A review of saproxylic beetle intra- and interspecific genetics: current state of the knowledge and perspectives

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Abstract
Forests are important habitats that harbor high biodiversity and have great economic value to humans. These ecosystems depend on saproxylic organisms, which play a crucial role in the decomposition of the main substrate of forests – wood. The highly important group of saproxylic organisms are beetles, with numerous species that are either of conservation concern (rare and threatened) or have economic value (“pests”). This review summarizes what is known about intra- and interspecific genetic information on species or populations of saproxylic beetles. A search of the literature yielded 110 articles published in 57 journals. The majority of molecular research has focused on “pests” (82 articles on 59 species), with fewer studies of the “non-pest” beetles (28 articles on 40 species, including 10 relicts of primeval forests). Most studies concerned Palearctic and Nearctic taxa, with only a few articles on beetles from (sub)tropical forests. Members of 11 families, 38 genera and 99 species were the subject of molecular studies. The majority of studies (71%) were conducted on beetles associated with conifers. Genetic metrics were found to have different overall values in “pests” and the “non-pest” species. Analyzes resulted in identification of units or either conservation (15 cases) or taxonomic (33) value, the discovery of hybridization (4), invasion routes, and common phylogeographic patterns with the localization of glacial refugial areas. This article is the first comprehensive summary of what is known about the history, present-day diversity, and relationships of highly important group of saproxylic beetles based on molecular studies. “Pests” found to be much wider studied than threatened taxa. A list of species that should be the subject of future molecular studies was provided along with a rationale. Finally, methodological and objective deficiencies in previous studies were characterized.

Keywords: Coleoptera, phylogeography, pests, primeval forest relicts, dead wood, forest

Introduction
Among forest-dwelling organisms, a remarkable high number of species is closely associated with woody parts of trees. Some of these species use living trees (Lieutier et al. 2004), but many of them are found only in dying trees or in the wood of dead trees (colloquially called “deadwood”). This group of organisms (hereafter referred to as saproxylic) (Siitonen 2001) has been neglected for many years in forest ecosystems. Their role in ecological processes in forests was finally noticed, leading to an increasing number of scientific studies focusing on various aspects of their biology, evolution, diversity and ecology (Kozák et al. 2021). Saproxylic organisms are crucial in natural forest ecosystems as they play many roles in different trophic levels (sapro-, xylo-, cambio- or mycetophages and predators) and are thus fundamental for forest functioning (Hjältén et al. 2012). In this respect, detritivores are particularly important as they depend on and are responsible for the decomposition of the most abundant substrate in this habitat, namely wood. Saproxylic organisms have received special attention from biologists and nature...
conservationists (Mason & Zapponi 2015), which has led to the protection of many rare, endangered or threatened species and the designation of numerous protected areas in forests of different areas and management regimes.

Division of saproxylic species into two opposing groups may be proposed. The first group includes rare, threatened, and often protected species, and is therefore of less concern to foresters, but may well conflict with forestry activities. Conservation of saproxylic organisms usually requires the designation of protected areas, or at least substantial changes in forest management practices that result in reduced logging and the preservation of large numbers of dying trees and large amounts of dead-wood in forests (Davies et al. 2008). Such measures are usually at odds with the needs of timber production (Grove 2002). Furthermore, these conservation measures are not always properly implemented, which can be easily seen by the distribution of rare and threatened deadwood-related species, which are usually absent from managed forest stands and “pushed back” into protected areas. The second group of saproxylic organisms of great concern in forestry are species colloquially referred to as “pests” (De Groot et al. 2019). These species are generally considered harmful to trees, as their outbreaks lead to weakening of trees, development of diseases in trees (e.g. fungal infections), usually resulting in death of infested trees and/or loss of large areas of forest. This is one of the most serious problems in timber production and the reason for many studies aimed at finding methods to prevent or mitigate such outbreaks (Klapwijk et al. 2016). Forest management neglects the natural role of these common saproxylic species in forest ecosystems. These organisms are natural elements in the life of trees (Müller et al. 2008).

The best-known group of saproxylic organisms are the beetles (Coleoptera). Approximately 400,000 species are known in this insect order and 50–60% of them are thought to live in the trunks or roots of trees, with many species relying on dying trees or deadwood (Slipiński et al. 2011; Gimmel & Ferro 2018). Saproxylic beetles are a focus of attention for biologists, conservationists and foresters due to their great diversity, abundance (in the case of common species) or rarity (in the case of threatened taxa), charismatic features (e.g. morphology, colors), and their role in forest ecosystems (either as flagship/umbrella/keystone species for forest ecosystems or as “pests” in timber production) (Dajoz 2000; Stokland et al. 2012). Saproxylic beetles are common in all types of forests and woodlands worldwide (Grove 2002; Gimmel & Ferro 2018).

While wood-dwelling Coleoptera are best known from temperate and boreal forests, our knowledge from tropical forests is still unsatisfactory (Gimmel & Ferro 2018). Saproxylic beetles are known from 122 of the 187 beetle families and in 32 of them all or the majority of taxa are saproxylic (Gimmel & Ferro 2018). Among the saproxylic beetles, there are many rare and threatened taxa. In Europe, for example, 168 species are listed as saproxylic relicts of primeval forests (Cálix et al. 2018; Eckelt et al. 2018). There are also dozens of taxa of saproxylic beetles designated as “pests”, including many species of weevils, bark and ambrosia beetles, and some of jewel beetles and longhorn beetles.

