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ORIGINAL ARTICLE

Insect Conservation and Diversity

Taxonomic and methodological biases in saproxylic beetles: Body size, trophic group and detection probability

Markus Franzén[1,2] | Nicklas Jansson[1] | Mustafa Avci[3] | Antoine Brin[4] | Hervé Brustel[4] | Jan Budka[5] | Jörn Buse[6] | Giuseppe Carpaneto[7] | Stefano Chiari[7] | Lukáš Čížek[8] | Mustafa Coskun[9] | Jeremy Dagley[10] | Peter M. Hammond[11] | Estefanía Micó[12] | Tuğba Öncül Abacıgil[13] | Tomáš Pavlíček[14] | Jiří Schlaghamerský[5] | Pavel Šebek[8] | Anne Sverdrup-Thygeson[15] | Sakin Vural Varli[16] | Lars Westerberg[1] | Inge Wilde[17] | Agnese Zauli[7] | Per Milberg[1]

[1]IFM Biology, Division of Ecology, Linköping University, Linköping, Sweden

[2]Department of Biology and Environmental Sciences, Linnaeus University, Kalmar, Sweden

[3]Department of Forest Entomology and Protection, Faculty of Forestry, Süleyman Demirel University, Isparta, Turkey

[4]École d'Ingénieurs de Purpan, Toulouse, France

[5]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

[6]Department for Ecological Monitoring, Research and Species Protection, Black Forest National Park, Seebach, Germany

[7]Department of Science, University of Rome, Rome, Italy

[8]Institute of Entomology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic

[9]Department of Biology, Faculty of Science and Literature, Adıyaman University, Adıyaman, Turkey

[10]Open Spaces Department, Epping Forest, City of London, The Warren, Essex, UK

[11]Natural History Museum, London, UK

[12]Research Institute CIBIO (Centro Iberoamericano de la Biodiversidad), University of Alicante, Alicante, Spain

[13]Olive and Olive Processing Technology Department, Vocational High School of Edremit, Balıkesir University, Balıkesir, Turkey

[14]Institute of Evolution, University of Haifa, Haifa, Israel

[15]Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

[16]Faculty of Science and Arts, Balıkesir University, Balıkesir, Turkey

[17]Nottinghamshire Wildlife Trust, The Old Ragged School, Nottingham, UK

Correspondence
Per Milberg, IFM Biology, Division of Ecology, Linköping University, SE-581 83 Linköping, Sweden.
Email: per.milberg@liu.se

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Abstract

1. Smaller insect species are routinely described later than larger species, perpetuating the Linnean shortfall.
2. Using 425 saproxylic beetle species from 28 veteran oak sites, we test whether body size varied with year of description and earliest georeferenced record year, and whether body length predicted detection probability.

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3. Linear models show a significant negative relationship between body length and both year of description ($\beta = -0.00063 \pm 0.00021$ SE, $p = 0.003$) and earliest georeferenced year ($\beta = -0.00057 \pm 0.00024$ SE, $p = 0.016$).
4. Single-season occupancy models reveal only a marginal size effect on detection ($\beta = -0.021$, $p = 0.055$); instead, the trophic group drives variation, with saproxylophagous species detected most readily.
5. Fourteen species remain undescribed, and 29% lack any georeferenced record, highlighting combined Linnean and Wallacean shortfalls.
6. Historical taxonomic bias towards conspicuous species and methodological undersampling of specific trophic guilds together impede accurate biodiversity assessment.
7. We recommend integrated taxonomic revision, diversified trapping protocols and trait-based occupancy models to rectify these biases and improve conservation planning.

KEYWORDS
biodiversity informatics, Coleoptera, conservation planning, flight interception traps, Linnean shortfall, occupancy modelling, sampling bias, trait-based ecology, veteran oaks, Wallacean shortfall

INTRODUCTION

Despite centuries of taxonomic effort, much insect diversity is still undescribed, creating severe Linnean and Wallacean shortfalls (Diniz-Filho et al., 2013; Hortal et al., 2015). Body size consistently predicts description probability across taxa, with large species named earlier (Blackburn & Gaston, 1994; Engel et al., 2021; Riedel et al., 2013). Yet the ecological and methodological mechanisms that generate this bias remain poorly quantified for many hyper-diverse groups, including saproxylic beetles.

