

What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database

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Abstract

1. The extinction of species is a non-random process, and understanding why some species are more likely to go extinct than others is critical for conservation efforts. Functional trait-based approaches offer a promising tool to achieve this goal. In forests, deadwood-dependent (saproxylic) beetles comprise a major part of threatened species, but analyses of their extinction risk have been hindered by the availability of suitable morphological traits.
2. To better understand the mechanisms underlying extinction in insects, we investigated the relationships between morphological features and the extinction risk of saproxylic beetles. Specifically, we hypothesised that species darker in colour, with a larger and rounder body, a lower mobility, lower sensory perception and more robust mandibles are at higher risk.
3. We first developed a protocol for morphological trait measurements and present a database of 37 traits for 1,157 European saproxylic beetle species. Based on 13 selected, independent traits characterising aspects of colour, body shape, locomotion, sensory perception and foraging, we used a proportional-odds multiple linear mixed-effects model to model the German Red List categories of 744 species as an ordinal index of extinction risk.
4. Six out of 13 traits correlated significantly with extinction risk. Larger species as well as species with a broad and round body had a higher extinction risk than small, slim

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and flattened species. Species with short wings had a higher extinction risk than those with long wings. On the contrary, extinction risk increased with decreasing wing load and with higher mandibular aspect ratio (shorter and more robust mandibles).

5. Our study provides new insights into how morphological traits, beyond the widely used body size, determine the extinction risk of saproxylic beetles. Moreover, our approach shows that the morphological characteristics of beetles can be comprehensively represented by a selection of 13 traits. We recommend them as a starting point for functional analyses in the rapidly growing field of ecological and conservation studies of deadwood.

KEYWORDS

deadwood, extinction risk, forest biodiversity, forestry, functional traits, morphometry, red lists, saproxylic beetles

1 | INTRODUCTION

Functional trait-based approaches have become a widely used strategy to study community ecology, with several advantages compared to purely species-based approaches (McGill et al., 2006). For example, in addition to providing mechanistic insights into community functioning and assembly processes, the use of functional traits allows a generalisation across scales (Albrecht et al., 2018; Carmona et al., 2016; Hagge et al., 2019; McGill et al., 2006). In conservation biology, analyses of traits can shed light on why certain species are at higher risk of extinction than others, thereby improving conservation concepts and practical management (Chichorro et al., 2019; Koh et al., 2004; Seibold et al., 2015). Trait-based approaches rely on the availability of common traits with standardised definitions and measurement protocols for all species present in the studied system (Schneider et al., 2019). Therefore, ecologists have increasingly called for an ecological trait-data standard particular for hyper-diverse groups as arthropods (Brousseau et al., 2018; Dawson et al., 2019; Moretti et al., 2017).

Deadwood-dependent (i.e. saproxylic) species are a taxonomic, phylogenetic and functional diverse group that accounts for roughly one-third of all forest-dwelling arthropod species (Kuuluvainen & Siitonen, 2013). Saproxylic organisms are, following Stokland et al. (2012), defined as 'any species that depends, during some part of its life cycle, upon wounded or decaying woody material from living, weakened or dead trees'. They substantially contribute to the important ecosystem function of wood decomposition and thus to the recycling of the largest terrestrial organic source of energy and nutrients (Harmon et al., 1986; Stokland et al., 2012; Ulyshen, 2014). However, diversity of saproxylic beetles is threatened and in the Red List for Europe (Nieto & Alexander, 2010) and for Germany (Schmidl & Büche, 2020; Schmidt et al., 2016), only half of the evaluated saproxylic beetle species are so far listed as unthreatened. Trait-based approaches to the study of saproxylic beetles have thus far been restricted to coarse ecological traits related to habitat preferences (e.g. decay niche, wood diameter niche, canopy niche) and foraging guilds (Gossner et al., 2013; Heikkala et al., 2016; Laaksonen et al., 2020; Seibold et al., 2015). Moreover,

most of these traits are 'soft' traits based on subjective estimates by a few experts (e.g. Freude et al., 1983; Köhler, 2000; Möller, 2009; Schmidl & Bussler, 2004). Although undeniably important, they are neither replicable nor applicable to other species in further studies or beyond the focal region where they were compiled. By contrast, replicable, independent measurements of morphological traits can be made if standardised protocols are available (as suggested by Dawson et al., 2019; Moretti et al., 2017). A standardised methodology would allow morphological trait databases to be applied in other forest ecosystems and expanded to other species and regions. With the exception of surveys of body size (Freude et al., 1983), however, morphological traits and a standardised protocol for their determination in saproxylic beetles are lacking.

Identifying the traits that make species prone to extinction is essential for conservation biology and for timely measures ensuring species protection (Chichorro et al., 2019). Previous extinction risk analyses of animals suggested several morphological traits that make species more prone to extinction. For instance, pale insect species seem to perform better under the conditions of a warming climate because of the thermoregulatory advantage conferred by a light colour (Zeuss et al., 2014). Moreover, body size, a strong surrogate for decreasing population size and increasing home range size and life span, is linked to a higher extinction risk in both vertebrates and invertebrates (Cardillo et al., 2005; Chichorro et al., 2019; Seibold et al., 2015). Species with a lower dispersal ability may also be more prone to extinction in fragmented landscapes (Kotiaho et al., 2005; Reinhardt et al., 2005; Sekar, 2012), whereas those with finely tuned sensory perception may be better able to adapt to changing environments and will thus be less threatened in human-modified landscapes (Cardé, 1984; Turlure et al., 2016). For saproxylic beetles in Europe, studies of species habitat preferences (ecological soft traits) revealed that species preferring large trees, sunny conditions and feeding in wood of broad-leaved trees are at greater risk of extinction. This risk tracks well with the ecological degradation of forests, in which natural broad-leaved forests are replaced by dense conifer-dominated forests while old growth and dead wood are lost (Seibold et al., 2015). Thus, in general, species whose morphological traits prevent adaptation to a set of environmental changes will have a

TABLE 1 The five hypotheses of the study along with the selection of 13 independent morphological traits of saproxylic beetles and the hypothesised functions reported in literature of those traits

