Contributed Paper

Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe

Sebastian Seibold,*† ¶ Roland Brandl,‡ Jörn Buse,§ Torsten Hothorn,** Jürgen Schmidl,†† Simon Thorn,*† and Jörg Müller*†

*Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
†Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, Center for Food and Life Sciences Weihenstephan, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85354 Freising, Germany
‡Department of Ecology, Animal Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch-Str. 8, 35032 Marburg, Germany
§Institute for Environmental Sciences, Ecosystem Analysis, University of Koblenz-Landau, Fortstr. 7, 76829 Landau, Germany
**Epidemiology, Biostatistics and Prevention Institute, University of Zurich, Hirschengraben 84, 8001 Zürich, Switzerland
††Ecology Group/Developmental Biology Division, Biology Department, University of Erlangen-Nuremberg, Staudtstr. 5, 91058, Erlangen, Germany

Abstract: *To reduce future loss of biodiversity and to allocate conservation funds effectively, the major drivers behind large-scale extinction processes must be identified. A promising approach is to link the red-list status of species and specific traits that connect species of functionally important taxa or guilds to resources they rely on. Such traits can be used to detect the influence of anthropogenic ecosystem changes and conservation efforts on species, which allows for practical recommendations for conservation. We modeled the German Red List categories as an ordinal index of extinction risk of 1025 saproxylic beetles with a proportional-odds linear mixed-effects model for ordered categorical responses. In this model, we estimated fixed effects for intrinsic traits characterizing species biology, required resources, and distribution with phylogenetically correlated random intercepts. The model also allowed predictions of extinction risk for species with no red-list category. Our model revealed a higher extinction risk for lowland and large species as well as for species that rely on wood of large diameter, broad-leaved trees, or open canopy. These results mirror well the ecological degradation of European forests over the last centuries caused by modern forestry, that is the conversion of natural broad-leaved forests to dense conifer-dominated forests and the loss of old growth and dead wood. Therefore, conservation activities aimed at saproxylic beetles in all types of forests in Central and Western Europe should focus on lowlands, and habitat management of forest stands should aim at increasing the amount of dead wood of large diameter, dead wood of broad-leaved trees, and dead wood in sunny areas.*

Asociación del Riesgo de Extinción de los Escarabajos Saproxílicos con la Degradación Ecológica de los Bosques en Europa

Resumen: *Para reducir la futura pérdida de biodiversidad y para asignar efectivamente los fondos para la conservación, los conductores principales detrás de los procesos de extinción a gran escala deben ser identificados. Un enfoque prometedor consiste en enlazar el estatus de lista roja de las especies y las características específicas que conectan a las especies de taxones funcionalmente importantes a los recursos de los que dependen. Dichas características pueden usarse para detectar la influencia de cambios de los ecosistemas antropogénicos y los esfuerzos de conservación sobre las especies, lo que permite realizar recomendaciones prácticas para la conservación. Modelamos las categorías de la Lista Roja Alemana como un índice ordinal de riesgo de extinción para 1025 escarabajos saproxílicos con un modelo lineal de efectos mixtos y probabilidades*

proporcionales para respuestas categóricas ordenadas. En este modelo, estimamos los efectos fijos para las características intrínsecas al categorizar la biología de las especies, los recursos requeridos y la distribución con intercepciones azarosas correlacionadas filogenéticamente. El modelo también permitió predecir riesgos de extinción para especies que no tienen categorías en la lista roja. Nuestro modelo reveló un riesgo de extinción mayor para las especies de tierras bajas y para las de gran tamaño, así como para las especies que dependen de maderas con un gran diámetro, árboles con hojas anchas o un dosel abierto. Estos resultados reflejan bien la degradación ecológica del bosque europeo a través de los últimos siglos causada por la silvicultura moderna, que es la transformación de bosques naturales de árboles con hojas anchas a bosques dominados densamente por coníferas y la pérdida de madera muerta y árboles de viejo crecimiento. Por esto, las actividades de conservación enfocadas a los escarabajos saproxílicos en todos los tipos de bosque en Europa central y occidental deben enfocarse en las tierras bajas, y el manejo de hábitat de los bosques debe centrarse en incrementar la madera muerta de gran diámetro, la de árboles de hojas anchas y la que se encuentra en áreas soleadas.

