requirements are met. It is important to note that some of these species might display different habitat requirements in regions with warmer climatic conditions outside their range in Central Europe, such as in the Mediterranean, possibly due to interactions between resource requirements and climatic conditions (Müller et al. 2015). Here, both the definition of primeval habitat features and the list of primeval forest relict species focused on saproxylic beetles. Some species in other taxonomic groups or among non-saproxylic beetles might be similarly restricted to primeval forests but these were beyond the scope of this publication.

The saproxylic beetle species were classified by 21 experts of beetles in Central Europe (U. Bense, H. Brustel, H. Bußler, Y. Chittaro, L. Cizek, A. Eckelt, A. Frei, E. Holzer, M. Kadej, M. Kahlen, F. Köhler, G. Möller, H. Mühle, J. Müller, A. Sanchez, U. Schaffrath, J. Schmidl, A. Smolis, A. Szallies, T. Németh, C. Wurst). All saproxylic beetle species of Central Europe were given full consideration for classification. In the first step, we created a preliminary list of 210 species that could potentially meet the criteria of primeval forest relict species as defined above based on information in the literature (Table S2) and expert knowledge. This list was then discussed and edited during a workshop in September 2015 held at the Kalkalpen National Park (Austria), in which 14 of the authors took part. The preapproved list was then sent to all 21 experts for revision and final approval.

Phylogeny and trait data

We used the phylogeny of saproxylic beetles of Central Europe published by Seibold et al. (2015). Thirty missing primeval forest relict species were added to this phylogeny following the approach used by Gossner et al. (2013). That means that missing species were added to the tree topology based on additional phylogenetic (Hunt et al. 2007) and taxonomic information (Freude et al. 1964–1983), and branch lengths were estimated (function *bladj* in the program *phylocom*; Webb et al. 2008) using the same 25 calibration points from fossil records as used in Seibold et al. (2015). The final phylogeny included 1465 species of saproxylic beetles including 168 primeval forest relict species (Fig. 1).

For a trait-based analysis of the ordinal primeval relict status, we used information on eight biological and resource-related traits and on elevational distribution in Central Europe (Seibold et al. 2015). Lacking additional species parameters were compiled from literature or scored according to our own experience. Biological traits included mean *body size* and *feeding type* of the larvae (xylophagous, mycetophagous, saprophagous, zoophagous), and resource-related traits included mean niche

positions with regard to *wood diameter* and *decay stage* of dead wood as well as *canopy cover* of forests in which a species was recorded; preference of each species for coniferous and/or broadleaf *host trees*; and the *microhabitat guild* of the larvae (wood and bark, cavities, fungal fruit-bodies). Elevational distribution (planar, coline, montane and subalpine) was transformed into an ordinal scale from which the mean *elevational* distribution was calculated. For the calculation of resource-related traits, we followed the procedure of Gossner et al. (2013), using the occurrence of species in defined classes: dead wood diameter: < 15, 15–35, 35–70, > 70 cm; decay: alive, freshly dead, initiated and advanced decomposition, extremely decomposed; and canopy cover: open, semi-open, closed. The frequency of occurrence of each species in each category was then described by weighting scores based on the mean niche positions calculated (for details, see Seibold et al. 2015 and; Gossner et al. 2013).

Statistical analyses

All statistical analyses were carried out in R 3.3.2 (R Development Core Team 2008). To assess whether primeval forest relict status (binary variable: 1 = primeval forest relict species category 1 or 2; 0 = not an primeval forest relict species) contains a phylogenetic signal, we calculated the *D*-statistic (Fritz and Purvis 2010; function *phylo.d* in package *caper*) for the full phylogeny including all 1465 species. *D* = 1 indicates that the binary trait has a phylogenetically random distribution across species, and *D* = 0 indicates that the observed trait is clumped.