Knowledge about saproxylic beetles is quite extensive thanks to the increasing number of studies (Horák et al. 2012). Many species have well-known distribution and population demography, reproductive biology, and ecology, including relationships with the environment and other organisms (such as fungi) (Evans et al. 2004; Schowalter 2012). Taxonomy and systematics of saproxylic beetles have been the subject of numerous studies, including recent revisions at various taxonomic levels (Knižek & Beaver 2007). Classification of these beetles has been additionally supported by phylogenetic and evolutionary biology studies, but mostly concerns higher units, e.g. elaboration of individual genera or families (De Santana Souza et al. 2020; Sun et al. 2020). The development of molecular tools and methods in recent decades has enabled a better understanding of the history of individual genera and species (particularly speciation, hybridization, and phylogeography), the diversity and connectivity of populations today (population genetics, demography, etc.) as well as reviewing the taxonomic status of known species, discovering new taxa (species delimitation, identification of Operational Taxonomic Units – OTU) or naming evolutionary units within species such as Evolutionary Significant Units (ESU) and Management Units (MU) (Blaxter et al. 2005; Allendorf et al. 2010; and other references in Supplementary Table S1 and in the next chapters). These findings have been sometimes focused on increasing basic knowledge about the species or group in question (Avise 2000; Kumar & Kumar 2018), but often had practical significance, e.g. identifying conservation priorities (in the case of discoveries of cryptic taxa, OTU, ESU, MU), or determining source areas for invasive species (especially those of economic importance). Moreover, the phylogeographic patterns revealed for saproxylic beetles follow (or not) some of the basic paradigms known for forest-dwelling taxa (e.g. Taberlet et al.
The available knowledge on the molecular diversity of saproxylic species is impressive but may also be highly unequal for particular taxa or groups (taxonomically, geographically, inhabiting particular forest types or tree species). Surprisingly, this topic has never been summarized before.

Considering the above reasons, we decided to conduct an intensive literature search for publications dealing with inter- and intraspecific studies of saproxylic beetles using molecular markers, focusing particularly on studies dealing with phylogeography, population genetics, landscape genetics and conservation genetics (or genomics).

The collected database of selected literature was processed to describe and summarize the knowledge related to the following issues:

1. Presentation of progress in intra- and interspecific genetic studies on saproxylic beetles (excluding deep phylogenies, see Material and methods), in particular, how many papers have been published over the years, in which journals, and for beetles from which parts of the world.
2. Taxonomic coverage of saproxylic beetles studied (how many species, genera, and families were subjected to molecular analyses).
3. Ecological coverage of saproxylic beetles studied (what trophic associations, microhabitats, and host trees of species studied have been genetically examined to date).
4. Technical details of genetic studies on saproxylic beetles, including: sampling effort (number of sites sampled and individuals analyzed), selection of laboratory and analytical methods, and choice of genetic markers.
5. Use of genetic metrics and statistics for a description of the variability of examined saproxylic beetles, and comparison of available values between taxa considered as “pests” and “non-pest” species (common and endangered beetles), as well as between “pests” from Old and New World.
6. Elaboration of intra- and interspecific partitioning, distances and divergence dating for saproxylic beetles, and, where applicable, with comparison of New and Old World “pests”, and between common and endangered species.
7. Presentation of taxonomic decisions made for saproxylic beetles based on their genetics (except for deep phylogenies, see Material and methods), and listing of examples of hybridizing taxa.
8. Discussion of the phylogeography of saproxylic beetles, with emphasis on determining glacial refugia for which sufficient data are available.

This review also summarises genetic knowledge for selected taxa, and for a total of two defined groups (“pests” and invasive species, and primeval relicts and threatened species) based on data from the literature. We intentionally use the term “pest” in quotation marks, because species are considered pests only based on their classification in forestry.

Finally, we described information missing from previous genetic studies on saproxylic beetles, focusing on i) species for which molecular data are lacking but deserve scientific attention; ii) methods that need to be applied; and iii) scientific objectives for future research.

**Material and methods**

The scientific literature was searched using two databases: Web of Science; WoS (webofknowledge.com; Clarivate Analytics) and Scopus (scopus.com; Elsevier).

The following combination of keywords associated with the Boolean operators was implemented: (phylogeny OR phylogenetic OR phylogeography OR phylogeographic OR “population genetic” OR “conservation genetic” OR “landscape genetic” OR “population genomic” OR “conservation genomic” OR “landscape genomic”) AND (beetle OR Coleoptera) AND (saproxylic OR xylophagous OR cambioxylophagous OR cambioxylophagic OR xylophagous OR saproyxylophagous OR cambioxylophagous OR deadwood OR “dead wood” OR bark) AND (forest OR tree) AND NOT (fungi OR fungus OR fungal OR myceto OR yeast OR microbe OR mycobiome OR mycobiome OR microorganism OR nematode). The first set of keywords was linked to the methods of the studies, the second to the objects of the studies, and the third to the microhabitat (i.e. the substrate for saproxylic beetle development), the fourth with the general habitat, and the fifth was added to avoid entries related to fungi, bacteria, and nematodes. The search was conducted on 17/01/2021, therefore the publication date limit was 2020; however, some recently published papers could not be present in the databases at the time of the search.

The search yielded 1795 hits (Scopus) and 270 hits (WoS) results.

Each document was read critically for the information it contained on molecular studies of intra- or interspecific relationships in beetles related to
“wood”, with particular reference to the study issues listed above. Figure 1 shows a flowchart for the systematic review following the PRISMA guidelines (Moher et al. 2009). Articles that had no relevance (e.g. all reports that did not focus on beetles, studies that did not use molecular = genetic data; studies on isozymes or allozymes) were excluded. This resulted in 152 (Scopus) and 132 (WoS) papers. Next, all publications dealing with i) higher-level phylogeny (we left only phylogenetic studies on species complexes or groups of closely related taxa, as such studies often contained data relevant to the objectives of this review); ii) barcoding studies on large data sets (exceptions were studies on small groups of closely related taxa as above); iii) genomics (presentation of genomes or mitogenomes); iv) marker development (mostly microsatellite loci) were excluded. Since an initial review of suitable articles revealed only two papers on predatory beetles (one on Cleridae and one on Cucujidae; all other papers found, i.e. on Carabidae or Staphylinidae, were not based on molecular data), we intentionally omitted these studies and narrowed the topic to taxa that feed on xylem, cambium, or phloem. Species associated with bracket fungi (e.g. Mycetophagidae) were also omitted because the search key excluded most papers on these taxa (only ambrosia beetles were included in the revision because they live in wood but feed on fungi that grow in the tree). Finally, 69 (Scopus) and 80 (WoS) articles were identified that met all search criteria and were appropriate for the purposes of this review. After removing duplicates (39), 110 publications remained for further review.