Recent studies reveal that species discovery follows discernible patterns driven by species' traits, including body size (Moura & Jetz, 2021). This size bias creates systematic distortions in our understanding of biodiversity patterns and can lead to skewed conservation priorities that favour larger, more charismatic taxa (Gardner et al., 2011; Troudet et al., 2017). The relationship between body size and discovery timing reflects both biological reality and methodological constraints. Larger species tend to have broader geographic distributions and higher abundance, increasing encounter probability (Blackburn & Gaston, 1994). Simultaneously, historical collecting methods have favoured the detection and description of larger organisms, as they are more conspicuous and easier to identify using traditional morphology (Fontaine et al., 2012).

Beyond initial description, the documentation of species' distributions—reflected in georeferenced occurrence records—may also exhibit body size bias. This aspect of the Wallacean shortfall (incomplete knowledge of species distributions) remains less explored but may similarly reflect trait-based biases (Lomolino et al., 2017; Meyer et al., 2015). Understanding how body size influences not only when species are described but also when their distributions become documented provides crucial insights into persistent knowledge gaps.

While body size represents a fundamental trait, ecological characteristics may further modulate detection probability (Bouget et al., 2008; Ferro & Flick, 2015; MacKenzie et al., 2005; Moura & Jetz, 2024). Trophic specialisation, in particular, shapes a species' microhabitat associations, population densities and activity patterns—all factors affecting detectability during biodiversity surveys (Burrascano et al., 2023; Yoccoz et al., 2001). Saproxylic beetles, as decomposers and predators in deadwood, exhibit diverse trophic strategies ranging from mycetophagous species within fungal fruiting bodies to xylophagous taxa boring through woody substrates (Speight, 1990; Ulyshen & Šobotník, 2018). Each guild presents different detection challenges, potentially creating systematic biases that remain poorly quantified.

The extensive dataset used here, spanning a wide latitudinal gradient, has already proven effective for examining macroecological patterns in saproxylic beetle richness and body size clines (Franzén et al., 2025). This dataset is ideal for addressing foundational questions about taxonomic history and methodological bias at present (Gossner et al., 2013; Seibold et al., 2015). In this study, we test two complementary hypotheses: (i) species discovery (formal description) and documentation (georeferenced records) are influenced by body size, with smaller beetles being recognised later due to biases favouring larger species; and (ii) contemporary detection probability during standardised sampling varies with both body size and trophic specialisation, reflecting trait-based differences in activity patterns and microhabitat use.

MATERIALS AND METHODS

Study sites

We analysed saproxylic beetle assemblages from 28 veteran oak (*Quercus* spp.) sites across 10 countries in Europe, Turkey and Israel. At each site, 10 mature oak trees with cavities (circumference 175–612 cm) were selected. The sites span an elevation range of 10–1500 m a.s.l.

and a latitudinal range from 31.5° N to 60.0° N (Franzén et al., 2025). Although multiple *Quercus* species were present across the study gradient, previous work suggests limited host-tree specificity among many saproxylic beetles in deciduous trees (Milberg et al., 2014), minimising potential confounding effects on assemblage composition. Further details on the study sites are provided in Franzén et al. (2025).