Hypotheses	Morphological trait	Hypothesised functions of the trait
H1: Colour	Lightness	Thermoregulation and thus species activity and habitat use (Clusella-Trullas et al., 2008); UV protection (Roulin, 2014; True, 2003); crypsis and aposematism (Roulin, 2014; True, 2003); pathogen resistance (Roulin, 2014; True, 2003)
H2: Body shape	Body length	Fundamental trait in the species biology, e.g. dispersal ability, oxygen transport, metabolic rate (den Boer, 1990; Kaiser et al., 2007; Peters, 1983)
	Body width	Microhabitat use (Barton et al., 2011; Gibb & Parr, 2010)
	Body roundness	Microhabitat use (Barton et al., 2011; Gibb & Parr, 2010; Raine et al., 2018)
	Head length	Prey size and foraging speed in ants (Kaspari & Weiser, 1999)
H3: Locomotion	Wing length	Dispersal ability (Rundle et al., 2007; Sekar, 2012)
	Wing aspect	Flight performance (manoeuvrability, speed, distance; Hassall, 2015; Wootton, 1992)
	Wing load	Dispersal ability (Angelo & Slansky, 1984; Bouget et al., 2015; Bowlin & Wikelski, 2008; Feldhaar & Schauer, 2018; Gibb et al., 2006)
	Leg length (front femur)	Dispersal ability (Hurlbert et al., 2008); resource acquisition and foraging efficiency (Teuscher et al., 2009); surface temperature (Hurlbert et al., 2008; Krasnov et al., 1996); oxygen transport (Kaiser et al., 2007)
H4: Sensory	Antenna length	Olfactory communication (Elgar et al., 2018); diurnal or nocturnal activity (Ribera et al., 1999)
	Eye length	Feeding type (Ribera et al., 1999); diurnal or nocturnal activity and microhabitat use (Talarico et al., 2011; Talarico et al., 2007)

(Continues)

TABLE 1 (Continued)

Hypotheses	Morphological trait	Hypothesised functions of the trait
	Hairiness (Pronotum dorsal)	Dehydration tolerance and mechanoreception (Wittlinger et al., 2007); hydrophobic functions (Suter et al., 2004); pollination (Stavert et al., 2016)
H5: Foraging	Mandibular aspect ratio	Feeding type (Bai et al., 2015); fighting (Goyens et al., 2016; Mills et al., 2016)

higher extinction risk. For example, large species and species with a round body shape are more adapted to large-dimension deadwood and should be thus more threatened than small, flattened species specialised for the small deadwood items that are likely to be available even in intensively managed forests. Furthermore, because coniferous trees were favoured over broad-leaved trees for centuries in Europe, species with robust mandibles adapted to the harder wood of broad-leaved trees are likely to be more prone to extinction.

In this study, we developed a protocol for standardised morphological trait measurements and then applied it to generate a comprehensive trait database for Central European saproxylic beetles. The database was then used to answer the question: What does a threatened saproxylic beetle look like? Based on the above argumentation, we hypothesised that threatened species are those with the following morphological traits: (H1) dark colouration, (H2) larger and rounder body and thus adapted to large-diameter wood, (H3) wing and leg morphologies restricting dispersal ability, (H4) reduced sensory perception and (H5) a higher mandibular aspect ratio (more robust mandibles adapted to hardwood) (Table 1).

2 | MATERIALS AND METHODS

2.1 | Species list

The 1,170 beetle species included in this study were identified by experts. Species names followed the taxonomy of the German beetle checklist (Bleich et al., 2020). Saproxylic beetles were selected based on the definition of Stokland et al. (2012) and on the German reference list of saproxylic beetles (Köhler, 2000; Schmid & Bussler, 2004). The vast majority of the studied specimens had been collected in Europe.

2.2 | Morphological traits

In all, 32 morphological traits were measured directly and five additional traits (wing load, wing aspect, mandibular aspect ratio, total hairiness and body roundness) were calculated based on these measured values (Figure 1, Table 2; a detailed measurement protocol and the morphological trait database of saproxylic beetles are published on Dryad Digital Repository <https://doi.org/10.5061/>