To facilitate description of the available data, analyzes, and discussion, the data set was divided into two groups: (i) “pests” (species considered harmful to trees, causing economic damage in production

![Figure 1. Prisma flow-diagram (see Moher et al. 2009) for literature search for the purposes of this study. Values indicate number of papers excluded at different assessment stages. Only articles retrieved from “Scopus” (Elsevier) and “Web of Science” (Clarivate Analytics) databases are presented.](image-url)
forests, invasive species, etc.); (ii) “non-pest” beetle species (those not referred to as “pests” in the publications and not considered to cause wood damage according to the literature and the authors’ expert knowledge) – the latter group was dominated by primate relicts or threatened taxa and other more common species. Although such classification of beetle species has neither a taxonomic nor ecological rationale (both groups include taxa from various families with different trophic associations and microhabitat preferences), it allowed us to present the available data in a simple design and to discuss the observed genetic patterns in terms of the economic importance of the “pests” and the conservation importance of the primate relicts, threatened and protected species. In addition, for some analyses (based on available genetic metrics), the “pests” were divided into two geographic groups: New World taxa (mostly Nearctic), and Old World taxa (mostly Palearctic). The remaining group of beetles was also divided into two subgroups based on their threat status, i.e. species with IUCN categories (see https://www.iucnredlist.org/). Thus, CR, EN, VU and NT were classified as “endangered”, while the species in the LC and DD categories and those not listed by the IUCN were classified as “common”.

We examined the collected data using the following criteria: (i) characteristics of publications [categorical], (ii) geographic distribution of studies and number of species studied from zoogeographic realms [categorical], (iii) trophic affinity and preferred microhabitats of the species studied [categorical], (iv) risk category and classification as a primate relict according to the IUCN [binary], (v) classification as a “pest” [binary], (vi) taxonomy (number of studies conducted on beetles of specific families, genera and species) [numeric], (vii) sampling design (number of sites and individuals studied) [numeric], (viii) tree hosts (number of studies conducted on beetles associated with specific trees) [numeric], (ix) molecular marker characteristics (type and method of recovery) [categorical], (x) characteristics of molecular methods and software used (phylogenetic, delimitation, population genetic, and demographic) [categorical], (xi) basic molecular metrics and statistics (such as haplotype number and diversity, nucleotide diversity, allelic richness, heterozygosity, fixation indices, pairwise distances, isolation by distance, molecular variance, etc.) [numeric], (xii) number of distinct genetic clusters, evolutionary units, or phylogenetic lineages [numeric]. Statistical analyzes for the data collected in numerical values (e.g. Chi² test for comparing some variables between “pests” and “non-pest” beetles) were performed in R Core Team (2020).

In addition, due to the nature of the data, the following characteristics were evaluated descriptively: (a) implications for conservation and management, (b) the phenomenon of hybridization, (c) invasion events, (d) taxonomic revisions, (e) phylogeographic history with the location of refugia and the distribution of distinct genetic units. Finally, for the part dealing with knowledge gaps and future challenges, data on beetle taxa characterized as primate relicts or threatened species were taken from the following publications: Carpaneto et al. (2010), Nieto and Alexander (2010), Eckelt et al. (2018), Cálix et al. (2018), García et al. (2018). In the case of “pests”, data on wood-dwelling species were taken from Lieutier et al. (2004). This information was supplemented by the expert knowledge of the authors of this study.

Results and discussion

Characteristics of genetic studies on wood-dwelling beetles

Basic information. The final list of publications included 110 papers (see Supplementary Table S1). The oldest articles with relevant information were published in 1998 (Juan et al. 1998; Stauffer & Zubler 1998), and the number of articles published since then increased significantly from year to year (correlation Rho = 0.693; Figure 2). The majority of these articles (82%) were published after 2005. Studies on “pests” dominated over studies on “non-pest” beetles, except for the last three years (since 2018), when a similar number of articles were published for both of these groups.

Selected studies were published in 57 scientific journals, most frequently in: Molecular Ecology (11 articles), PLoS ONE, Biological Journal of the Linnean Society and Agricultural and Forest Entomology (5 articles each) (Supplementary Figure S1).

A total of 82 articles were on beetles classified as “pests”. The “non-pest” species were the subject of studies in only 28 articles.

The objectives of the selected articles could be classified into seven categories. The majority of studies were conducted for population-genetic or landscape-genetic (40 cases), phylogeography (38), and phylogenetic-delimiting-barcoding (36) purposes. Fewer studies were conducted for invasion detection (14 cases), dispersal (11), conservation genetics (8), and reproductive mating kinship (5) (Supplementary
Figure S2). Some works involved the resolving of multiple objectives.

Regarding the geographical localization of the studies performed and the number of species studied, most of them were conducted in the regions of Western Palearctic (73 articles with 57 taxa), Eastern Palearctic (43 and 42) and Nearctic (45 and 29). Significantly fewer studies were conducted and less taxa were examined in the Neotropical (14 and 12), Indomalayan (6 and 5), Afrotropical (2 and 2) and Australasian (2 and 2) regions, with no study conducted in Oceania (Figure 3).

Taxonomy of examined beetles. The selected publications covered eleven beetle families. The vast majority of studies were conducted and taxa examined on Curculionidae (76 articles and 53 species), followed by Cerambycidae (17 and 19), Scarabaeidae (7 and 11), Buprestidae (2 and 2) and Lucanidae (2 and 2), Euchiridae (1 and 3), and Pythidae (1 and 3). Single species of Elateridae, Passalidae, Scarabidae, Tenebrionidae were studied in single papers (Supplementary Figure S3).

Thirty-eight genera were studied in the selected articles (18 considered as “pests” and 20 “non-pest” species). Some studies were performed more than once on the same genera, such as Dendroctonus (22 papers and 10 species), Ips (15 and 7), Tomicus (12 and 7), Pissodes (7 and 5), Pityogenes (6 and 1), Xylosandrus (5 and 7), Osmoderma (5 and 5), Euwallacea (3 and 3), Cerambyx (3 and 2), Agrius (2 and 2), Lucanus (2 and 2), Protaetia (2 and 2), Crypturgus (1 and 9), Cetonia (1 and 5), Anastrangalia (1 and 5), Propomacrus (1 and 3), Pytho (1 and 3), Aphanarthrum (1 and 2), and Morimus (1 and 2) (Supplementary Figure S3).

The most intensively studied species were pests: Dendroctonus ponderosae (11 papers), Ips typographus (8), Pityogenes chalcographus (7), Tomicus destructus and T. pimperda (each 7), and one endangered species: Osmoderma barnabita (5). Several species were studied in 2–3 papers, and the majority of “non-pests” was presented only in single articles (Supplementary Figure S3).