Beetle collection and identification

Each site was sampled for one season between 1994 and 2012. Sampling duration (3–6 months) was aligned with local beetle activity periods. A flight interception trap (30 cm × 50 cm transparent window; collection container with ethylene glycol, water and detergent) was installed on each tree at 1–7 m height, typically near a cavity entrance. Traps were checked monthly. The ethylene-glycol mixture was disposed of following local environmental regulations. Although each site was sampled only once across the study period (1994-2012), the staggered sampling design means that any temporal trend in beetle abundance, such as the broad insect declines documented across Europe during this period (e.g., Hallmann et al., 2017; Seibold et al., 2019), would be confounded with site identity and cannot be partitioned from spatial variation; we acknowledge this as a limitation of the dataset. We focused on 425 species from 11 beetle families: Anobiidae (106 species), Buprestidae (28 species), Cleridae (16 species), Dermestidae (55 species), Elateridae (67 species), Erotylidae (10 species), Histeridae (32 species), Lucanidae (6 species), Mycetophagidae (11 species), Scarabaeidae (16 species) and Tenebrionidae (78 species). These families were selected based on reliable taxonomic expertise (Packer et al., 2018). Families presenting substantial identification difficulties at species level—including Latridiidae, Cryptophagidae and Staphylinidae—were excluded, as consistent determination across contributors and countries could not be assured; this conservative constraint likely means the detection and taxonomic biases reported here are underestimates (Sebek et al., 2012). Taxonomic nomenclature followed Fauna Europaea (de Jong, 2016).

Taxonomic validation

Species identifications were performed by the authors and external taxonomic specialists. Detailed information regarding identification methods (e.g., keys used), taxon concepts (e.g., citation of recent revisions) and specimen vouchering (e.g., deposition in named collections) for this dataset are provided in Franzén et al. (2026). Fourteen species collected were new to science and await formal description (Göktepe et al., 2023; Mazur et al., 2013; Novák et al., 2011; Platia et al., 2011).

Trait data

Body size was measured as body length (anterior edge of the head to posterior end of the abdomen, nearest 0.1 mm) using callipers; species-level averages were calculated from three male specimens. Each species was classified into one of five larval trophic groups: mycetophagous (37 species), saprophagous (99 species), sapro-xylophagous (96 species), xylophagous (78 species) or zoophagous (115 species), following Bouget et al. (2005) with updates from author expertise.

The year of formal species description was obtained from taxonomic literature. To assess distributional documentation, we queried the Global Biodiversity Information Facility (GBIF.org, accessed 30 January 2024) for all Coleoptera records. For each of our 425 species, we extracted the earliest year a georeferenced occurrence record was available.

Statistical analyses

All analyses were conducted in R version 4.4.3 (R Core Team, 2024). To test for trends in body size over time, we regressed $\log_{10}$(body length) against (i) year of description and (ii) earliest georeferenced record year, using separate linear models (lm function). Model assumptions were assessed by inspecting quantile–quantile plots and residuals; no violations were detected. A regression slope ≥ ±0.0005 year^{-1} was considered biologically meaningful (≈12% change per century).

To model detectability, we used single-season occupancy models in the unmarked package version 1.4.3 (Kellner et al., 2023). Using the detection history (presence/absence across the 10 traps per site), we fitted a constant detection probability model for each species (occu function) and extracted the estimate using backTransform. We then assessed the relationship between detection probability and traits. First, we regressed species-specific detection probabilities on $\log_{10}$(-body length). Second, to test for trophic group differences, we used a generalised linear model with detection probability as the response and trophic group as a fixed effect. We used Type II Wald χ^2 tests (car package version 3.1-3; Fox et al., 2019) for overall significance and emmeans version 1.10.6 (Lenth, 2022) for post-hoc pairwise comparisons with Tukey's adjustment. To assess whether differences in detection probability among trophic guilds could reflect underlying body size differences, we compared $\log_{10}$-transformed body length across guilds using a Kruskal–Wallis test, as Shapiro–Wilk tests indicated departures from normality in four of five guilds (sapro-xylophagus: $W = 0.938$, $p < 0.001$; saprophagus: $W = 0.891$, $p < 0.001$; xylophagus: $W = 0.899$, $p < 0.001$; zoophagus: $W = 0.932$, $p < 0.001$). Pairwise post-hoc comparisons were conducted using Dunn's test with Bonferroni correction. Guild-level means and standard deviations are reported in untransformed units (mm). The relationship between body length and detection probability is additionally shown with species coloured by family for reference (Figure S1).