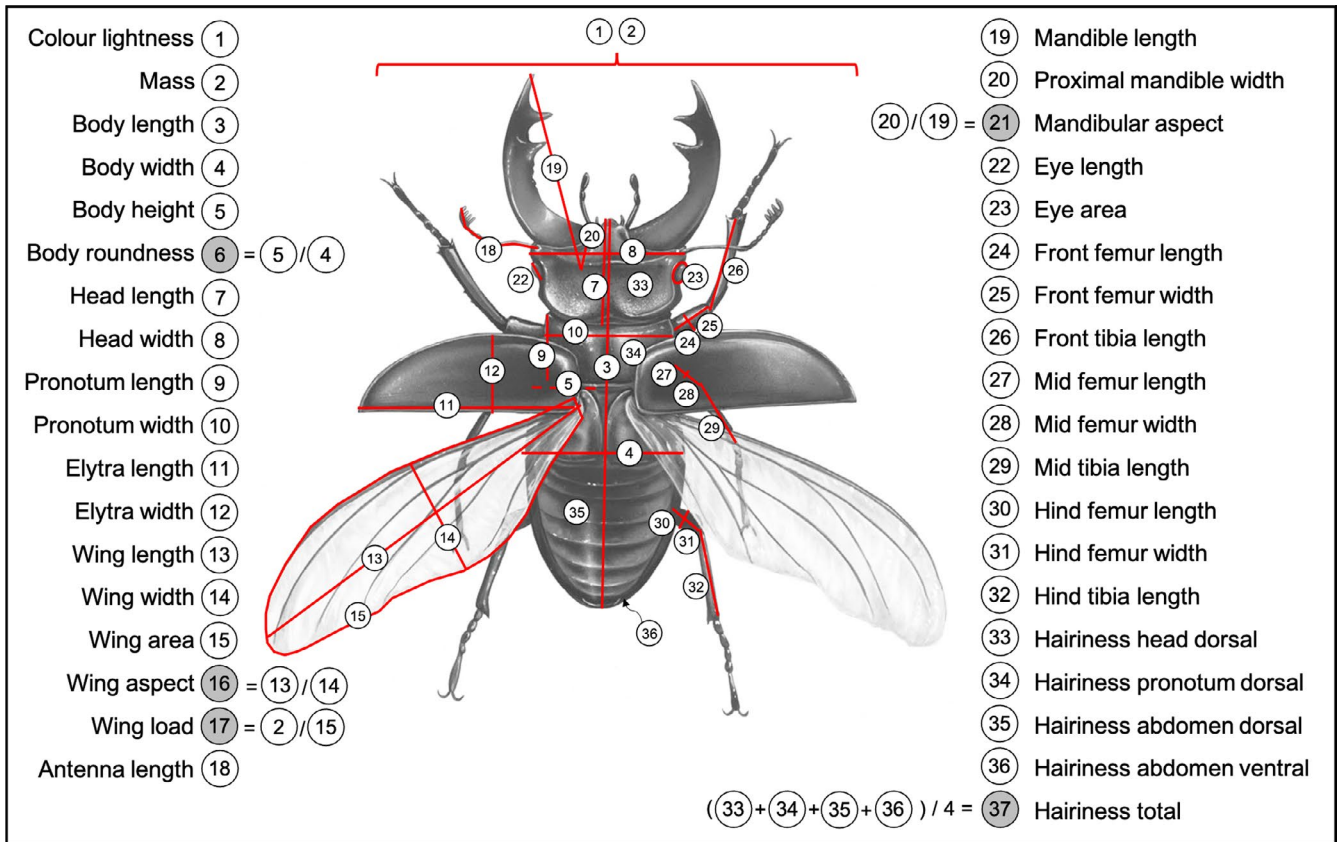


FIGURE 1 The 37 morphological investigated traits, including five traits that were calculated from combinations of the measured traits (grey circles). All traits were measured on the right body side of the beetles, but in the illustration for clarity they are shown on both body sides

dryad.2fqz612p3; Hagge et al., 2021). All traits were measured on the right side of the beetles' bodies, with the left side measured only when body parts were damaged or missing. Although we acknowledge the importance of intraspecific variability (see the discussion part), due to the physical limitations (more details in Appendix S5), most of the species were represented by a single individual. For 180 species (15%), however, two or more individuals of the same species were measured (Hagge et al., 2021). In that case, the average value of each trait was calculated. Furthermore, information on morphological differences between sexes reported in taxonomic literature was collected (Freude et al., 1983) focusing on the 13 traits selected for the extinction risk analyses (see below and Table 1). Substantial sexual differences were classified and reported in the trait database together with the recorded sexes for those species.

The morphological measurements of the beetles were made using a Leica M205 C (Leica Microsystems CMS GmbH., Switzerland) stereomicroscope with a magnification range of 7.8x to 160x and an optical resolution of 0.952 μm . The line, segmented-line and area measurement tools of the Leica LAS Core (version LAS V4.1.0) measurement software were used in combination with the Leica DFC295 digital colour camera (Leica Microsystems CMS GmbH., Switzerland). Beetle mass was measured using Sartorius M5P microbalances (Sartorius AG, Germany) with a resolution of 0.001 mg.

The colour lightness of the beetle species was estimated using the workflow of a computer-assisted digital image analysis system (Schweiger & Beierkuhnlein, 2016; Zeuss et al., 2014). Digital photos published in the book 'Käfer Mitteleuropas' (Dries, 2016) served as the reference. The beetle species in the book were photographed under standardised conditions in dorsal view against a white background. Subsequently, the white background of the red, green and blue (RGB) photographs was removed and the mean of the RGB colour channel across all pixels of each image was calculated. Possible colour lightness values thus ranged from 0 for completely blackish to 255 for completely whitish species.

2.3 | Red List and phylogeny

The extinction risk analysis was restricted to saproxylic beetle species occurring in Germany for the following reasons: (a) a current comprehensive national Red List is available for all of the beetle species (Schmidl & Büche, 2020; Schmidt et al., 2016); (b) the German checklist of saproxylic beetle species is comprehensive, with 1,374 species from 70 different families (Schmidl & Bussler, 2004) and (c) Germany is representative of both the climate and the history of silviculture in Western and Central Europe (Seibold et al., 2015). Therefore, the results should be broadly transferrable to surrounding countries.

TABLE 2 Summary statistics of 37 morphological traits, their allometric regressions with body length and their respective phylogenetic signal (Pagel's λ with lower and upper confidence interval). Intercept, slope and Pagel's λ based on phylogenetic generalised least squares regression model between each log-transformed measured trait and the log-transformed body length using the *gls* function in the add-on package *nlme* (Pinheiro et al., 2020)