To test which traits characterize primeval forest relict species, we related the primeval forest relict status (ordinal variable: 0 = not an primeval forest relict species; 1 = primeval forest relict category 2; 2 = primeval forest relict category 1) of 1292 species for which trait information was available (including all primeval forest relict species) to the eight biological and resource-related traits described above. Species, however, might not form independent data points as closely related species may share similar traits, including a similar primeval forest relict status (Harvey and Pagel 1991). We used a proportional-odds model (function *clmm* in the add-on package *ordinal*; Christensen 2013) to describe the distribution of the ordinal primeval forest relict category as a function of the trait predictors. Phylogenetic correlation between species was modelled by species-specific intercepts with a fixed correlation structure defined by the phylogenetic distance between each pair of species to avoid inflation of degrees of freedom due to relatedness of species (for more details, see Seibold et al. 2015). Post-hoc tests for categorical predictor variables based on this model were performed with the add-on package *multcomp* (Hothorn et al. 2008).

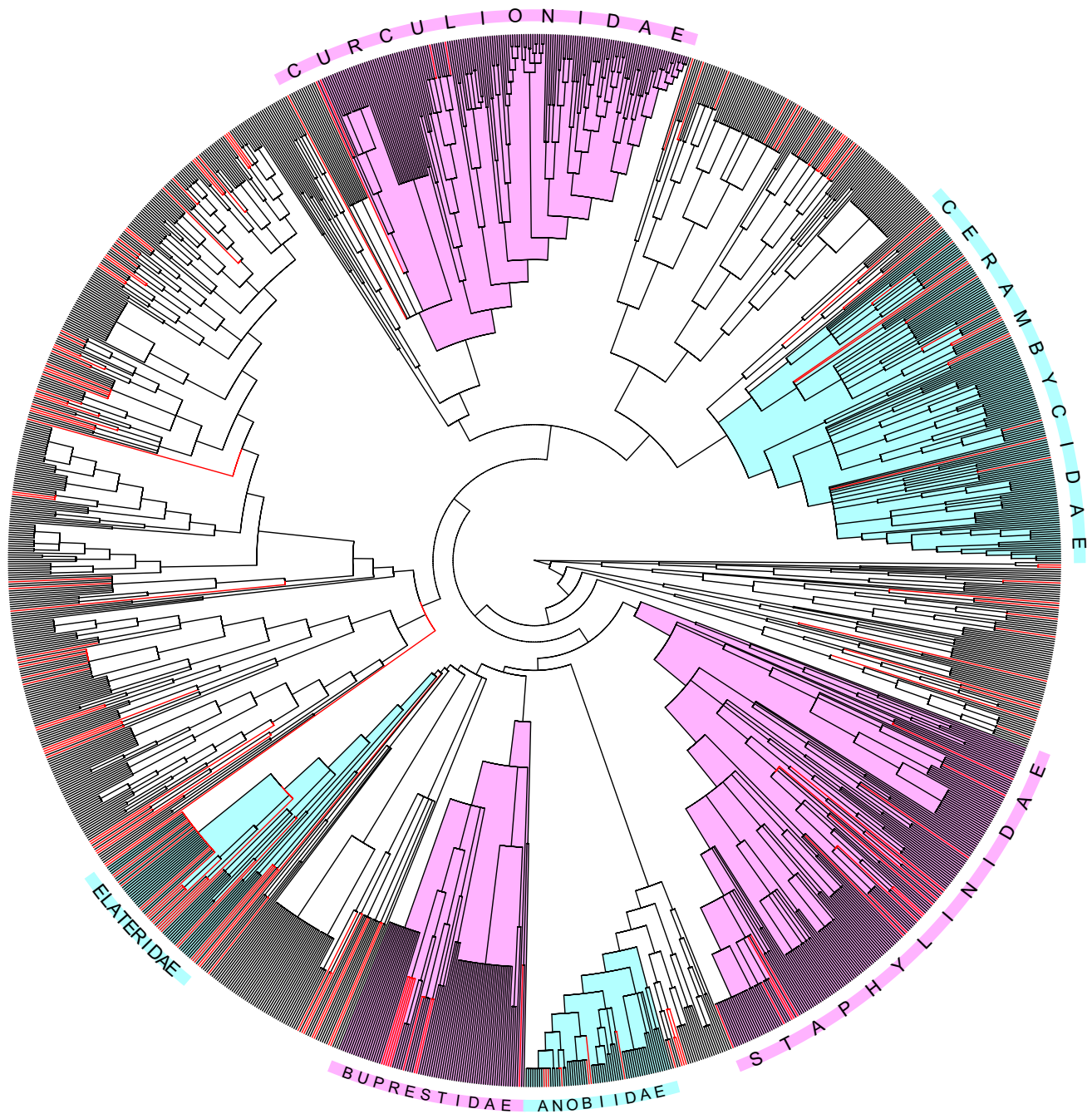


Fig. 1 Phylogeny of 1465 saproxylic beetles in Central Europe. Primeval forest relict species (168 species) are marked by red branches, and larger families are named

Results

We classified 168 saproxylic beetle species as primeval forest relict species in Central Europe (Table 4 and S1). Sixty species were classified as primeval forest relict species *sensu stricto* (category 1), and 108 as primeval forest

relict species *sensu lato* (category 2). Except *Xylolaemus fasciculosus*, all species were recorded in at least one of the nine Central European countries in the last fifty years. Eight species were in the last fifty years exclusively recorded in one country (*Trigonurus mellyi*, *Lopheros lineatus*, *Lasonotus jelskii*, *Dolichocis laricinus*, *Pytho kolwensis*,

Dircaea quadriguttata, *Alosterna ingrlica*, and *Stictoleptura variicornis*).