Trophic associations, microhabitats and host trees. One hundred articles dealt with species that feed on living trees (xylo- & cambiophages) – 82 of these were considered “pests” (59 species) and 18 were about “non-pest” beetles (24 species). Ten articles were about species that feed on dead trees (saprofagophages) – all taxa were not classified as “pests” (16 species).

Eighty-eight articles dealt with species living in fresh wood of dying and dead trees (81 “pests” and 7 “non-pest” species), 13 articles concerned species living in decomposed wood of dead trees (1
“pest” and 12 “non-pest” beetles), and 9 articles dealt with beetles living in wood mould (rotten holes) (all were not classified as “pests”).

The vast majority of studies (72%) involved beetles associated with conifers (Figure 4), with pines Pinus spp. (ca. 49%) and spruces Picea spp. (ca. 19%) clearly dominating. Among deciduous trees, species associated with oaks Quercus spp. (ca. 5%), maples Acer spp. (ca. 4%) and beeches Fagus spp. (ca. 3%) were used most frequently. The differences between “pests” and “non-pest” beetles were significant ($\chi^2 = 1392.7, p < 0.001$).

**Sampling effort.** The average number of populations (or sites sampled, as these two categories were listed in different papers, often interchangeably or without direct definition) was 10 (ranging from 1 to 121) per study and species studied (as some papers included studies on multiple taxa). This value was similar ($Z = 0.50, p = 0.617$) for “pests” (mean 12) and “non-pest” beetles (mean 9) (Supplementary Figure S4).

In contrast, the mean number of individuals examined was significantly different ($Z = 2.62, p = 0.009$) for “pests” (98) and “non-pest” beetles (36). The mean number of individuals examined per paper and species was 74 (from 1 to 4607) (Supplementary Figure S4).

**Molecular methods and markers.** There were 10 types of methods used to collect genetic data. The most commonly used method was Sanger sequencing (in 64% of studies), followed by microsatellite genotyping (17%), next-generation sequencing (NGS) with single nucleotide polymorphism (SNP) genotyping (6%) and Amplified Fragment Length Polymorphism Genotyping (5%). The remaining methods were used in individual studies (Supplementary Figure S5).

Considering only mitochondrial markers, fragments of the Cytochrome Oxidase (CO) subunit I gene were used most frequently (78% of cases), followed by CO subunit II (12%) and 16S (4%). Other mtDNA genes were used in individual studies. Except COI, COII and 16S, other genes were used only in studies on “pests”.

Regarding nuclear sequences, Internal Transcribed Spacers of rDNA (29%) and 28S of rDNA (25%) were most frequently used, followed by Elongation Factor 1-α gene (18%), and the remaining markers were used in individual studies. Most nuclear sequences were used in studies on “pests”, while only individual studies on the “non-pest” beetles used some of these markers (mostly rDNA).

The number of loci in microsatellite markers varied from 2 to 17 (mean 9), while the mean number of loci in SNPs was 1450 (min 89, max 19,904).
Microsatellites were used in studies on different beetles, while SNPs were used only in studies on “pests”.

Among phylogenetic methods, Maximum Likelihood (27% of cases), Bayesian Inference (27%) and Maximum Parsimony (20%) were chosen with similar frequency, and the remaining methods were used in individual studies (Supplementary Figure S5). Phylogenies were most frequently reconstructed using Phylogenetic Analysis Using Parsimony (26%), Molecular Evolutionary Genetics Analysis (16%), PHYLogeny Inference Package (15%), MrBayes (13%), and Bayesian Evolutionary Analysis Sampling Trees (13%). The remaining tools were used occasionally (Supplementary Figure S5).

Delimitation methods were used infrequently (9 cases in 6 articles), with the following tools being used with similar frequency: Automatic Barcode Gap Discovery, Poisson Tree Processes and Generalized Mixed Yule Coalescent, but Bayesian Phylogenetics and phylogeography were used only once.

There were numerous population genetic methods used in conjunction with various software. These methods may be grouped as follows: molecular variance (used in 26% of studies), assignment tests (21% of studies), network reconstructions (20%), isolation by distance (Mantel test) (17%), multidimensional methods (9%), and nested clade analysis (6%) (Supplementary Figure S5).

Similarly, many methods and tools used in the reviewed studies for demographic analyzes could be categorized into the following groups: demographic tests (mostly Tajima and Fu tests) (used in 80% of articles), demographic Bayes methods (14%), and effective population size estimators (6%).

Genetic metrics variability. Mitochondrial haplotype diversity data were available from 43 studies. Haplotype diversity values were similar in “pests” (mean $H_{div} = 0.86$; $0.33–1.00$; SD = 0.19) and for “non-pest” beetles (mean $H_{div} = 0.95$; 0.40–1.00; SD = 0.23), but overall differences were significant ($Chi^2 = 19.09$, $p = 0.024$) (Figure 5). The mean haplotype diversities were significantly different ($Chi^2 = 33.33$, $p < 0.001$) between endangered (mean $H_{div} = 0.96$; 0.65–1.00; SD = 0.14) and common species (mean $H_{div} = 0.52$; 0.21–0.72; SD = 0.18). Also, “pests” from Old World (mean $H_{div} = 0.84$; 0.33–1.00; SD = 0.18) and New World (mean $H_{div} = 0.96$; 0.53–1.00; SD = 0.17) have significantly different haplotype diversities ($Chi^2 = 45.66$, $p < 0.001$) (Supplementary Figure S6).

Data on heterozygosity were found in 26 articles. Mean heterozygosity was also similar in “pests” (mean $He = 0.45$; 0.09–1.00; SD = 0.29) and “non-pest” beetles (mean $He = 0.56$; 0.21–0.86; SD = 0.22), but again, overall differences were
The mean heterozygosity values were significantly different ($\chi^2 = 65.96, p < 0.001$) between endangered (mean $He = 0.52; 0.21–0.72; SD = 0.18$) and common species (mean $He = 0.79; 0.29–0.86; SD = 0.25$). Also, “pests” from Old World (mean $He = 0.48; 0.10–1.00; SD = 0.32$) and New World (mean $He = 0.45; 0.23–0.88; SD = 0.24$) have significantly different haplotype diversities ($\chi^2 = 51.82, p < 0.001$) (Supplementary Figure S6).