Morphological trait	Unit	Min	Max	Mean	SE of mean	Intercept	Slope	SE of slope	Pagel's λ	Lower C.I. λ	Upper C.I. λ
Colour lightness	RGB ^b	73.19	159.33	116.48	0.43	116.90	-3.73	0.90	0.53	0.43	0.62
Mass	mg	0.01	3,438.30	43.81	6.05	-2.94	2.66	0.04	0.77	0.70	0.83
Body length	mm	0.65	46.96	6.56	0.17	-	-	-	0.97 ^c	0.95	0.98
Body width	mm	0.25	22.37	2.26	0.06	-0.76	0.90	0.01	0.95	0.93	0.97
Body height	mm	0.13	15.66	1.75	0.05	-1.11	0.90	0.01	0.94	0.92	0.96
Body roundness ^a	-	0.30	1.25	0.78	0.00	-0.35	0.00	0.01	0.88	0.83	0.92
Head length	mm	0.14	9.52	1.11	0.03	-1.60	0.92	0.02	0.76	0.70	0.83
Head width	mm	0.17	17.72	1.24	0.03	-1.36	0.83	0.01	0.93	0.90	0.96
Pronotum length	mm	0.13	13.25	1.40	0.03	-1.27	0.90	0.01	0.88	0.85	0.92
Pronotum width	mm	0.20	16.06	1.80	0.05	-1.03	0.88	0.01	0.95	0.93	0.97
Elytra length	mm	0.22	29.95	4.09	0.11	-0.48	0.95	0.01	0.89	0.86	0.92
Elytra width	mm	0.12	10.65	1.12	0.03	-1.45	0.90	0.01	0.94	0.92	0.96
Wing length	mm	0.95	38.77	6.39	0.15	0.29	0.85	0.01	0.83	0.78	0.89
Wing width	mm	0.25	16.34	2.38	0.06	-0.66	0.86	0.01	0.83	0.78	0.89
Wing area	mm ²	0.21	533.00	19.51	1.18	-0.60	1.72	0.03	0.82	0.76	0.88
Wing aspect ^a	-	1.59	4.75	2.72	0.01	0.94	0.00	0.01	0.78	0.73	0.84
Wing load ^a	mg/mm ²	0.01	9.37	0.86	0.03	-2.42	0.98	0.04	0.62	0.53	0.72
Antenna length	mm	0.20	70.70	2.88	0.15	-1.08	0.90	0.02	0.96	0.94	0.98
Mandible length	mm	0.03	19.00	0.47	0.02	-2.51	0.95	0.02	0.79	0.72	0.85
Proximal mandible width	mm	0.01	5.92	0.20	0.01	-3.38	0.94	0.03	0.57	0.47	0.68
Mandibular aspect ratio ^a	-	0.08	1.67	0.44	0.01	-0.85	-0.01	0.03	0.31	0.20	0.41
Eye length	mm	0.03	4.18	0.52	0.01	-2.51	0.84	0.02	0.89	0.86	0.92
Eye area	mm ²	0.00	6.35	0.23	0.01	-5.45	1.63	0.03	0.86	0.82	0.90
Front femur length	mm	0.16	12.57	1.19	0.03	-1.54	0.91	0.02	0.82	0.76	0.88
Front femur width	mm	0.05	3.25	0.38	0.01	-2.56	0.93	0.02	0.83	0.77	0.88
Front tibia length	mm	0.14	11.58	1.13	0.03	-1.66	0.95	0.02	0.86	0.82	0.90
Mid femur length	mm	0.15	11.32	1.31	0.04	-1.51	0.93	0.02	0.80	0.75	0.86
Mid femur width	mm	0.05	3.38	0.39	0.01	-2.60	0.92	0.01	0.81	0.76	0.87
Mid tibia length	mm	0.14	10.70	1.26	0.04	-1.59	0.97	0.02	0.89	0.85	0.92
Hind femur length	mm	0.15	14.02	1.52	0.05	-1.46	0.96	0.02	0.86	0.81	0.90
Hind femur width	mm	0.05	4.16	0.41	0.01	-2.60	0.93	0.02	0.81	0.75	0.86
Hind tibia length	mm	0.14	11.66	1.50	0.05	-1.51	0.99	0.02	0.91	0.87	0.94
Hairiness head dorsal	hairs/mm	0.00	179.19	27.17	0.72	3.05	-0.53	0.08	0.57	0.48	0.66
Hairiness pronotum dorsal	hairs/mm	0.00	203.88	27.74	0.73	3.12	-0.68	0.08	0.65	0.57	0.73
Hairiness abdomen dorsal	hairs/mm	0.00	170.89	29.72	0.77	3.17	-0.68	0.08	0.79	0.72	0.85
Hairiness abdomen ventral	hairs/mm	0.00	155.84	31.02	0.83	2.99	-0.61	0.08	0.73	0.65	0.80
Hairiness total ^a	hairs/mm	0.00	130.42	28.76	0.65	3.24	-0.63	0.06	0.83	0.77	0.89

^aCalculated traits.

^bColour lightness value averaged from RGB (red, green and blue) channels, ranging from 0 (completely black) to 255 (completely white).

^cPhylogenetic signal (Pagel's λ) of body length was calculated as an intercept-only model.

The categories of the German Red List follow the International Union for Conservation of Nature (IUCN) classification. As in Seibold et al. (2015), the six sequential categories of saproxylic beetles of the German Red List were converted into an ordinal scale of extinction risk as follows: 0 = least concern (LC), 1 = near threatened (NT), 2 = vulnerable (VU), 3 = endangered (EN), 4 = critically endangered (CR) and 5 = regionally extinct (RE).

Due to the non-independency of individual species, phylogenetic information was included in the analyses of species extinction risk (see below). This was achieved by adding species to the phylogenetic tree of saproxylic beetles published by Seibold et al. (2015). We assigned 43 new species to the tip next to the closest known relative using the *phangorn* package (Schliep, 2011; Appendix S1). Placing some of the missing taxa into a phylogenetic tree using the taxonomic information can, however, lead to the higher uncertainty in the trait-related analyses compared to the phylogeny based on pure genetic data (Rabosky, 2015). To check the robustness of our results, we therefore created a phylogeny for a subset of 519 species for which most recent molecular data were available and repeated the analyses of species extinction risk for this subset (Appendix S7).

2.4 | Data analysis

All analyses were conducted in R 3.6.1 (<http://www.r-project.org>). Descriptive statistics of untransformed data were calculated for all traits across all species (min, max, mean, SE of the mean). To investigate the relationship between each of the morphological trait and body size, we fitted an allometric model (Cheverud, 1982) between log-transformed measured trait and the log-transformed body length [$\log(\text{TRAIT}) \sim \log(\text{body length})$] of the same species using phylogenetic generalised least squares regression (PGLS) model with help of the *gls* function in the add-on package *nlme* (Pinheiro et al., 2020). As species are not statistically independent, the PGLS method allows correcting for phylogeny during the fitting process by considering a specific variance-covariance matrix that captures the correlation structure in a trait among species. The phylogenetic correlation structure of the model was represented by parameter λ (Pagel, 1999) using the function *corPagel* (Freckleton et al., 2002). Pagel's λ is the most widely used index quantifying the strength of the phylogenetic signal, with values ranging from 0 (trait's evolution independent of phylogeny) to 1 (trait's evolution according to Brownian motion). The fitted regression was used to calculate the approximate parameter estimates (intercept, slope, SE of the slope) and the phylogenetic signal (Table 2). We applied the *intervals* function from the *nlme* package (Pinheiro et al., 2020) to calculate 95% confidence intervals of the phylogenetic signal.