RESULTS

Our sampling across 28 sites yielded 425 saproxylic beetle species from 11 families and five trophic groups (Figure 1a, Table S1). As of

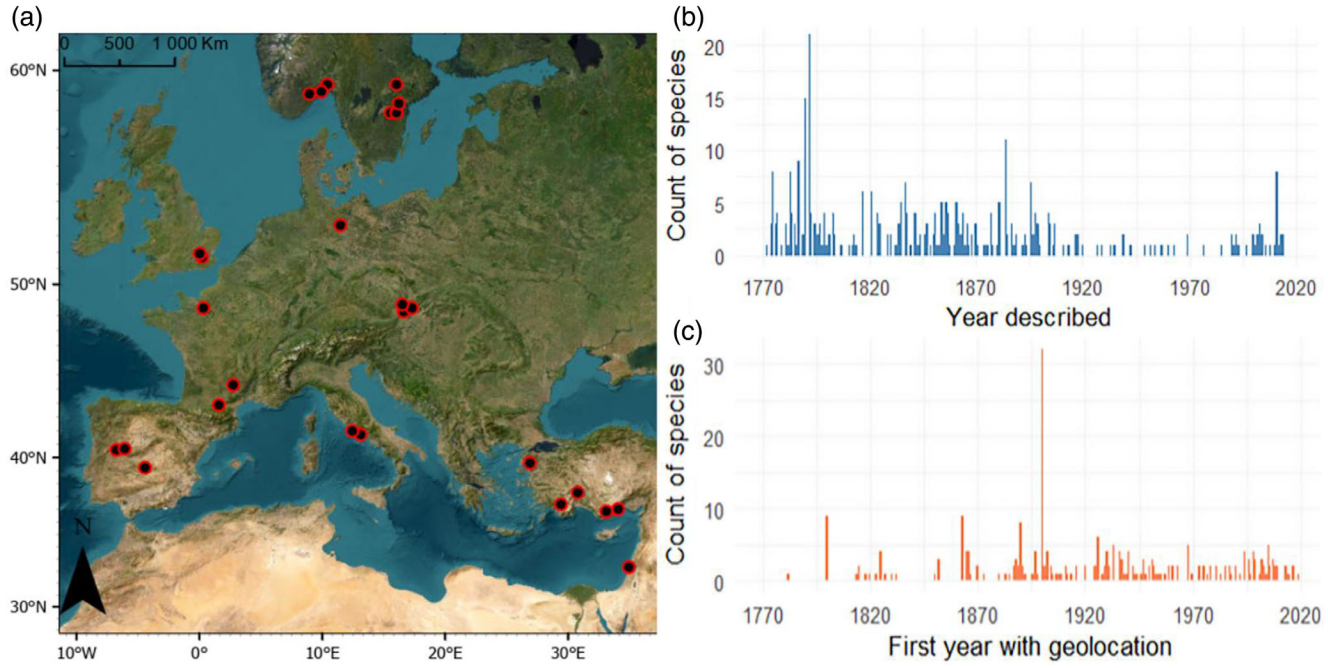

FIGURE 1 Study sites and temporal patterns in beetle documentation. (a) Map of the 28 study sites across Europe, Turkey, and Israel. (b) Temporal distribution of species descriptions showing the count of species described each year. Fourteen out of 425 species remain undescribed as of 2023. (c) Earliest year of georeferenced occurrence records in GBIF. Of the 425 species, 123 (29%) lack georeferenced records as of 2023.

2023, 14 of these species remained formally undescribed. Furthermore, 123 species (29%) lacked any georeferenced records in the GBIF database (Figure 1b,c).

We found a significant negative relationship between $\log_{10}$(body length) and the year of formal species description ($\beta = -0.00063 \pm 0.00021$ SE; $F_{1,409} = 9.17$, $p = 0.003$, $R^2 = 0.022$), indicating that smaller species have been described more recently (Figure 2). A similar significant pattern emerged for the earliest georeferenced record year ($\beta = -0.00057 \pm 0.00024$ SE; $F_{1,287} = 5.82$, $p = 0.016$, $R^2 = 0.020$), showing that smaller species are also documented later in biodiversity databases.