The countries with the highest numbers of recent and historic records of primeval forest relict species are Austria (144 species) and Poland (144 species), followed by Slovakia (143 species; Table 1). The highest percentage of primeval forest relict species with only historic records was found in Poland (15.4%), followed by Austria (13.8%; Table 2). The lowest percentage of only historically recorded primeval forest relict species was found in Slovakia (1.4%), Hungary (3.8%) and Czechia (5%), which indicated that these countries have lost the lowest percentage of primeval forest relict species.

Analysis of the *D*-statistic revealed a phylogenetic signal of $D=0.56$ in the primeval forest relict status, which differed significantly ($p < 0.001$) from both 0 and 1. This indicates that the primeval forest relict status exhibited moderately strong phylogenetic clumping (Fritz and Purvis 2010). The proportional-odds model revealed that primeval forest relict species were characterized by a higher dead-wood diameter niche and by a larger body size (Table 3). The other traits had no significant effects on the primeval forest relict status, as indicated by the model (Table 3) and post-hoc tests (results not shown).

Discussion

We provide the first list of primeval forest relict species that can serve as a common standard to classify and rank the conservation value of forest stands throughout Central Europe and to raise public awareness for the conservation of natural forests. This list expands an earlier list that focused only on species in Germany (Müller et al. 2005) and benefits from both experience in applying the German list and expert knowledge gained over the last decade (Bußler 2010; Lorenz 2010).

Table 1 Total numbers of primeval forest relict species *sensu stricto* (category 1) and *sensu lato* (category 2) recorded per country

Country/region	Category 1	Category 2	Σ (Category 1 + 2)
Central Europe	60	108	168
Austria	46	98	144
Switzerland	23	72	95
Czechia	45	94	139
Germany	43	93	136
Hungary	32	74	106
Poland	49	95	144
Slovakia	47	96	143

Table 2 Total number of primeval forest relict species recorded recently and historically per country, and percentage of primeval forest relict species with only historic (<1965) or also recent (>1965) records