Palabras Clave: características funcionales, filogenia, historia del bosque, lista roja, madera muerta, silvicultura orientada a la conservación

Introduction

Numerous national strategies seek to reduce the rate of global biodiversity loss. In these strategies, red lists represent, despite numerous drawbacks, a valuable tool for ranking the potential extinction risk of species on various spatial scales (Rodrigues et al. 2006). Furthermore, analyses that link red-list status to species' traits allow an understanding of and perhaps allow one to predict the red-list status of particular species (Fritz et al. 2009). However, most red-list analyses have focused only on vertebrates (e.g., Purvis et al. 2000; Krüger & Radford 2008) and charismatic invertebrate groups, such as butterflies, dragonflies, and damselflies (Kotiaho et al. 2005; Clausnitzer et al. 2009). This leads to a biased understanding of the ecological and evolutionary background for the red-list status.

Factors that affect the extinction risk of a species can be either intrinsic (i.e., they accrue from the species properties) or extrinsic (i.e., drivers act independently of species, such as habitat loss, species overexploitation, or climate change) (Fisher et al. 2003). Intrinsic factors, for example, body size or life history characteristics, affect reproduction and mortality rates (Calder 1996) and thus the risk of extinction by demographic stochasticity (Gaston & Blackburn 1996; Payne & Finnegan 2007). Recently, Di Marco et al. (2014) proposed 4 sets of predictors of extinction risk: species distribution state and biological traits (both intrinsic) and human pressures and conservation response (both extrinsic). Any analysis of extinction risk should incorporate factors of all 4 types as far as possible and account for potential interactions, such as biological properties of species mediating effects of human pressures (Price & Gittleman 2007; Di Marco et al. 2014).

Studies of extinction risk are sometimes criticized for failing to link their results to practical conservation (Fisher & Owens 2004; Cardillo & Meijaard 2012). To increase the relevance of a study for conservation practice, Cardillo and Meijaard (2012) suggest restricting the geographic and taxonomic scope of a study and working out clear implications from the results. To be able to draw clear implications, the scale and the detail of the predictors are crucial. For example, for species threatened by anthropogenic habitat changes, well-defined traits that describe the resource on which a species relies (Mouillot et al. 2012; Gossner et al. 2013) can help identify limited resources driving the extinction risk.

Forests in Europe are a prominent example of an anthropogenically changed ecosystem; such forests have been affected by humans for >5000 years (Grove 2002). By around AD 1750, forest cover reached its smallest extent since the last glacial maximum (Whitehouse 2006). With the beginning of modern forest management in the late 18th century, indigenous broad-leaved tree species were replaced by fast-growing conifers, and moribund and old trees were extracted (Grove 2002). Recently, increasing fuel wood prices have increased pressure on dead trees and logging residues, even of small diameter (Lassauce et al. 2012). Therefore, even if forests still cover a considerable proportion of our landscape, structures of these production forests differ considerably from those of pristine forests (Gossner et al. 2013).

These changes in forests have affected many forest species and especially those associated with dead wood (Siitonen 2001). Saproxylic beetles, which depend at some stage of their life cycle on dead wood or the presence of other saproxylic species (Speight 1989), are highly diverse and functionally important in the decay process in forests (Grove 2002). These species can be characterized by several intrinsic traits that mechanistically link to the required resource (Gossner et al. 2013). For example, body size is a proxy for the size of required dead-wood objects (larger species have longer larval development times and thus need large dead-wood objects) and species requirements link to canopy cover, dead wood diameter, and decay stage. Zoophagous saproxylic beetle species can be expected to be at a

relatively higher risk of extinction because species at higher trophic levels are generally more affected by habitat fragmentation (Dupont & Nielsen 2006).

Red-list categories can be used as an ordinal index of extinction risk (Verde Arregoitia et al. 2013), but the differences between consecutive levels are unknown. Their modeling has 2 methodological problems. First, an ordinal scale requires ordinal regression models (Verde Arregoitia et al. 2013) or transformation of the response variable (Mooers et al. 2008). Second, phylogenetically related species are not independent from a statistical point of view. Related species are often assigned to similar red-list categories because related species share traits that determine the susceptibility of these species to environmental pressures (Purvis 2008).