Species-specific detection probability showed only a marginal, non-significant negative association with $\log_{10}$(body length) ($\beta = -0.021$, $p = 0.055$, $R^2 = 0.009$; Figure 3). In contrast, trophic group had a highly significant influence on detectability ($\chi^2 = 31.41$, df = 4, $p < 0.001$; Figure 4). Sapro-xylophagous beetles exhibited the highest mean detection probability (0.316 ± 0.019 SE, 95% CI: 0.278–0.354), which was significantly greater than that of mycetophagous (0.196 ± 0.018 SE, 95% CI: 0.161–0.231) and zoophagous taxa (0.222 ± 0.011 SE, 95% CI: 0.200–0.244) based on post-hoc tests.

Body length differed significantly among trophic guilds (Kruskal–Wallis: $\chi^2 = 57.93$, df = 4, $p < 0.001$). Mycetophagous (mean 3.85 ± 1.76 mm) and saprophagous species (4.10 ± 2.57 mm) were significantly smaller than sapro-xylophagous (8.55 ± 6.20 mm), xylophagous (7.99 ± 9.69 mm) and zoophagous species (8.43 ± 5.62 mm; all Dunn pairwise $p < 0.05$ after Bonferroni correction). No significant difference in body length was detected between mycetophagous and saprophagous species, nor among sapro-xylophagous, xylophagous and zoophagous species (all $p > 0.05$; Figure 3).

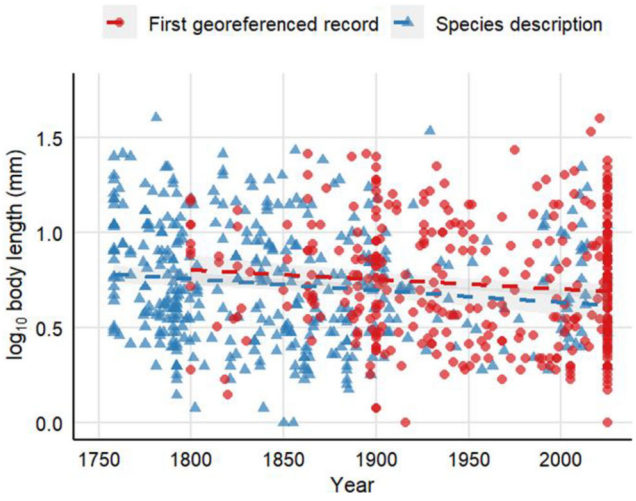

FIGURE 2 Relationship between $\log_{10}$-transformed body length and year of formal species description (blue triangles, solid line) and year of first georeferenced occurrence record (red circles, dashed line). Lines represent linear regression fits with 95% confidence intervals (shaded areas). Analyses based on 411 described species and 289 georeferenced species, respectively.

DISCUSSION

Our analysis of 425 saproxylic beetle species reveals a clear historical bias where smaller species are described and documented later than their larger counterparts. However, in the context of contemporary field surveys, trophic ecology emerges as a more critical determinant of detection probability than body size. These findings confirm our