Country/region	Number of primeval forest relict species	Historic records (%)	Recent records (%)
Central Europe	168	0.6	99.4
Austria	144	13.8	86.2
Switzerland	95	12.5	87.5
Czechia	139	5.8	94.2
Germany	136	12.5	87.5
Hungary	106	3.8	96.2
Poland	144	15.4	84.6
Slovakia	143	1.4	98.6

Species lists of saproxylic taxa across large areas are often incomplete, but lists of rare species, such as primeval forest relict species, tend to be compiled more carefully. Such species are thus better suited than others to identify forest stands and tree aggregations of high value for conservation. Potential applications of the primeval forest relict species list include prioritization of conservation measures by ranking forest stands according to the number of recent primeval

Table 3 Results of a proportional-odds linear mixed-effects model with species-specific random intercepts based on the phylogeny (Fig. 1) to estimate effects of biological and habitat-related traits on the ordinal primeval forest relict status of 1229 saproxylic beetle species in Central Europe

Trait	Estimate	Std. error	z value	p value
Elevational distribution	0.241	0.214	1.12	0.26
Body size	0.0561	0.0248	2.26	0.02
Wood-diameter niche	1.85	0.239	7.74	<0.001
Canopy niche	-0.00336	0.315	-0.011	0.99
Decay niche	-0.0771	0.204	-0.377	0.71
Host tree specificity ^a				
Broadleaf	-0.0618	0.354	-0.175	0.86
Conifer	0.791	0.418	1.89	0.06
Guild ^b				
Fungal fruit-bodies	0.351	0.612	0.573	0.57
Wood & bark	-0.233	0.487	-0.479	0.63
Feeding type ^c				
Saprophagous	-2.30	1.28	-1.80	0.07
Mycetophagous	-0.0126	0.511	-0.025	0.98
Xylophagous	0.496	0.423	1.17	0.24

^aLevels of host tree specificity are compared to the category “both broadleaf and conifer”

^bLevels of guild are compared to the category “cavities”

^cLevels of feeding type are compared to the category “predatory”

forest relict species records and evaluation of conservation and forest management strategies aiming at the protection of biodiversity typical for near-natural and natural forests (Müller et al. 2016; Chylarecki and Selva 2016; Kindlmann and Křenová 2016). Primeval forest relict species could be used as outstanding trademarks in media and policy campaigns to raise broader public awareness and support for conservation of these species and especially for their last remaining habitats. Habitat conservation for primeval forest relict species creates an umbrella effect which benefits a broad range of other taxa affiliated with dead wood, such as wood-inhabiting fungi, other insect groups, arachnids, lichens and mosses (e.g. Ranius 2002; Foit et al. 2016). The umbrella effect is even enhanced due to the well-known and documented habitat requirements of primeval forest relict species and allows thereby conservation measures to be tailored more specifically (e.g. Djupström et al. 2012; Gutowski et al. 2014; Foit et al. 2016).

Primeval forest relict species—trademarks for conservation of primeval forests

With their rather small size, beetles might not exactly meet the commonly expected criteria of typical flagship species, such as charismatic, large mammals or birds (Favreau et al. 2006). However, owing to their strong association with primeval forests, the term “primeval forest relict” seems to have a positive connotation of wilderness and pristine nature, which makes them particularly appealing and charismatic. Experience gained in the applications of the German list of primeval forest relict species demonstrated this high attractiveness of primeval forest relicts to the public. For example, protected areas in Germany report and advertise the number of primeval forest relict species occurring within their boundaries, and even timber companies use these species to show the effectiveness of their conservation strategies (Bußler 2010; Lorenz 2010). The iconic status of primeval forest relict species benefits from the rarity of natural forests in Central Europe, but in regions where natural forests are still common (Müller et al. 2013, 2016), these relicts might not have the same charisma. Nevertheless, attempts have been made to demonstrate the value of forests in Eastern Europe (Bußler and Müller 2006; Lachat et al. 2016) and at the Caspian Sea (Müller et al. 2016) by pointing out the high number of occurring primeval forest relict species.