To identify potential drivers of the extinction risk of a functionally important insect group on a national level, we modeled the red-list categories as an ordinal index of extinction risk (for simplicity hereafter called extinction risk) of saproxylic beetles; biological traits and intrinsic traits described required resources and distribution. We used a linear mixed ordinal regression model, which allows consideration of phylogenetically correlated random intercepts. This model was then used to predict the extinction risk of species for which no red-list status is available. Based on our results, we offer simple but important suggestions for sustainable forest management across all forest types.

Methods

Study Group

More than 1400 saproxylic beetle species have been recorded in Germany. Globally, they are considered indicators of forest degradation (Grove 2002) due to their ecological diversity and functional importance. In Europe, the over 400-year-old tradition of field entomology, starting with Aldrovandi's "De Animalis Insecta" in 1602, has led to the accumulation of a unique body of literature on taxonomy, distribution, ecology, and traits of Central and Western European beetles, which is the basis of our study (Supporting Information).

Study Area and Red-List Categories

We restricted our analysis to saproxylic species considered in the German Red List of Beetles (Supporting Information; J. Schmidl & B. Büche, unpublished data). This red list covers all saproxylic beetle families. The categories of the German Red List follow the International Union for Conservation of Nature (IUCN) classification and include the categories rare (R) and indeterminate (I), which were used by the IUCN until 2001 (www.bfn.de/0322_kat.html). Germany is representative

for both the climate and the history of silviculture in Western and Central Europe. Therefore, our results should be broadly transferrable to surrounding countries. We converted the categories of saproxylic beetles of the German Red List into an ordinal scale of extinction risk ranging from 0 (least concern [LC]) to 5 (regionally extinct [RE]). Of 1064 saproxylic species assigned to a category in the German Red List of Beetles, 28% are listed as threatened or regionally extinct (not including the categories data deficient [DD], I, and R). The categories contain the following number of species: RE, 39 (4%); critically endangered (CR), 57 (5%); endangered (EN), 75 (7%); vulnerable (VU), 128 (12%); near threatened (NT), 63 (6%); and LC, 704 (66%).

Predictors of Extinction Risk

Traits of mammals, such as distribution, are well known. However, spatial scales on which mammals live may cover more than several hectares and are therefore rather coarse. Thus, it is possible to derive predictors of extinction risk for mammals with remote-sensing data on human pressures (e.g., Di Marco et al. 2014). In contrast, saproxylic beetles act on small spatial scales, such as single trees or forest stands of less than a few hectares (Ranius 2006). Information of sufficiently high resolution on their distribution and occurrence in or outside protected areas and means of deriving measures of human pressure on the national scale using remote sensing are not available (Müller & Brandl 2009). However, for the 1213 saproxylic species on the German Red List of Beetles (including the categories DD, I, and R, which are not part of our ordinal scale of potential extinction risk), we were able to compile information on 8 biological and resource-related traits as well as geographic and elevational distribution in Germany (Table 1; for references and the complete data set, see Supporting Information). Those traits that describe required resources are intrinsic but link species mechanistically to potential habitat changes caused either by human pressure or conservation (for instance hollow tree inhabitants are more threatened than others [Müller et al. 2014]), which represent both sides of a gradient of forest-use intensity (see fig. 1 in Gossner et al. 2013 for conceptual framework). We used the following resource-related traits that mirror human pressure and conservation: mean niche positions with regard to wood diameter and decay stage of dead wood and canopy cover of forests in which a species was recorded; whether adult beetles visit flowers; preference of species for coniferous, broad-leaved, or both types of trees as host trees; and microhabitat guild of larvae (wood and bark, cavities, fungi). We used the biological traits mean body size and feeding type of larvae (xylophagous, mycetophagous, detritivorous, predatory). Distribution since recording of beetles began was characterized by range size measured as the number of German regions (maximum 18) in which a

Table 1. List of explanatory variables used to estimate the extinction risk of saproxylic beetles.[a]