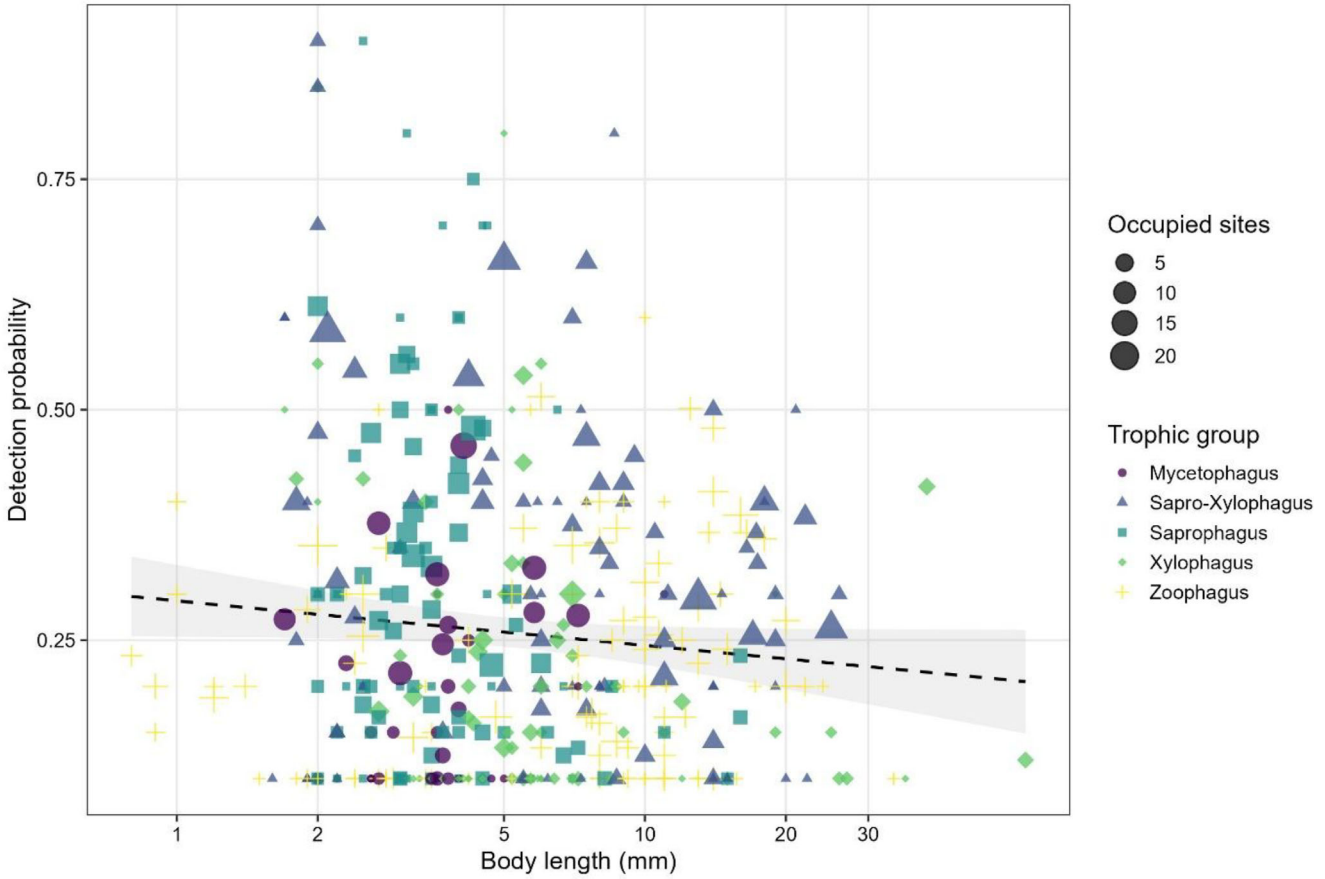

FIGURE 3 Relationship between body length and per-species detection probability estimated from single-season occupancy models across 28 oak forest sites. Each point represents one species, with shapes and colours indicating trophic guild; point size scales with the number of occupied sites. The dashed line shows the fitted ordinary least-squares regression on $\log_{10}$-transformed body length (shaded band: 95% CI).

hypotheses and highlight how distinct trait-based biases shape our knowledge of saproxylic beetle biodiversity.

The delayed description of smaller species demonstrates a persistent size bias contributing to the Linnean shortfall (Blackburn & Gaston, 1994; Diniz-Filho et al., 2023; Gaston, 1991; Hortal et al., 2015; Moura & Jetz, 2024). This pattern likely arises because larger species are more conspicuous and historically easier to study, whereas identifying smaller taxa often requires specialised collection and advanced taxonomic methods (e.g., molecular phylogenetics) that have only recently become widespread (Fontaine et al., 2012). Similarly, the later appearance of smaller species in georeferenced databases points to a size-biased Wallacean shortfall (Lomolino et al., 2017). This lag in documentation, even after formal description, suggests that factors beyond field detectability, such as limited research attention or taxonomic expertise for diminutive fauna, hinder our understanding of their distributions (Troudet et al., 2017).

From a conservation standpoint, these shortfalls are problematic (Cardoso et al., 2011; Leather, 2013). Macroecological analyses based on size-biased data may underestimate the diversity and functional importance of smaller species, which often constitute the majority of individuals and biomass in forest ecosystems (Gardner et al., 2011). Conservation strategies that overlook these cryptic taxa risk failing to protect the full spectrum of biodiversity and the ecological processes they support.