The fixation index ($F_{ST}$) was present in 46 publications. This index varied significantly ($\chi^2 = 239.87, p < 0.001$) between “pests” (mean $F_{ST} = 0.34; 0.00–1.00; SD = 0.33$) and “non-pest” beetles (mean $F_{ST} = 0.12; 0.01–0.93; SD = 0.40$) (Figure 5). The mean fixation indices were significantly different ($\chi^2 = 30.86, p < 0.001$) between endangered (mean $F_{ST} = 0.19; 0.01–0.92; SD = 0.36$) and common species (mean $F_{ST} = 0.03; 0.29–0.93; SD = 0.41$). Also, “pests” from Old World (mean $F_{ST} = 0.39; 0.00–1.00; SD = 0.33$) and New World (mean $F_{ST} = 0.14; 0.01–0.55; SD = 0.19$) have significantly different haplotype diversities ($\chi^2 = 47.43, p < 0.001$) (Supplementary Figure S6).

Intra- and inter-specific division, distances and divergence dating. Isolation by distance (IBD) was investigated in 28 studies which reported results for 20 taxa. Significant IBD was reported for the following
taxa of “pests”: *Agrilus planipennis, Dendroctonus rufipennis*, *D. approximatus*, *D. ponderosae*, *D. pseudotsugae*, *Ips typographus*, *I. sitchensis*, *Pissodes nemorensis*, *P. strobi*, *Tomicus destruens*, *T. piniperda*, *T. yunnanensis* (Stauffer et al. 1999; Laffin et al. 2004; Horn et al. 2006, 2009; Vasconcelos et al. 2006; Maroja et al. 2007; Mock et al. 2007; Sallé et al. 2007; Ruiz et al. 2009; James et al. 2011; Cullingham et al. 2012; Gayathri Samarasekera et al. 2012; Sánchez-Sánchez et al. 2012; Keever et al. 2013; Lü et al. 2014; Wondafrash et al. 2016; Avtzis et al. 2019). The Mantel test also proved significant in some “non-pest” beetle species: *Cetonia aurata, Cerambyx wedenii*, *Elater ferrugineus*, *Osmotherma barnabita*, *Protactia marmorata*, *Rosalia alpina* (Ahrens et al. 2013; Oleksa et al. 2013, 2015; Drag et al. 2015; Torres-Vila & Bonal 2019). IBD was found to be insignificant in studies on populations of: *Ips typographus*, *Masicus raddei* and *Pityogenes chalcographus* (all “pests”) (Gugerli et al. 2008; Bertheau et al. 2012; Némethy et al. 2018; Schebeck et al. 2018; Zhang et al. 2020).

Analysis of Molecular Variance (AMOVA) also found a significant and large (over 30%) proportion of variance between population groups of several “pests”: *Agrilus planipennis, Dendroctonus valens*, *D. ponderosae*, *Ips typographus*, *Semanotus germanus* and *Crypturgus proximus*, *Tomicus destruens*, *T. piniperda*, *T. yunnanensis* and *Xylasandrus germanus* (Kerdelhué et al. 2002; Shoda et al. 2003; Horn et al. 2006; Mock et al. 2007; Cai et al. 2008; Ito et al. 2008; Keever et al. 2013; Lü et al. 2014; Mayer et al. 2014; Kononov et al. 2016; Wondafrash et al. 2016; Sarikaya & Şen 2017). For many “non-pest” species, AMOVA revealed low inter-group variance (e.g. *Anaspis ruficollis*; Schauer et al. 2018 and *Acrocinus longimanus*; Zeh et al. 2003).

In 65 articles, genetic data illustrated the existence of distinct genetic clusters (in the case of allelic markers) or phylogenetic lineages/evolutionary units (in the case of nucleotide markers). The total number of such distinguishable groups (regardless of their intra- or interspecific status) per taxon studied was similar (Z = 1.40, p = 0.161) for “pests” (mean N = 3.0; 2.0–5.0; SD = 1.0) and “non-pest” beetles (mean N = 4.0; 2.0–8.0; SD = 2.0) (Figure 5). The mean number of clusters was significantly different (Z = 0.00, p = 1.00) between endangered (mean N = 4; 2–7; SD = 1.7) and common species (mean N = 3; 2–8; SD = 2.1). Also, “pests” from Old World (mean N = 3; 2–6; SD = 1.3) and New World (mean N = 3; 2–9; SD = 1.5) have significantly different haplotype diversities (Z = 0.57, p = 0.57) (Supplementary Figure S6).

Information on pairwise distances calculated on mitochondrial markers between different taxa was available in 43 articles. These distances differed significantly (Chi² = 44.81, p = 0.004) between “pests” (mean d = 8.1; 0.8–19.4; SD = 6.5) and “non-pest” beetles (mean d = 9.0; 1.3–23.1; SD = 6.6) (Figure 5). The mean pairwise distances were significantly different (Chi² = 62.50, p < 0.001) between endangered (mean d = 10.5; 3.0–23.1; SD = 7.2) and common species (mean d = 7.3; 1.3–16.4; SD = 5.6). Also, “pests” from Old World (mean d = 2.5; 0.0–19.4; SD = 7.4) and New World (mean d = 3.3; 0.0–16.0; SD = 5.8) have significantly different haplotype diversities (Chi² = 35.81, p < 0.001) (Supplementary Figure S6).

These distances were next used to estimate divergence times in 21 articles. Mean divergence times were much lower for “pests” (mean D = 0.4 Mya; 0.0–2.5; SD = 0.7) than for “non-pest” beetles (mean D = 4.6 Mya; 0.1–9.0; SD = 3.7) (Chi² = 57.33, p < 0.001) (Figure 5).