Sixteen saproxylic beetle species have been listed in the appendices of the Habitats Directive, which ensures the conservation of a wide range of rare, threatened or endemic animal and plant species by the NATURA 2000 framework

(European Council 1992). These species can also be considered flagship species; most are colourful or otherwise visually spectacular, such as *Lucanus cervus*, *Cerambyx cerdo*, *Rosalia alpina* and *Cucujus cinnaberinus*, and are representative of certain important habitats. Some of these Habitat Directive species have become increasingly relevant in urban and rural landscape management, such as *Osmoderma eremita* (Carpaneto et al. 2010). However, the saproxylic beetle species listed in the Habitats Directive possess a strong emphasis on old oaks and hollow trees and therefore they cover only a fraction of old-growth habitats. To promote conservation of a broader range of old-growth habitats, we suggest using primeval forest relict species—which include some of the Habitats Directive species—as focal and umbrella species.

Many saproxylic beetle species listed as threatened in Central Europe require habitat structures that have become rare in production forests owing to forest management and thus most primeval forest relict species are considered threatened (Seibold et al. 2015). However, a typical criterion of Red List assessments is a small or decreasing geographic distribution within the considered region, which is also evident for the German Red List of saproxylic beetles (Seibold et al. 2015). Thus, a species can be assigned a high Red List status even if its small distribution within the study area is caused by preferences for climatic conditions and not for high habitat quality. For the classification as primeval forest relict, not the size of a species range in Central Europe is a criterion *per se*, but rather its association with primeval habitat features. Therefore, the list of primeval forest relict species in Central Europe might be less biased by the distribution of a species within the study area, and thus might be a better indicator of the requirements of a species for high-quality habitat. This, however, does not mean that an relict species cannot be locally common within or outside Central Europe if old-growth attributes are locally common (Müller et al. 2013) or if the habitat preferences of a species change with the biogeographical region.

Characteristic traits of primeval forest relict species

Similar to the Red List status of saproxylic beetles (Seibold et al. 2015), the primeval relict status showed a phylogenetic signal, which indicated that some families comprise more relict species than others (Table 4). Our model shows that primeval forest relict species are primarily characterized by a strong association with dead wood or dying trees of large diameter (Table 3). These parameters are also the most

apparent attributes of old-growth forests in Central Europe (Bauhus et al. 2009).

Primeval forest relict species were further characterized by larger body size compared to non-relict species, possibly because large-bodied species need pieces of dead wood of a minimum size that provide microhabitat conditions for a time long enough to complete larval development (Foit 2010). Using a similar approach, Seibold et al. (2015), showed that saproxylic beetle species that need dead wood of large diameter and have larger bodies are more threatened (i.e., have a higher Red List status) than species that occur in small diameter dead wood and species that have small bodies. Moreover, species of the lowlands and species that prefer sunny forests and broadleaf trees were also more threatened than species of higher elevations, species that prefer shady forests and deciduous trees. These three traits (elevational distribution, canopy cover niche and tree species specificity) had no effect on the primeval forest relict status. This underlines that primeval forest relict species are limited to structure-rich forests with primeval habitat attributes.

Why do some countries have more primeval forest relict species than others?