Variable	Unit	Range or definition	Mean
Range size	numerical[b]	0–18	14.05
Elevation	numerical[c]	1–4	2.02
Body size	mm	0.7–50.0	6.04
Wood diameter niche	numerical	1–4 (small–high)	2.30
Canopy niche	numerical	1–3 (sunny–shady)	1.65
Decay niche	numerical	1–5 (fresh–decomposed)	2.90
Flower visitor	binomial	yes or no	0.19
Host tree	categorical	conifer, broad-leaved, both	–
Guild	categorical	wood and bark; cavity; fungi	–
Feeding type	categorical	xylophagous, mycetophagous, detritivorous, predatory	–

[a]*For more details and references, see Supporting Information.*
[b]*Number of German regions in which a species was reported during the last 200 years.*
[c]*Mean of a species' elevational distribution covering the zones planar, colline, montane, and subalpine.*
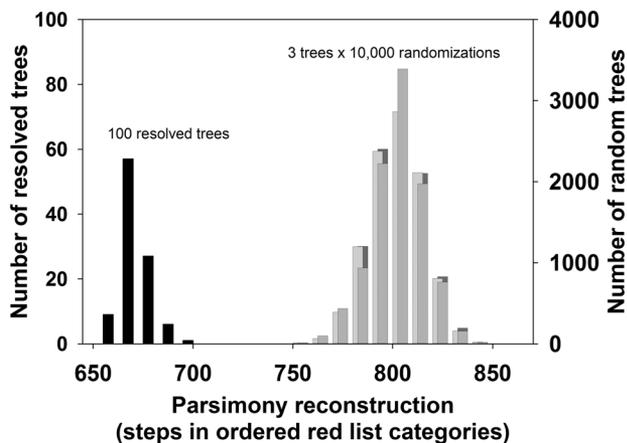

Figure 1. Number of evolutionary steps necessary to explain the distribution of the German Red List categories (ordinal variable) of 1025 saproxylic beetles (German Red List of Beetles; J.S. & B. Büche, unpublished data) across tips of the phylogenetic trees. From 100 randomly selected resolved trees (black bars), we selected 3 trees, 1 with the minimum number of steps, 1 with maximum number of steps, and 1 near the average to derive the expectation of the number of steps for randomly distributed categories across tips. For each of the 3 trees, we randomly reshuffled the categories across tips 10,000 times and calculated the number of steps for each of these trees (gray bars).

species was reported during the last 200 years. We are aware that former and current distributions may produce different results (Hanna & Cardillo 2013), but no comprehensive distribution for the time before 1950 is available for all species and analyses restricted to records of only the last 60 years produced similar results (not shown). Elevational distribution (planar, colline, montane, and subalpine) according to Böhme (2005) was transformed into an ordinal scale from which the mean elevational distribution was calculated. For the calculation of the resource-related traits, we followed the procedure of

Gossner et al. (2013), that is the occurrence of species in ordered classes: diameter, <15, 15–35, 35–70, >70 cm; decay, alive, freshly dead, initiated, advanced decomposition, extremely decomposed; canopy cover, open, semi-open, closed. The frequency of occurrence of each species in each category was then described by weighting scores based on which mean niche positions were calculated (for details, see Supporting Information & Gossner et al. 2013).

Phylogeny

In cross-species analysis, species are not independent, which inflates the degrees of freedom. For a phylogenetically informed analysis, we followed the approach used by Gossner et al. (2013), who created a topology based mainly on Hunt et al. (2007) with additional phylogenetic and taxonomic information for some genera (Supporting Information). Because DNA sequence data were available only for a small subset of our species, we estimated branch lengths for our topology using 25 calibration points from fossil records (Supporting Information; function bladj in program phylocom [Webb et al. 2008]; see Supporting Information for phylogeny). To obtain fully resolved trees, we used BEAST (Drummond et al. 2012), following the procedure suggested by Kuhn et al. (2011). This approach allows input of partially resolved trees with the known topology and node ages as constraints and applies an MCMC algorithm to permute polytomies with a constant rate birth–death model. From this analysis, we obtained a random sample of 100 fully resolved trees, which we used to estimate the variability of the phylogenetic signal in our red-list category.

Data Analyses

We tested the phylogenetic signal in the ordinal variable red-list category with the program Mesquite (Maddison & Maddison 2011). We selected the parsimony model for an ordered variable. Then, we used the function trace character history based on the parsimony ancestral state

Table 2. Results of a proportional-odds linear mixed-effects model with species-specific random intercepts based on the phylogeny (Gossner et al. 2013) to estimate the effects of intrinsic traits characterizing species, required resources, and distribution on the extinction risk of 1025 saproxylic beetles.