**Taxonomic revisions.** A total of 34 taxonomic recommendations were proposed in 25 articles. Eight of them concerned the description of new taxa (*Dendroctonus beckeri, Euwallacea fornicator, E. whitfordiodendrus, E. kuroshio, Ips subelongatus, Tomicus armandi*) (Stauffer et al. 2001; Cai et al. 2008; Li et al. 2010; Gomez et al. 2018), one designation of a new subspecies (*Dendroctonus pseudotsugae barragani*) (Ruiz et al. 2009), seven confirmed previous taxonomic revisions (*Crypturgus subcribrosus* distinct from *C. cinereus*, *Monochamus sartor sartor* distinct from *M. sartor urussovi*, *Tomicus destruens* as a valid species; distinctness of five species of *Osmotherma* (Kerdelhué et al. 2002; Jordal & Knížek 2007; Audisio et al. 2008; Plewa et al. 2018), six delimited new taxa but without taxonomic decisions (new taxa distinct from: *Dendroctonus brevicomis, D. frontalis, Euwallacea interjectus, Hégert politus, Protactia hypocrita, Odontotaenius disjunctus and Tomicus piniperda*) (Juan et al. 1998; Kelley et al. 1999; Duan et al. 2004; Armendáriz-Toledano et al. 2014; Cognato et al. 2015; Vondráček et al. 2018; Garrick et al. 2019), eight synonymized extant taxa (*Anastrangalia reyi* and *A. sequensi* to be subspecies of *A. dubia*; *Ips amitinus* var. *montana* as a race of *I. amitinus*; rejection of the existence of five taxa related to *Morimus asper*, *Propomacus cypricatus* reduction to *P. bimuscronatus cypricatus*) (Stauffer & Zuber 1998; Solano et al. 2013; Sfenthourakis et al. 2017; Zamoroka...
et al. 2019), one rejected the distinctness of putative taxa in the Cetonia aurata complex (Ahrens et al. 2013) and two present uncertain taxonomic implications (doubts about the monophyly of Protactia cuprea in relation to P. cuprina and uncertain species status of P. metallica) (Vondráček et al. 2018).

Hybridization. Individuals with mixed genotypes have been reported in natural populations of: Anastrangalia reyi and A. dubia in Europe (Zamoroka et al. 2019), Cerambyx cerdo and G. zelensis (Torres-Vila & Bonal 2019) in Iberia, and Lucanus cervus and L. tetrodon in Italy (Solano et al. 2015). In addition, artificial interspecific crosses have been induced for Dendroctonus frontalis and Dendroctonus sp. nov. from Middle America (Armendáriz-Toledano et al. 2014).

Refugia. Phylogeographic analyzes indicating the localization of potential refugial areas (mostly glacial) were presented in 61 articles and concerned 47 beetle taxa.

Details of the phylogeographic patterns observed for all species studied are presented in Supplementary Table S2. In addition, important data on divergent lineages of some bark and ambrosia beetles are available in the barcoding study by Jordal and Kambestad (2014) (not included in the review because it was identified as a large-scale barcoding study).

Several patterns of phylogeographic distribution of genetic lineages were observed for saproxylic beetles and are listed in Table I.

There are several areas in the world that could be identified as important refugia for saproxylic beetles, but unfortunately the available studies limit this list to the Palearctic and Nearctic regions. The best known glacial refugium in the Mediterranean Basin with several areas identified as genetic hotspots (Iberia, Apennines, Balkans, Anatolia, Maghreb) has been reported for 17 species, both relicts, common species and “pests”. Central European mountain systems (mainly Alps and Carpathians) proved to be refugia for at least four beetle taxa. About 20 species had distinct refugia over Eastern Europe and/or the southern Ural Mountains, Siberia, and East Asia (Far East Russia, Korea, East and South China). Another refugium for saproxylic beetles was noted in the Japanese archipelago, but the significance of this area requires further investigation, as data are available for only three taxa. In the New World, refugia were reported from eastern North America (Appalachians) (for four species), midwestern North America (Rocky Mountains) (for five taxa), the Pacific coast of North America (Cascade Mountains) (six species), and Middle America (Sierra Madres Occidental & Oriental) (two taxa) (Supplementary Figure S7). In addition, unique refugia were reported for only four species in both the Palearctic and Nearctic realms. These identified refugia, particularly in Europe, eastern Asia, and North America, fit very well with the general phylogeographic patterns known for the Palearctic and Nearctic species (Taberlet et al. 1998; Avise 2000; Hewitt 2000). Many of the saproxylic beetles show

Table I. Distribution of identified refugia for saproxylic beetles with lists of matching species.

| Refugia | Exemplary taxa |
|---------|----------------|
| Multiple within the Mediterranean region | Scarabaeidae (Osmothera eremita complex, Cetonia aurata, Protactia cuprea); Lucanidae (Lucanus cervus, L. tetrodon); Curculionidae (Anastrangalia reyi, Monochamus sartor); Curculionidae (Pityogenes chalcographus) |
| Central-west vs north-east Europe | Cerambycidae (Anastrangalia reyi, Monochamus sartor); Curculionidae (Pityogenes chalcographus) |
| Europe with Siberia vs east Asia | Pythidae (Pytho abieticola, P. depressus, P. holotensis); Curculionidae (Anastrangalia reyi, Monochamus sartor); Curculionidae (Dendroctonus micans, Ips cembri, I. duplicatus, I. acuminatus, I. svecicus, I. typographus, Tomius piniperda, T. minor, Crypturgus hispidulus, C. suberibius, Dryocoetes hystrix, Hylurgus pallsiatus, Hylastes bruneus, Orthotomicus loricatus, Pityogenes chalcographus, Polygraphus subopacus) |
| East vs central Asia (or east vs west China) | Cerambycidae (Anastrangalia sequens, Massicus raddei); Curculionidae (Pissodes yunnanensis) |
| The Japanese Islands vs east mainland Asia | Curculionidae (Polygraphus proximus, Xylosandrus germanus) |
| The Japanese archipelago only | Curculionidae (Semanotus japonicus) |
| West vs east North American | Curculionidae (Dendroctonus brevicomis, D. frontalis, D. ponderosae, Pissodes strobi) |
| West part of North America | Curculionidae (Dendroctonus ponderosae, D. pseudotsugae, D. rufipennis, D. valens, Ips confusus, I. pini) |
| The Middle America | Curculionidae (Dendroctonus approximatus, D. mexicanus) |
| West Palearctic vs east Palearctic vs Nearctic | Curculionidae (Dryocoetes autographus, Hylastes opacus, Trypodendron lineatum) |
| Europe vs North America | Curculionidae (Orthotomicus naturalis) |
evidence of range contraction to southern refugia (such as the Mediterranean) during the Pleistocene. This is especially true for taxa associated with deciduous trees (e.g. Scarabaeidae, Lucanidae, Cerambycidae), whose distribution was restricted to southern areas at mid-elevations, but also for some beetles associated with conifers, especially pines (e.g. Scolytinae). Most boreal taxa of saproxylic beetles (especially Scolytinae and some Cerambycidae) were restricted to eastern refugia in Asia, from where they spread across the boreal zone into Eurasia. In addition, some of them survived the ice ages in local mountainous regions in Europe or Asia. In the case of the North American taxa, many species had refugia in the mountains of the western and eastern coastal areas and then spread in either a northeasterly or northwesterly direction. Notable is the lack of phylogeographic studies for subtropical and tropical saproxylic beetles, whose history was also influenced by glaciations, when thermophilic forests shrank, which must have consequences for the genetics of Neotropical, Afrotopical, Indomalayan and Australasian beetles.