The number of primeval forest relict species per country varied between 95 in Switzerland and 144 in Austria and Poland. There are several reasons that might explain the difference in species numbers between countries. The most obvious reason is the lack of suitable habitats for organisms that depend on primeval forest with an adequate and continuous supply of dead wood. Primeval forests in Europe are nowadays restricted to the eastern and south-eastern Carpathian Mountains, to boreal forests in Fennoscandia and to a few small remnants in Central Europe (Leibundgut 1982; Parviainen 1999). Poland possesses the Białowieża Forest, which is one of the largest lowland primeval forests in Europe (Bobiec et al. 2000), and Slovakia and Poland share highly intact forest habitats with primeval forest attributes in the Carpathians (Paulenka and Paule 1994; Parviainen 2005). Thus, the comparatively higher presence of primeval forests in Poland and Slovakia might explain why these two countries host the highest numbers of primeval forest relict species, including some outstanding species, e.g. *Phryganophilus ruficollis*, *Pytho kolwensis*, *Boros schneideri*, *Cucujus haematodes* and *Rhysodes sulcatus*. These species have become extinct in most parts of Central Europe owing to strong negative effects of increasing forest management intensity (Horak et al. 2011; Gutowski et al. 2014; Siitonen and Saaristo 2014).

Another explanation for the high numbers of primeval forest relict species in Austria, Poland and Slovakia could be topography. Primeval forest stands could have persisted in inaccessible valleys and on steep slopes, where forestry has been impossible or restricted. Moreover, the mountainous terrain can lead to higher disturbance frequencies through avalanches, fires, landslides or storms, creating high amounts and diversity of dead wood (Stokland et al. 2012; Müller et al. 2013).

Within the Kalkalpen National Park (Austria), 22 primeval forest relict species have survived, despite intensive forestry during the last 150 years, possibly because of frequent natural disturbance events in the region (Eckelt and Kahlen 2012; Degaspari and Eckelt 2015; Nationalpark Kalkalpen Ges.m.b.H. 2016).

Yet another explanation for the differences in the number of primeval forest relict species found in the different countries might be biogeography. Several boreal species, for example, reach only Poland. And lastly, the sampling intensity has probably not been equal across Central Europe as many data on beetle distribution are based on beetles collected by amateur entomologists, and the popularity of beetle collecting varies between countries and over time.

Conclusions

We hope to stimulate efforts to protect and maintain the last remaining primeval forests in Central Europe and the unique species communities that they hold by providing a list of primeval forest relict species of this region. This species list can help to identify so far unrecognized but valuable forest stands, to prioritize conservation efforts and to raise awareness for conservation issues related to old-growth forests.

Acknowledgements We thank Erich Mayrhofer, Erich Weigand and their team at the Kalkalpen National Park (Austria) for assistance during the workshop and financial support; Ottó Merkl (Budapest, HNHM) for advice on species selection; and Jerzy M. Gutowski, Lech Buchholtz, Andrzej Melke, Karol Komosiński (Poland), O. Konvička (Zlín), D. Hauck (Brno), P. Průdek (Brno), and J. Vávra (Ostrava) for advice on the distribution and status of several primeval forest relict species.

Appendix

See Table 4.

Table 4 List of Central European primeval forest relict species of saproxylic beetles compiled in September 2016

Family/Species	Cat.
Rhysodidae	
<i>Omoglymmius germari</i>	1
<i>Rhysodes sulcatus</i>	1
Histeridae	
<i>Abraeus parvulus</i>	2
<i>Epierus comptus</i>	2
<i>Platylomalus complanatus</i>	2
<i>Platysoma deplanatum</i>	1
Leiodidae	
<i>Dreposcia umbrina</i>	1
Staphylinidae	
<i>Abemus chloropterus</i>	2
<i>Batrisodes hubenthali</i>	2
<i>Bibloporus ultimus</i>	1
<i>Bolitochara lucida</i>	2
<i>Euryusa coarctata</i>	2
<i>Gyrophaena nitidula</i>	2
<i>Hesperus rufipennis</i>	2
<i>Lordithon pulchellus</i>	2
<i>Lordithon speciosus</i>	2
<i>Olisthaerus substriatus</i>	2
<i>Phymatura brevicollis</i>	2
<i>Quedius infuscatus</i>	2
<i>Quedius truncicola</i>	2
<i>Sepedophilus binotatus</i>	2
<i>Stenichnus foveola</i>	1
<i>Tachysida gracilis</i>	1
<i>Thoracophorus corticinus</i>	2
<i>Trigonurus mellyi</i>	2
Lycidae	
<i>Lopheros lineatus</i>	2
Cleridae	
<i>Dermestoides sanguinicollis</i>	2
Derodontidae	
<i>Derodontus macularis</i>	2
Trogositidae	
<i>Calitys scabra</i>	1
<i>Grynocharis oblonga</i>	2
<i>Peltis grossa</i>	1
<i>Temnochila caerulea</i>	2
Elateridae	
<i>Ampedus auripes</i>	2
<i>Ampedus brunnicornis</i>	1
<i>Ampedus cardinalis</i>	1
<i>Ampedus elegantulus</i>	2
<i>Ampedus melanurus</i>	2
<i>Ampedus quadrisignatus</i>	1
<i>Ampedus suecicus</i>	1
<i>Ampedus tristis</i>	2
<i>Brachygonus ruficeps</i>	1
<i>Cardiophorus gramineus</i>	2