Our results reveal two complementary biases. First, a historical taxonomic bias has produced a body of knowledge where small-bodied species are systematically underrepresented (Diniz-Filho et al., 2023). Second, a contemporary methodological bias is evident within the 11 families analysed: mycetophagous and predatory species showed lower detection probabilities, a pattern likely to be further pronounced had taxonomically challenging families such as Latridiidae, Cryptophagidae and Staphylinidae been included. These families predominantly comprise small-bodied mycetophagous and predatory taxa, and their exclusion results in conservative estimates of the detection biases reported here (Sebek et al., 2012). The lower detectability of mycetophagous species is at least partly attributable to their smaller average body size. Together, these biases mean that small-bodied species belonging to less-detectable trophic groups face a dual jeopardy of being overlooked, reinforcing both Linnean and Wallacean shortfalls. Addressing these mutually reinforcing trends requires integrated solutions. On the historical side, targeted taxonomic revisions using modern tools like micro-CT imaging and DNA barcoding can accelerate the description of neglected taxa (Fontaine et al., 2012). On the contemporary side, diversifying field methods to include emergence traps, baited traps or direct substrate surveys will mitigate sampling bias against specialised guilds and provide a more complete picture of local assemblages (Brin & Bouget, 2018; Økland et al., 1996).

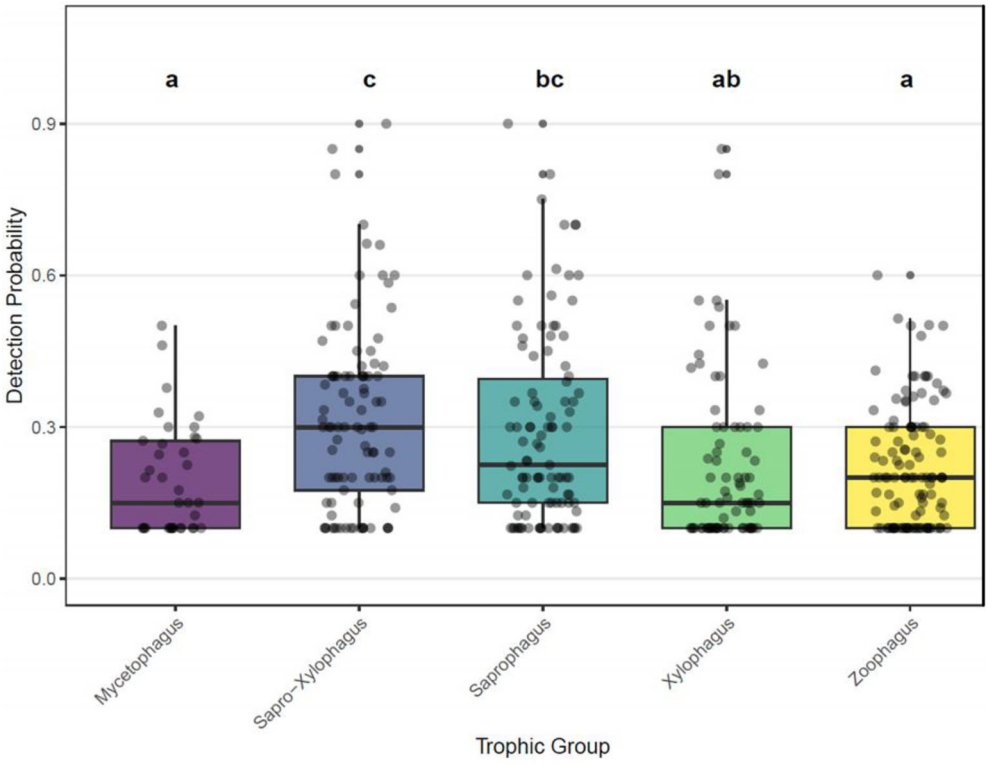

FIGURE 4 Variation in detection probability across saproxylic beetle trophic groups. Boxplots show median (horizontal line), first and third quartiles (box boundaries), and whiskers extending to 1.5 × interquartile range. Letters above boxes indicate significant differences ($p < 0.05$) from Tukey's post-hoc tests. Sample sizes: Mycetophagous ($n = 37$), Saprophagous ($n = 99$), Sapro-xylophagous ($n = 96$), Xylophagous ($n = 78$) and Zoophagous ($n = 115$).