Variable	Estimate	z	p^a	Post hoc comparison[b]
Range	−0.366	−14.7	<0.001***	
Elevation	−0.485	−2.64	0.008**	
Body size	0.0689	3.30	<0.001***	
Wood diameter niche	1.10	6.74	<0.001***	
Canopy niche	−0.937	−3.40	<0.001***	
Decay niche	−0.0750	−0.448	0.65	
Flower visitor	−0.425	−1.51	0.13	
Host tree				
Broad-leaved[c]	0.653	2.08	0.037*	broad-leaved >>> conifer
Coniferous[c]	−1.48	−3.57	<0.001***	both >> conifer
Guild				
Wood + bark[c]	−0.752	−1.94	0.053	
Fungi[c]	−0.0560	−0.103	0.92	
Feeding type				
Detritivorous[c]	0.807	1.06	0.29	
Xylophagous[c]	0.568	−0.426	0.67	
Mycetophagous[c]	−0.206	1.54	0.12	

[a] *Significant differences for the model:* *p < 0.05; **p < 0.01; ***p < 0.001.
[b] *For categorical variables, significant differences:* >>p < 0.01; >>>p < 0.001.
[c] *Levels of host tree are compared to the category* both, *levels of guild are compared to the category* cavity, *and levels of feeding type are compared to the category* predatory.

and calculated the number of evolutionary steps necessary to evolve the observed distribution of red-list categories across each of the 100 randomly selected resolved trees. These values were compared with an expectation derived by tip shuffling (10,000 times). A lower number of steps than expected indicated that the red-list categories were not randomly distributed across the tips of the tree. All further analyses were conducted in R 3.1.0 (www.r-project.org). Species without trait information and species listed as DD, I, and R were excluded from the total list of 1213 saproxylic species of beetles before modeling, resulting in analysis of a total of 1025 species.

To evaluate which traits influence extinction risk, we related the ordinal red-list categories of 1025 species of saproxylic beetles to all 10 traits. We used a proportional odds model (Tutz 2011) to describe the distribution of the ordinal extinction risk categories as a function of our predictors. Phylogenetic correlation between species was modeled 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 (Harvey & Pagel 1991). We fitted this proportional-odds linear mixed-effects model using the function clmm in the add-on package ordinal (Christensen 2013) with de-correlated random intercepts (Fahrmeir et al. 2004; details in Supporting Information). Post hoc tests were performed based on this model with the add-on package multcomp (Hothorn et al. 2008). This modeling framework allowed us to analyze ordinal extinction risk of phylogenetically related species without violating strict model assumptions, such as normality, linearity of the mean, and

independence of species. The model contained all 10 variables without interactions and was not simplified. In a preliminary model, we also tested for potential interactions between variables and body size (Cardillo et al. 2005), but none of the interactions showed significant effects. Therefore, we did not include interactions. Body size and wood diameter niche are both related to the dimension of dead wood but were only weakly correlated ($r = 0.13$, $p < 0.001$; Supporting Information); thus, both were included in the model.

For 188 species listed as DD, I, and R, for which trait information was available, we used our final model, including the correlated species-specific random intercepts derived from our phylogeny, to estimate their extinction risk. In this case, we used the class with the maximum probability value as the estimated extinction risk category.

Results

When we tested the red-list status for a phylogenetic signal, we obtained on average 667 steps across the 100 randomly selected trees, which is far lower than expected by chance (Fig. 1). In some families (e.g., Elateridae, Tenebrionidae, Melandryidae, and Buprestidae), more than 45% of the species were threatened, while others (e.g., Nitidulidae, Pselaphidae, and Staphylinidae) had only a small percentage of threatened species (Supporting Information).

In the proportional-odds linear mixed-effects model, geographic range had the highest z value (Table 2). The

extinction risk decreased with increasing mean elevation of the distribution of a species. Body size was positively correlated with extinction risk. With regard to resources, species requiring dead wood of larger diameters and preferring areas with an open canopy had a significantly higher risk of extinction. Species using conifers as host trees had a lower extinction risk than species using broad-leaved trees or both broad-leaved trees and conifers. Preferences for different decay stages, flower visitation, microhabitat guild, and larval feeding type had no significant influence on the extinction risk in our model.