Table 4 (continued)

Family/Species	Cat.
<i>Crepidophorus mutilatus</i>	2
<i>Danosoma conspersum</i>	1
<i>Denticollis borealis</i>	1
<i>Elater ferrugineus</i>	2
<i>Ischnodes sanguinicollis</i>	2
<i>Lacon lepidopterus</i>	1
<i>Lacon punctatus</i>	2
<i>Lacon querceus</i>	1
<i>Limoniscus violaceus</i>	1
<i>Megapenthes lugens</i>	2
<i>Podeonius acuticornis</i>	1
<i>Reitterelater dubius</i>	1
Cerophytidae	
<i>Cerophytum elateroides</i>	2
Eucnemidae	
<i>Dirrhagofarsus attenuatus</i>	1
<i>Farsus dubius</i>	1
<i>Microrhagus pyrenaeus</i>	2
<i>Nematodes filum</i>	2
<i>Otho sphondyloides</i>	1
<i>Thambus friwaldskyi</i>	1
<i>Xylophilus testaceus</i>	2
Buprestidae	
<i>Acmaeodera degener</i>	1
<i>Buprestis splendens</i>	1
<i>Dicerca aenea</i>	2
<i>Dicerca alni</i>	2
<i>Dicerca berlinensis</i>	2
<i>Dicerca furcata</i>	1
<i>Dicerca moesta</i>	2
<i>Eurythyrea austriaca</i>	1
<i>Eurythyrea quercus</i>	1
Bothrideridae	
<i>Oxylaemus variolosus</i>	2
<i>Teredus cylindricus</i>	2
<i>Teredus opacus</i>	1
Cerylonidae	
<i>Philothermus evanescens</i>	2
Rhizophagidae	
<i>Rhizophagus brancsiki</i>	2
Cucujidae	
<i>Cucujus haematodes</i>	1
Erotylidae	
<i>Dacne notata</i>	1
<i>Dacne pontica</i>	2
<i>Triplax collaris</i>	2
<i>Triplax elongata</i>	1
<i>Triplax melanocephala</i>	1
<i>Tritoma subbasalis</i>	2
Cryptophagidae	
<i>Cryptophagus confusus</i>	2

Table 4 (continued)