Since body size is a pervasive trait that influences all other morphological traits of beetle species, there was a strong correlation among most of the measured traits (Appendix S2). To remove the effect of body size for the process of the selection of complementary morphological traits, we extracted the residuals from the same phylogenetically corrected regression model as described above. Based on

these values, we created the correlation matrix between the individual traits using Pearson's correlation coefficients in *corrplot* package (Wei & Simko, 2017). As the number of hairs per millimetre was already standardised for body size, only a logarithmic transformation was applied. For the colour lightness values, no previous logarithmic transformation was needed, nor was a standardisation of body size. Out of five calculated traits (all subsequently log-transformed), only wing load strongly correlated with body length (Appendix S3), and so it was standardised for body length in the same way as the measured traits.

Some traits proved to be strongly correlated with each other even after body length had been considered and they clustered into several distinct groups (e.g. leg lengths, wing size, hairiness of different body parts). Therefore, only one representative trait from each group was selected for the subsequential extinction risk analyses, as this substantially reduced the correlation coefficients among the selected traits (Appendix S4). Traits characterising the different aspects of ecological functions (colour, body shape, locomotion, sensory and foraging; Table 1) were emphasised, with a preference for those that are easy to measure (linear instead of squared measurements). Based on all three conditions, that is, independent, easily measurable and representing specific ecological functions, 13 morphological traits were selected for the extinction risk analyses.

To model the extinction risk according to morphological traits, the ordinal red list categories were related to the 13 selected morphological traits. All species not listed in German Red lists for beetles (Schmidl & Büche, 2020; Schmidt et al., 2016) were excluded, resulting in 1,125 beetle species. Species with missing trait data (for one or more predictor trait variables) or listed as data deficient (D), indeterminate (I) or of restricted range (R) in the Red list were also excluded such that the analysis included a total of 744 species. For these species, a proportional-odds multiple linear mixed-effects model was fitted using the function *clmm* in the add-on package *ordinal* (Christensen, 2020). The six ordinal Red List classes (LC, NT, VU, EN, CR and EX, see above) were treated as response variable and the log-transformed raw values of 13 selected morphological traits (for colour lightness no logarithmic transformation was needed, Table 1) as predictor variables in the model. Phylogenetic correlations between species were modelled from the species-specific random intercepts with a fixed correlation structure defined by the phylogenetic distance between each pair of species, to avoid inflation of the degrees of freedom due to species relatedness (Harvey & Pagel, 1991; for details, see Seibold et al., 2015).

3 | RESULTS

3.1 | Trait database on European saproxylic beetles

In the following, our comprehensive trait database focused on saproxylic beetles in Central and Northern Europe and based on the newly developed standardised measurement protocol is presented. The database can be accessed via Dryad Digital Repository <https://doi.org/10.5061/dryad.2fqz612p3> (Hagge et al., 2021). Overall, it includes 37 traits covering a wide range of the morphological variability of the

studied beetles. The traits were measured in 1,376 specimens, covering 1,170 different beetle species and 64 families (Table 2). Of these species, 1,157 were European saproxylic species and 13 species were either non-saproxylic or a saproxylic species from outside Europe.

Among the 1,170 species included in this study, very strong, positive correlations ($r > 0.76$, $p < 0.001$; Appendix S2) were determined between each of the measured traits and body length, with the exceptions of hairiness and colour. The correlation of the hairiness of different body parts with body length was marginally negative ($r > -0.3$, $p < 0.001$), whereas colour was not significantly related to body length. Wing load (as the ratio of body mass to wing area) was the only calculated trait with a close positive relationship to body

length ($r = 0.82$, $p < 0.001$; Appendix S3). For most of the linear traits, the slopes of the allometric relationships with body length were close to one (isometry), ranging from 0.83 to 0.99 (Table 2), while for nonlinear variables (mass, wing area and eye area) the slopes were substantially higher (2.66, 1.72 and 1.63, respectively).

3.2 | Selection of 13 independent traits

After standardisation of the traits for body length, several remained highly correlated with each other (Figure 2), as strong correlations were found within the groups relative leg length ($r = 0.67-0.92$),