Primeval forest relics, threatened species and conservation implications. Beetles considered to be primeval forest relicts (10 species) were studied in 18 articles.

Twenty-three publications included studies on threatened beetles. Of the taxa studied, one species had IUCN category CR (Propomacrus cypriacus: Sfenthourakis et al. 2017), three were EN (Osmoderma lassalei, O. italicum, O. cristinae: Audisio et al. 2008), four were VU (Cerambyx cerdo, Rosalia alpina, Morimus funereus and M. asper: Solano et al. 2013; Drag & Čižek, 2015; Drag et al. 2015, 2018; Melosik et al. 2018; Molfini et al. 2018; Torres-Vila & Bonal 2019), six were NT (Osmoderma eremita, O. barnabita, Lucanus cervus, Elater ferrugineus, Propomacrus bimumonatus and Cerambyx welensii: Audisio et al. 2008; Svensson et al. 2009; Oleksa et al. 2013, 2015; Solano et al. 2015; Landvik et al. 2017; Sfenthourakis et al. 2017; Cox et al. 2019; Torres-Vila & Bonal 2019; Melosik et al. 2020), and 12 species were in the LC category (Anastrangalia sequens, A. sangumia, Batocera lineolata, Lucanus tetraodon, Monochamus sartor, Protaetia marmorata, Pytho depressus, P. abieticola, Rhagium inquisitor, Primobius myardi, Protaetia cuprina, Trichoferus campestris: Painter et al. 2007; Oleksa et al. 2013; Solano et al. 2015; Plewa et al. 2018; Vondráček et al. 2018; Torres-Vila & Bonal 2019; Zamoroka et al. 2019; Çakmak et al. 2020; Peng et al. 2020; Wu et al. 2020). One species (Pytho kolwezis: Painter et al. 2007) was assigned to the category DD.

Implications for conservation were presented in 13 articles for 9 taxa. For example, the probable extinction of an isolated population of Cerambyx cerdo in Poland within 19 years was reported (Melosik et al. 2018), but, at the same time, reintroductions proved effective in Czech Republic (Drag & Čižek 2015). Within the range of Rosalia alpina, distinct evolutionary units have been found in Greece and Italy, for which separate conservation measures have been recommended (Drag et al. 2018; Molfini et al. 2018). In the case of Morimus, the conservation status of M. funereus should be extended to the entire M. asper species (Solano et al. 2013). For Osmoderma barnabita, inbreeding in local populations has been reported (Oleksa et al. 2013), and the need for separate conservation of northern and central European populations has been highlighted (Landvik et al. 2017). Inbreeding in local populations has also been listed for Protaetia marmorata (Oleksa et al. 2013). Oleksa et al. (2015) highlighted the importance of tree alleles for the dispersal of Elater ferrugineus. Evolutionary units of conservation value have been proposed for Lucanus cervus and L. tetraodon (Solano et al. 2015), with particular attention to the Greek population of the former species (Solano et al. 2015).

Endangered species (see Materials and methods for their assignment) were found to have significantly 0.7-fold lower haplotype diversities than common beetles (excluding “pests”), and the same pattern was observed for heterozygosity (0.65-fold lower) and fixation indices (0.3-fold lower). Contrary, pairwise distances occurred to be 1.8-fold higher among endangered species than within common taxa, and the number of identified genetic clusters or clades was 1.5-fold higher in endangered than common beetles. These differences in genetic metrics strongly suggest that populations of endangered saproxylic beetles have overall lower genetic diversities and are more structured genetically than common species. These general genetic patterns could have important implications for the proper conservation of rare and threatened saproxylic beetles, which are probably more vulnerable to environmental constraints.

“Pests” and invasive species. Beetle species of economic importance to forestry were studied in 80 articles containing data for 59 species (53 Curculionidae, 4 Cerambycidae and 2 Buprestidae). These studies (apart from invasion described below) investigated barcoding and species distinctiveness (Kohlmayr et al. 2002; Allender et al. 2008; Li et al. 2010; Cognato et al. 2019), intraspecific diversity and phylogeography (Kelley et al.
European populations of *Pissodes castaneus* have invaded South America and also Southern Africa (Zaleski et al. 2013; Pereyra et al. 2016; Wondafrash et al. 2016). North America was the source of invasion of *Pissodes nemorensis* to Africa (Wondafrash et al. 2016), and of *Dendroctonus valens* to Asia (Cognato et al. 2005; Cai et al. 2008; Taerum et al. 2016). Intracontinental invasions have been reported for *Xylosandrus germanus* from East Asia to Middle East (Dzurenko et al. 2021), *Agrius mali* from eastern to western China (Bozorov et al. 2019), and *Pissodes strobi* from eastern to western North America (Lewis et al. 2001). In addition, *Aphanarthrus glabrum* has been reported as invasive in the Canary (Jordal et al. 2006). The weevil *Allaetes niger* was introduced to Cuba from China but is not considered as “pest” (Grebennikov 2020). The graphical representation of the “invasion routes” is shown in Supplementary Figure S6.

Available information for selected taxa. The articles on saproxylic beetle taxa with available molecular data on their intra- or interspecific diversity and relationships are abundant, and it is therefore difficult to comprehensively characterize all species covered. On the other hand, many of these taxa have been studied only for specific objectives, on a very limited sample size, and with only simple methods, so that knowledge about many beetles is superficial. In the Supplementary File S1, we have selected some characteristic species from two groups: “pests” and “primeval relicts” together with threatened taxa, for which the available information is briefly summarized.