Family/Species	Cat.
<i>Cryptophagus lyscholmi</i>	2
<i>Cryptophagus quercinus</i>	2
Laemophloeidae	
<i>Cryptolestes abietis</i>	2
<i>Laemophloeus muticus</i>	1
Latridiidae	
<i>Corticaria interstitialis</i>	2
<i>Corticaria lapponica</i>	2
<i>Corticaria lateritia</i>	2
<i>Corticaria orbicollis</i>	2
<i>Latridius brevicollis</i>	2
Mycetophagidae	
<i>Mycetophagus ater</i>	2
<i>Mycetophagus decempunctatus</i>	2
Zopheridae	
<i>Colydium filiforme</i>	2
<i>Endophloeus marcovichianus</i>	2
<i>Lasconotus jelskii</i>	1
<i>Pycnomerus terebrans</i>	2
<i>Rhopalocerus rondanii</i>	2
<i>Synchita separanda</i>	2
<i>Xylolaemus fasciculosus</i>	1
Endomychidae	
<i>Leiestes seminiger</i>	2
<i>Pleganophorus bispinosus</i>	1
Ciidae	
<i>Dolichocis laricinus</i>	1
<i>Ennearthron palmi</i>	2
Endecatomidae	
<i>Endecatomus reticulatus</i>	1
Bostrichidae	
<i>Lichenophanes varius</i>	2
<i>Stephanopachys linearis</i>	2
<i>Stephanopachys substriatus</i>	2
Ptinidae	
<i>Anitys rubens</i>	2
<i>Dorcatoma ambjoerni</i>	1
<i>Ernobius explanatus</i>	2
<i>Ernobius kiesenwetteri</i>	2
<i>Ernobius laticollis</i>	2
<i>Stagetus borealis</i>	2
<i>Xestobium austriacum</i>	2
Oedemeridae	
<i>Ditylus laevis</i>	1
Pythidae	
<i>Pytho abieticola</i>	1
<i>Pytho kolwensis</i>	1
Prostomidae	
<i>Prostomis mandibularis</i>	2
Melandryidae	
<i>Dircaea australis</i>	2

Table 4 (continued)

Family/Species	Cat.
<i>Dircaea quadriguttata</i>	1
<i>Mycetoma suturale</i>	2
<i>Phryganophilus auritus</i>	1
<i>Phryganophilus ruficollis</i>	1
<i>Rushia parreyssi</i>	2
Pyrochroidae	
<i>Agnathus decoratus</i>	2
Tenebrionidae	
<i>Allecula rhenana</i>	2
<i>Bius thoracicus</i>	1
<i>Bolitophagus interruptus</i>	1
<i>Corticeus bicoloroides</i>	2
<i>Corticeus fasciatus</i>	2
<i>Corticeus suturalis</i>	1
<i>Corticeus versipellis</i>	1
<i>Eledonoprius armatus</i>	1
<i>Hymenophorus doublieri</i>	1
<i>Mycetochara obscura</i>	2
<i>Mycetochara quadrimaculata</i>	2
<i>Neatus picipes</i>	2
<i>Platydema dejeani</i>	2
<i>Prionychus melanarius</i>	2
<i>Tenebrio opacus</i>	1
Boridae	
<i>Boros schneideri</i>	1
Scarabaeidae	
<i>Gnorimus variabilis</i>	2
<i>Osmoderma eremita</i> s.l	2
Lucanidae	
<i>Aesalus scarabaeoides</i>	2
<i>Ceruchus chrysomelinus</i>	2
Cerambycidae	
<i>Aegosoma scabricorne</i>	2
<i>Akimerus schaefferi</i>	2
<i>Alosterna ingrica</i>	2
<i>Cerambyx cerdo</i>	2
<i>Cornumutilla lineata</i>	2
<i>Evodinus borealis</i>	1
<i>Macroleptura thoracica</i>	1
<i>Necydalis ulmi</i>	2
<i>Nivellia sanguinosa</i>	2
<i>Nothorhina muricata</i>	2
<i>Rosalia alpina</i>	2
<i>Saperda punctata</i>	2
<i>Stictoleptura erythroptera</i>	1
<i>Stictoleptura variicornis</i>	2
<i>Tragosoma depsarium</i>	2
Curculionidae	
<i>Camptorhinus statua</i>	1
<i>Euryommatus mariae</i>	2
<i>Gasterocercus depressirostris</i>	2

Table 4 (continued)

Family/Species	Cat.
<i>Hexarthrum duplicatum</i>	2
<i>Rhyncolus reflexus</i>	2

Cat. Category

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