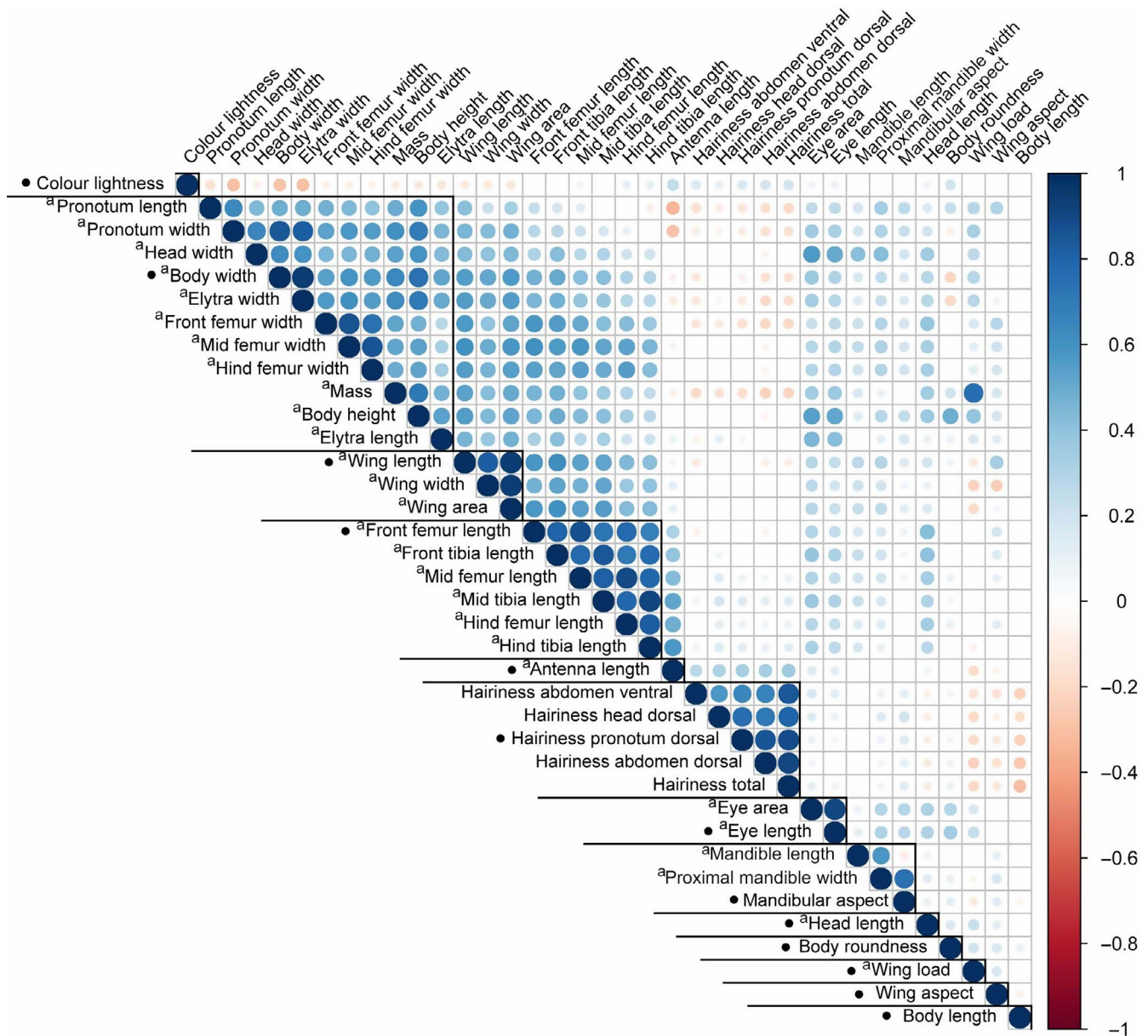


FIGURE 2 Correlation matrix between the individual traits using Pearson's correlation coefficients (corrplot package; Wei & Simko, 2017). The colour intensity (light to dark) and the size of the circles are proportional to the Pearson's correlation coefficients; positive correlations are represented in blue and negative correlations in red. Only significant ($p < 0.05$) values are shown. The 13 independent morphological traits representing individual groups are marked by a black dot. ^aIndicate relative traits based on the residual values of the regressions with body length (see Section 2)

relative wing size ($r = 0.83\text{--}0.95$), hairiness of different body parts ($r = 0.58\text{--}0.9$) and different relative body shapes ($r = 0.35\text{--}0.94$). Therefore, in the list of independent traits only one representative of each group was included, that is, relative front femur length, relative wing length, hairiness pronotum dorsal and relative body width. Similarly, given the positive correlation between relative eye area and relative eye length ($r = 0.92$) as well as between proximal mandible width and mandibular aspect ratio ($r = 0.75$) and relative mandible length (0.59), only relative eye length and mandibular aspect ratio were entered into the list. As traits within the group relative leg width were highly correlated with each other ($r = 0.74\text{--}0.86$) and with the many traits describing body shape and locomotion, these traits were excluded from the list of independent traits. The remaining traits (colour lightness, body length, body roundness, relative head length, relative antenna length, relative wing load and wing aspect) were largely independent of the others such that all were included in the final list. Thus, in total, the 13 independent traits that correlated only weakly with each other, after accounting for body length were selected for the subsequential extinction risk analyses ($r = -0.29\text{--}0.56$; Figure 2; Appendix S4).

3.3 | Morphology explains the extinction risk

Our ordinal model for Red List status clearly showed a correlation between extinction risk and species morphology (Figure 3, Appendix S6). Among the 13 traits, six correlated significantly with extinction risk while for the remaining seven there was no effect. Colour lightness had no significant effect on extinction risk. Among

the traits related to size and shape, the extinction risk was higher for larger than for smaller species, and for species with a broad and round body than for slim and flattened species. The relative head length was not significantly related to extinction risk. Among traits associated with locomotion and dispersal, extinction risk decreased with relative wing length, whereas it increased with decreasing relative wing load. Neither wing aspect nor relative leg length had a significant effect on the extinction risk, nor did the three traits related to sensory perception (relative antenna length, relative eye length and hairiness). Among the traits related to foraging, species with a higher mandibular aspect ratio (more robust mandibles) were at higher risk of extinction. Additional analyses of subsets of species showed that the results were robust to the use of a pure genetic phylogeny (Appendix S7) and for variation originated from species with sexual dimorphism (Appendix S8).

4 | DISCUSSION

The extinction risk of saproxylic beetles was significantly related to 6 out of the 13 assessed morphological traits. The known ecological aspects and functional roles of these 13 independent traits are presented in Table 1 and discussed in detail in the Appendix S9. Our analyses supported our hypotheses that species with a larger and rounder body shape (H2) and those with a higher mandibular aspect ratio (more robust mandibles; H5) are at higher risk of extinction. By contrast, there was no support for a relationship of colour lightness (H1) or sensory perception (H4) with the risk of extinction. For the hypothesis regarding locomotion