Our study is based on 11 beetle families and one trapping method; therefore, the patterns observed may not be universal across all saproxylic insects or sampling techniques. Future research should expand this trait-based approach to other taxonomic groups and incorporate a wider array of sampling protocols to build a more comprehensive understanding of detection biases. Furthermore, integrating our findings into spatially explicit frameworks, such as species distribution models that explicitly account for imperfect detection, could help correct for biases in occurrence records and refine our understanding of species' true ranges (Kodric-Brown & Brown, 1993; Roberts et al., 2017).

Body size has profoundly shaped the taxonomic history of saproxylic beetles, leading to significant knowledge gaps for smaller species. In modern ecological surveys, however, trophic specialisation is a more decisive factor in determining detection probability (Grove, 2002; Stokland et al., 2012). Recognising these distinct historical and methodological biases is essential for developing accurate biodiversity assessments and effective conservation strategies.

AUTHOR CONTRIBUTIONS

Markus Franzén: Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; project administration; formal analysis; data curation; supervision; resources. **Nicklas Jansson:** Conceptualization; funding acquisition; writing – original draft; methodology; validation; formal analysis; supervision; resources. **Mustafa Avci:** Investigation; validation; methodology; visualization; funding acquisition. **Antoine Brin:** Investigation; validation; methodology; formal analysis; visualization. **Hervé Brustel:** Investigation; funding acquisition; methodology; validation. **Jan Budka:** Methodology; validation; funding acquisition; investigation. **Jörn Buse:** Methodology; validation; investigation. **Giuseppe Carpaneto:** Investigation; validation; methodology. **Stefano Chiari:** Methodology; validation. **Lukáš Čížek:** Methodology; validation; visualization; investigation. **Mustafa Coskun:** Validation; visualization; methodology; investigation; funding acquisition. **Jeremy Dagley:** Methodology; validation; visualization; investigation; funding acquisition. **Peter M. Hammond:** Methodology; validation; visualization; funding acquisition; writing – original draft. **Estefanía Micó:** Writing – review and editing; visualization; methodology; validation; funding acquisition; writing – original draft. **Tuğba Öncül Abacıgil:** Investigation; funding acquisition; validation; methodology; writing – review and editing. **Tomáš Pavlíček:** Validation; methodology; funding acquisition. **Jiří Schlaghamerský:** Methodology; validation; funding acquisition. **Pavel Šebek:** Methodology; investigation; funding acquisition. **Anne Sverdrup-Thygeson:** Visualization; methodology; funding acquisition; validation. **Sakin Vural Varli:** Methodology; validation; visualization; funding acquisition. **Lars Westerberg:** Validation; methodology; funding acquisition; formal analysis; project administration; data curation; supervision; conceptualization; investigation; writing – original draft. **Inge Wilde:** Validation; methodology; funding

acquisition; writing – original draft. **Agnese Zauli:** Methodology; visualization; validation; funding acquisition. **Per Milberg:** Methodology; conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; software; project administration; formal analysis; data curation; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The dataset supporting the results of this study is available in the Dryad Digital Repository: Franzén et al. (2026) (https://doi.org/10.5061/dryad.gf1vhhn3w).

ETHICS STATEMENT

This work complied with all relevant national and international ethical guidelines. No ethical approval was required for invertebrate sampling. All necessary collection permits were obtained for sampling in protected areas.

ORCID

Per Milberg https://orcid.org/0000-0001-6128-1051

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Relationship between body length and per-species detection probability as in Figure 3, with points coloured and shaped by family. The dashed regression line is fitted across all species (shaded band: 95% CI). Provided to allow comparison of family-level body size distributions with the trophic guild patterns in Figure 3.

Table S1. Complete species list with family, larval trophic group and body length measurements for 425 saproxylic beetle species collected from 28 veteran oak sites across Europe, Turkey and Israel.

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