Our model assigned 67% of the species to the same category as in the red list and 81% to either the same or one of the 2 neighboring categories (Fig. 2a). No species was classified as NT in our model. Instead, the majority of the species categorized as NT on the red list were ranked as LC in our model. More than 50 species classified by the present red list as LC were ranked as VU, EN, or CR in our model. For each species, we predicted a range of extinction risk categories that were in agreement with the model. These "confidence intervals" reflected the model uncertainty and showed that variation differed across the risk categories (additional data in Supporting Information). When we used the model to predict the extinction risk of species not yet assigned to one of the red-list categories by experts, 33% of I, 35% of DD, and 80% of R species were ranked as likely to be threatened (Fig. 2b).

Discussion

Cross-species data need to consider phylogenetic relatedness (Freckleton et al. 2002), and analyses of red-list categories are no exception. Furthermore, red-list categories represent an ordinal variable with probably unequal differences between consecutive levels (Matthews et al. 2011). Most previous studies ignored the ordinal scale of the red-list categories (Purvis 2008; Verde Arregoitia et al. 2013), even though by ignoring this issue type I errors may be inflated (Matthews et al. 2011). We introduced species-specific random intercepts for the proportional-odds linear mixed-effects model in a way that allowed both modeling ordinal response variables and a correction for phylogenetic relatedness. The model not only allowed an estimation of inference statistics for traits correlated through phylogeny, but it could also be used to take phylogenetic information into account for the prediction of extinction risk of species not scored in the current German Red List.

Our prediction for the training species did not assign a single species to the category NT. This category is assigned when a species does not qualify for one of the threatened categories but is likely to be so assigned in the near future (Rodrigues et al. 2006). The rather high number of species recently listed as unthreatened that were

Figure 2. (a) Comparison of the number of saproxylic beetle species in the German Red List of Beetles (J. Schmidl & B. Büche, unpublished data) across categories and the extinction risk predicted by the model based on intrinsic traits and phylogeny (dark gray, assignments to the same class; light gray, assignments to neighboring classes; LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; RE, regionally extinct). (b) Modeled extinction risk of 188 species that could not be classified by experts (species assigned to the category with the highest probability; DD, data deficient; I, indeterminate; R, rare).

assigned to a higher extinction risk category in our model sounds a note of caution that the status of these species is underestimated in the current German Red List (Fig. 2a & Supporting Information). Furthermore, according to our predictions, a number of unassigned species may also be threatened. However, the small geographic range size of R species may have led to an overestimation of their predicted extinction risk. We suggest considering our predicted extinction risk for species whose status is possibly underestimated and for species likely to be threatened but not yet included in the red list. Both groups should also be included in future conservation programs (e.g., Kotiaho et al. 2005).

Independent of human influence, the risk of extinction owing to stochastic events increases as population size and geographic range decrease (e.g., Payne & Finnegan 2007). Therefore, population sizes as well as shrinking distributions are used as criteria for scoring red-list categories of species (Rodrigues et al. 2006) and thus circularity can enter into the analyses. Our model also identified a strong effect of geographic range on the extinction risk of saproxylic beetles. However, even after controlling for geographic range size, we found significant effects of elevation, biological traits, and resource-related traits on extinction risk.

Since Diamond (1989) called habitat loss one of the drivers in the "evil quartet of extinction," several studies have proven the devastating effect of habitat loss on biodiversity across various taxa (Owens & Bennett 2000; Hof et al. 2011; Di Marco et al. 2014). Within forests, the loss

of dead wood has been identified as one of the main threats to biodiversity (e.g., Grove 2002). Whitehouse (2006) analyzed fossil beetle records of the British Isles, which contain the strongest anthropogenically altered forests in Europe, and listed forest clearance, lack of temporal continuity, change of host tree distribution, lack of fires, and the decline of open forests as possible reasons for extinctions. Assuming that distribution and abundance of saproxylic beetles is determined primarily by the availability of required resources (e.g., Seidl et al. 2011), our results corroborate most of these mechanisms. Overall, our model revealed that lowland species, large species, and species using dead wood of large diameter have a higher extinction risk than others. The same was found for species of open forests and broad-leaved host trees. This pattern can be traced back to the main changes in Europe's forest landscape over the last centuries.