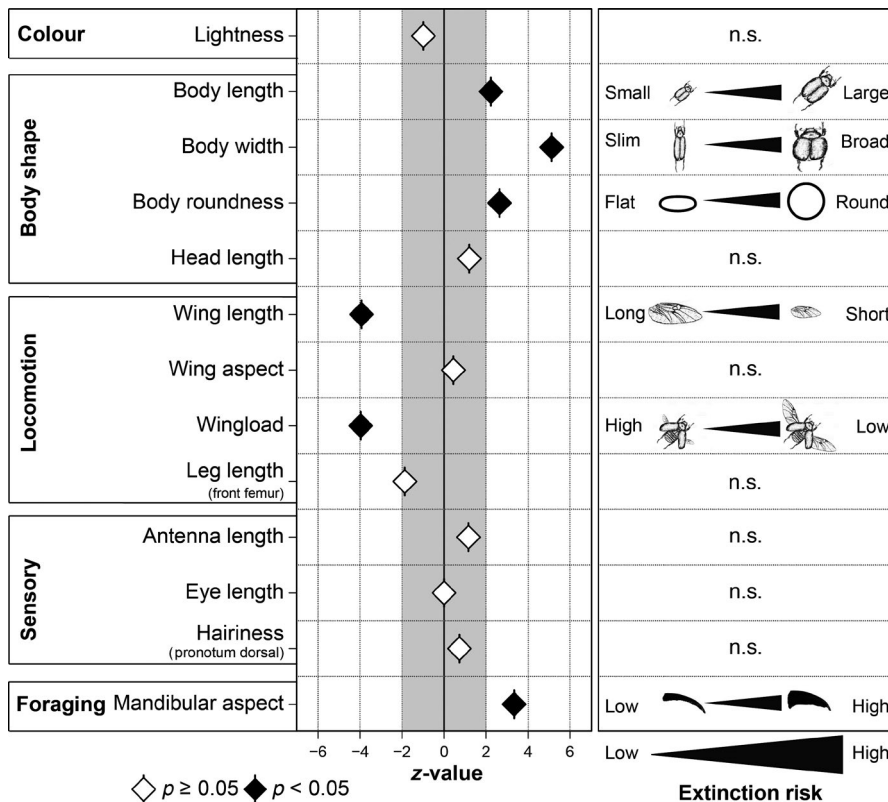


FIGURE 3 Results of the proportional-odds multiple linear mixed-effects model (z-values) with species-specific random intercepts based on the phylogeny to estimate the effects of morphological traits on the extinction risk of saproxylic beetles. Grey shading in the left panel refers to insignificant values ($p > 0.05$). Right panel visualises change in significant morphological traits from low to high extinction risk

(H3), evaluated using different morphological features as dispersal proxies, the results were mixed.

Our analysis showed an increased extinction risk with increasing body size. Previous studies of different organisms reported correlation of large body size with extinction-promoting traits such as low population density, long generation time and larger home-range requirements (McKinney, 1997). For example, the increased body length of several larger carabid species predicts their decline, possibly because of a lower reproductive output and a reduced dispersal capacity (Kotze & O'Hara, 2003). Our finding that body size is strongly linked to the extinction risk of saproxylic beetles is consistent with previous results using body size values derived from the literature (Seibold et al., 2015). For large-bodied species, deadwood of a minimum size is needed as it provides the required microhabitat conditions for a time long enough to allow the completion of larval development (Brin et al., 2011; Foit, 2010). Therefore, the gradual decrease over the last few centuries of old-growth forests, with the resulting loss of their structural properties (Grove, 2002a) together with the generally slower responses of larger species to environmental changes (Beissinger, 2000) has especially impacted species that prefer dead wood of large diameters. A finding which can be generalised in a way that forest-dwelling species associated with old-growth forest attributes are particularly prone to extinction (Lindenmayer & Franklin, 2002; Nieto & Alexander, 2010). Another explanation of the higher extinction risk of larger than of smaller species may be their larger area requirements (Slade et al., 2013). Indeed, analyses of life-history traits have shown that larger European moth species are vulnerable to population decline (Coulthard et al., 2019; Potocký et al., 2018), a pattern that is particularly pronounced in woodland species.

This study also found a lower extinction risk for flattened and slim species. Both properties are typical for saproxylic species living under bark in the phloem layer (Stokland et al., 2012). The extinction risk of these species may be lower because (a) suitable host trees are those that have recently died, and in managed forests such trees are more likely to be available than more-decayed trees, which are often removed; (b) most phloem feeders and their associated species have a relatively fast life cycle, with at least one generation per year and (c) species inhabiting short-lasting habitats are usually better dispersers than those living in long-lasting habitats. This finding thus illustrates how different functional specialisation of species can have diverging consequence for species extinction risk due to land-use change, which is in line with findings on land-use effects on the functional distinctness of Araneae, Carabidae and Heteroptera species (Birkhofer et al., 2015).

Species with shorter relative wing length were also found to have a higher extinction risk. A long relative wing length is considered to be related to a high dispersal ability (Southwood, 1966). Species with longer wings have larger distribution ranges (Rundle et al., 2007) and are generally better colonisers (Harrison, 1980). A relation between wing length and dispersal ability was also reported by Reinhardt et al. (2005), who showed that Orthoptera species with a lower dispersal ability have a higher extinction risk. However, we also found that more threatened species had a low relative wing load. Although this was in

contrast to the result for wing length, similar results were reported for two red-listed and three common species of saproxylic beetles within the genus *Epuraea* (Gibb et al., 2006). The explanation may lie in the dependence of potentially good dispersers (species with low wing load) on ephemeral or highly scattered resources (McLachlan, 1985), which makes these species more endangered despite their high dispersal ability. The ambiguity of these findings together with the other arguments that have been suggested (see the detailed discussion on traits in Appendix S9) questions the use of wing load as a general dispersal proxy for a wide range of saproxylic beetle species and points out the need for physiological studies comparing the different dispersal proxies of beetles across species (e.g. Goyens et al., 2015).