The intensification of land use in Europe began in the lowlands and along rivers, leaving, after millennia of deforestation and pasturing, only patches of disturbed forests (Whitehouse 2006; Radkau 2007). Today, the Atlantic region has the lowest amount of forest cover (Larsson 2001), and the formerly species-rich and structurally diverse floodplain forests have virtually disappeared (e.g., Klimo & Hager 2000). In contrast, mountainous regions were colonized later, and near-natural forests remained, at least in areas difficult to access (Scheifele 1988). Thus, taxa of lowland and riparian forests are at higher risk of extinction than species in other types of forests (Mikusiński & Angelstam 1998; Rust-Dubié et al. 2006), which emphasizes the importance of the few lowland forests with long habitat continuity for conservation (Buse 2012).

In addition to the massive decline of forest area, the remaining forests were heavily altered by forest management. One major change was the extraction of old-growth trees and dead wood, particularly of large diameters. Forestry literature of the 19th century gives a vivid example of this practice; it instructs foresters to "repeat thinning as often as dry or repressed trees are found" (Hartig 1808) and to cut dead, wounded, or insect-infested trees of large diameter (Cotta 1865). Hartig (1808) disagreed with some of his contemporary foresters, who suggested "leaving dead trees to decay as a fertilizer of forests" to deprive species considered pests, such as bark beetles, of any resource that could host them. The removal of old growth affected species that prefer dead wood of large diameters and large-bodied species that need pieces of dead wood of a minimum size that provide microhabitat conditions for a time long enough for larval development to complete (Foit 2010). An example of such a large-bodied species of large diameter wood (>60 cm) is *Cerambyx cerdo*. At the beginning of the 20th century, this longhorn beetle was considered a widespread pest species on old oaks, but due to the loss of such overmature oak trees, it is now listed as CR (Buse et al. 2008).

A further aspect that has changed greatly in forests is light conditions. Natural forests are influenced by disturbances that regularly open the canopy and create dead trees in sunny conditions (Schelhaas et al. 2003). Furthermore, the multiple uses of forests including coppicing and forest pasture provided the full gradient of canopy closure until the 18th and 19th century. Thereafter, agricultural land and forests were separated, wood pasturing ceased, and trees and hedgerows between fields were cleared (Radkau 2007; Rackham 2008). Forests used for fuel wood were transformed to high forests for the production of construction timber (Scheifele 1988; Radkau 2007). After World War II, the growing stock in European countries increased by more than 300%, although the forest area increased only slightly by about 10% (Schelhaas et al. 2003). As a consequence, formerly open forests developed into dark even-aged stands (Larsson 2001), and species of various taxa affiliated with sun-exposed structures became rare (Jonsell et al. 1998; Stehlik et al. 2007). The increase in growing stock affected light conditions and was accompanied by a tremendous shift in the tree species composition of European forests. Naturally occurring broad-leaved trees were still dominant in traditional coppice and pasture woodlands, but with changing demands during the early 19th century, conifer species were planted at their expense (Dirkx 1998; Radkau 2007).

We conclude that for diverse and cryptic arthropods, such as saproxylic beetles, distribution, traits characterizing the species biology, and particularly resource-related traits that allow linking the extinction risk of the species to human pressure or conservation response (Di Marco et al. 2014) are valuable in deriving comprehensive implications for national conservation strategies in biomes, such as temperate forests of Central and Western Europe. Based on our results, we suggest that the amount of dead wood of large diameter should be increased, including artificially created dead wood; more dead wood should be supplied in sunny areas by intentional accumulation in gaps, cutting of shading trees neighboring habitat trees, or benign neglect after natural disturbances; the proportion of the naturally dominant broad-leaved tree species should be increased; and lowland forests should be set aside for conservation rather than forests on remote mountains, which are usually chosen simply because they are associated with fewer conflicting interests with humans.

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Supporting Information

Further information on Red List, trait data and phylogeny of saproxylic beetles in Central and Western Europe (Appendix S1), description of the linear mixed proportional odds model (Appendix S2) including the complete data for analyses (Appendix S3), and a table containing red-list information, modeled extinction risk, and species traits of 1213 saproxylic beetle species (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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