In addition, we found a higher extinction risk for species with a higher mandibular aspect ratio (more robust mandibles). Although the shape and size of mandibles is typically associated with different fighting strategies and may represent a sexually selected trait (Goyens et al., 2016; Mills et al., 2016), this concerns only a few species and families (especially within family Lucanidae, Ciidea and some *Agathidium* spp.) and did not affect our overall observed pattern (Appendix S8). Often, the shape of mandibles is linked to different foraging strategies. In carabid beetles, the wider and shorter mandibles are associated with phytophagous species (Deroulers & Bretagnolle, 2019). In dung beetles (Bai et al., 2015), in checkered beetles (Vega & Hofstetter, 2015) and grasshoppers (Ibanez et al., 2013; Kang et al., 1999), morphological differences in mandible shape are linked to the quality (shape, texture or toughness) of the food resource. In saproxylic beetles, however, the functional adaptations of the morphological mandible characteristics to food exploitation are still not fully explored. Various wood characteristics are reflected in the mandibular structure of the larvae of individual saproxylic beetle species (Kundanati et al., 2020), whereas adults typically feed on other resources than wood. However, unlike for larvae, for which wood is a shelter and food source, for adult beetles it represents the barrier they have to overcome when leaving the tree after pupation in the case of xylem-feeding species (50%–60% of saproxylic beetle species, Schmidl & Bussler, 2004) or when gnawing galleries in the wood for growing fungi in case of ambrosia beetles (Hulcr & Stelinski, 2017). Thus, it can be hypothesised that even for adults, a higher mandibular aspect ratio implies specialisation in certain wood properties (e.g. harder oak wood exploited by species like *Cerambyx cerdo*) which would make these species more prone to extinction. In Europe, coniferous trees have been favoured over natural broad-leaved tree species for centuries (Grove, 2002b) and thus saproxylic beetle species specialised on broad-leaved tree species have a higher risk of extinction (Seibold et al., 2015). As most dominant broad-leaved tree species in Central Europe have harder wood than most conifer species, the change in tree species may explain our finding that species with more robust mandibles adapted to harder wood are more likely to face extinction.

The lack of evidence supporting our hypotheses regarding colour lightness and sensory perception may reflect the specialist lifestyle of saproxylic organisms. Since most of their life cycle is spent within the wood, saproxylics are buffered from many of the changes in the

surrounding environment such that thermoregulation associated with colour lightness is a less relevant or less effective function. In addition, the general ecological functions of morphological traits may vary such that between different species groups the same traits are responsible for different, perhaps even conflicting functions (Table 1, see also detailed discussion on trait in the Appendix S9). However, the contrasting energy allocation strategies of species may offset the function and thus the effect of a single morphological trait (Pinkert et al., 2020).

In this study, we focused on those morphological traits of saproxylic beetles which were correlated with extinction risk of species. These morphological traits have the advantage of being directly measurable and reproducible, based on the standardised protocol presented here. However, we are aware that other species characteristics including ecological (Seibold et al., 2015), physiological and behavioural traits play an important role and can contribute significantly to the overall picture. The potential multi-functionality of individual morphological traits (see Table 1 and the Appendix S9) restrains interpreting interactions between traits and the environment, and thus strictly hypotheses-driven analyses are essential (Brousseau et al., 2018; Sosiak & Barden, 2021). In addition, intraspecific variation in morphological traits, including variation between sexes (Bouget et al., 2015), could be important for several ecological and evolutionary processes (e.g. Griffiths et al., 2016; Molleman et al., 2016). However, for our extinction risk analyses covering the interspecific variability of several hundred deadwood beetle species, we were able to demonstrate that such variation played a minor role and could not alter the results from the extinction risk analyses (Appendices S5 and S8). In the broader context, our study highlights the general need in functional trait-based approaches that provide a better understanding of the relationship between individual species traits and species fitness. This would also allow a deeper understanding of the relative importance of individual traits for different functions, and thus for ecological functioning in general.

Our database provides measurements made following a standardised protocol of 37 morphological traits for 1,157 European saproxylic beetles and can be extended to other species and regions. Furthermore, the database and the measurement protocol can be used as a blueprint for other species-rich arthropod groups. The presented database contributes substantially to the rapidly growing field of ecological and conservation studies on deadwood and provides a solid background for new functional applications (Petchey & Gaston, 2002). The functional trait responses of species assemblages have also been applied to understand the changes in biodiversity caused by different drivers (Muscarella & Uriarte, 2016) as well as the consequences of functional community change for ecosystem processes (Moretti et al., 2013). The availability of multiple complementary species traits is essential to calculate valid measures of the functional diversity of species assemblages (Petchey & Gaston, 2006). In the field of deadwood ecology, such measures can be applied to explain the responses of saproxylic beetles to climate and local habitat properties (Pérez-Sánchez et al., 2020; Thorn et al., 2018). Functional diversity

measures of saproxylic species have also been integrated in biogeographical studies (Hagge et al., 2019) as well as in studies on interaction networks (Wende et al., 2017). Integrating functional diversity increases the certainty of conclusions drawn from survey studies (Thorn et al., 2020). In the experimental approaches frequently used in the field of deadwood ecology (e.g. Gossner et al., 2016; Seibold et al., 2018), the integration of functional diversity analyses would be a promising addition.

In general, our study shows that species extinction risk is not a random process. Instead, certain morphological characteristics of species that are negatively impacted by human resource exploration or, more generally, by land-use change, lead to a higher risk of extinction for these species. In the case of saproxylic beetles, these are traits linked to forest structures and deadwood features that have been suppressed or removed by forestry in the last centuries. To protect these threatened species, the amount of large-diameter deadwood should be increased (relevant especially for species with large body size), the supply of deadwood should be targeted across the landscape (relevant especially for species with low dispersal ability) and the proportion of the naturally dominant broad-leaved tree species should be increased (relevant especially for species adapted to naturally dominant tree species; see also Seibold et al., 2015). More generally, the morphological diversity of species as it emerged from functional evolution might be most appropriately maintained by balancing human land use with the preservation of the greatest possible complexity and heterogeneity of natural ecosystems.

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AUTHORS' CONTRIBUTIONS

J.H. and J.M. conceived the idea of the trait database and extinction risk analysis; J.H., J.M., J.B., M.M.G. and S.S. designed the measurement protocol; J.H., J.M., T.B., A.G., A.J.-M., J.S., A.S.-T., S.T. and L.D. contributed beetle specimens for measurement; J.H. and J.G.S. conducted the morphological trait measurements; C.H. created the genetic-based phylogeny; J.H. and L.D. analysed the data; J.M., R.H.B.C., S.S. and S.T. supported the statistical analyses; J.H., J.M. and L.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

A detailed measurement protocol and the morphological trait database of saproxylic beetles are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2fqz612p3> (Hagge et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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