Missing data and understudied topics

Species missed in molecular studies. The numerous studies listed and characterized in this review represent only “the tip of the iceberg” of saproxylic beetle biodiversity worldwide, both in terms of species considered “pests” (at least in some areas), beetles known to be relicts of primeval forests and threatened and protected (globally or regionally) taxa. Between these two extremes are thousands of wood-dwelling beetles that are of neither economic nor conservation importance, but all of these taxa are natural elements of forest ecosystems that are critical to the proper functioning of ecological networks because of the role of saproxylic beetles in wood decomposition (Harmon et al. 1986; Speight 1989; Stokland et al. 2012). In addition, all these beetles are an important food source for numerous organisms (Scherzinger 1996; Gutowski et al. 2004) and often create microhabitats for other organisms.
(Dajoz 2000; Gutowski et al. 2004; Stokland et al. 2012).

It is not possible to summarize all taxa that have been overlooked in molecular studies to date. Below, we briefly list and characterize knowledge gaps in molecular studies of important saproxylic beetles of economic importance (“pests”, with special attention to invasive taxa) and of primeval relicts and/or beetles of highest conservation interest. As knowledge about these groups (especially about rare and threatened taxa) is mostly limited to the western Palearctic, we have focused on the European (west Palearctic) taxa.

“Pests”. In the Palearctic region, there are numerous saproxylic beetle species that are capable of building their populations to outbreak densities, resulting in damage to entire forest stands. Details of these beetles, which should be the object of future molecular studies are provided in Supplementary File S2. In summary, knowledge of the genetics of “pests”, particularly bark and ambrosia beetles, is quite impressive with respect to some genera that are of greatest economic importance to timber production worldwide (i.e. Ips, Pityogenes, Dendroctonus, Tomicus, Xylodendrus, Xyleborus and Eucoccodera). However, some other genera of bark and ambrosia beetles have not yet been covered by molecular studies (e.g. Xyleborinus, Anisandrus, Trypodendron, Gnathotrichus, Platypus). Furthermore, for many other “pests” of conifers (e.g. Dryocoetes, Hylastes, Pityokytenes) and deciduous trees (e.g. Scolytus, Hylesinus, Taphrorychus), intraspecific genetic studies are not available. The exception is studies aimed at developing barcodes for some of these taxa in large-scale studies of pests (e.g. Hulcr et al. 2015), or deep phylogenies (e.g. Cognato & Sperling 2000; Cognato & Sun 2007).

Primeval forest relics and threatened beetles. The current European Red List of saproxylic beetles includes 688 taxa (Cálix et al. 2018). Of these, 113 species have been classified as threatened on the European continent (IUCN categories CR, EN, and VU), another 69 species are near threatened (category NT), and knowledge about the conservation status of another 168 species is insufficient (category DD). Thus, about 50% of the red listed saproxylic beetles in Europe are endangered or about to be classified in this status. To date, 26 beetle species from the above-mentioned European Red List and 8 taxa considered threatened in Europe have been genetically studied (Supplementary Table S1), representing 3.8% and 1.1% of assessed taxa, respectively.

A valuable category of threatened saproxylic beetles are primeval forest relicts, whose current distribution in Europe is closely linked to remaining patches of natural/pristine forests. The list of primeval forest relict beetles in Central Europe includes 168 species from 38 families (Eckelt et al. 2018), of which, only 8 species have been genetically studied representing about 4.8% of this group (Supplementary Table S1).

In conclusion, despite the observed progress in the number of articles in the last decade (Figure 2), the above data show that our knowledge of the intra- and interspecific genetics of endangered species, including primeval relicts, is still very incomplete, insufficiently explored, and in an initial phase.

As indicated by the attached data in Supplementary File S3, the need for research on the genetics of threatened and relict beetles is pressing. In Supplementary File S3 we provide a short list of beetles that have not yet been studied in this manner but are worth knowing about because they: i) belong to an unstudied family, ii) are protected by international initiatives for the conservation of continental biodiversity, iii) are associated with coniferous forests that dominate many areas and zones of the European continent, iv) belong to different ecological and feeding guilds (predators, mycophagous taxa, pyrophilous species), or v) are characterized by an unclear and unresolved taxonomic status.

Methodological limitations. The most important prerequisite for future studies on the genetics of saproxylic beetles is the introduction of next-generation sequencing (e.g. SNPs) or whole genomes. These methods allow for the simultaneous use of thousands of loci across the genome, greatly improving analysis capabilities. These modern methods should be used primarily on relict and endangered protected taxa, as none of them have yet been studied using these modern methods and tools.

Another necessary step would be the further development of barcode libraries for saproxylic beetles using the standard animal barcode – COI. This should be pursued to allow easy and rapid detection of saproxylic beetles in samples collected in the field and in environmental samples (bulk samples) collected from trees/wood (metabarcoding). Genomic data should be obtained for numerous species to facilitate genetic studies between and within populations. Genetic/genomic databases for saproxylic beetles should be developed and linked to taxonomy, species traits, and conservation or management requirements of barcoded/genotyped species.
Because of the rarity and low abundance of many saproxylic beetles, methods for non-invasive DNA extraction based on either live sampling (of beetle body parts), remains sampling (of insect remains), or environmental sampling (e.g. wood samples) should be implemented. Some of these methods have already been developed (see Garrick & Bouget 2018) and implemented (Redlarski et al. 2021).

**Topics needed for future studies.** There is still ongoing need for further studies on the phylogeography, population, and conservation genetics of selected beetle species characterized as relicts of primeval forests, and of these particularly endangered species that are highly threatened by forestry practices. In addition, molecular research continues on populations of as yet unstudied beetle species that are considered “pests” in managed forests and tree plantations, including tracking dispersal pathways for invasive species.

There is a great imbalance in terms of the geographic origin of the saproxylic beetles studied, with a lack of data from subtropical and tropical taxa and areas (especially “non-pest” taxa).

Surprisingly, there are no multi-species studies linking genetic polymorphism of saproxylic beetles (of both primeval relicts and “pests”) to quality and quantity of forest habitats and microhabitats, and to duration of forest protection or management intensity. These types of studies would improve understanding of the role of saproxylic beetles in forest ecosystem functioning and allow conservation priorities to be set, measures to protect rare and threatened taxa to be better implemented, or the mechanisms behind outbreaks of “pests” to be better understood. This research could be extended to other elements of forest ecosystems such as host trees, associated fungi, and predatory vertebrates to better understand the history of entire woodland-dwelling communities and present-day interactions in forest ecosystems.

**Conclusions**

The present work is the first comprehensive summary of what is known, based on molecular studies, about the history, present-day diversity, and relationships of an extremely important group of organisms, namely saproxylic beetles. Species of economic importance to forestry (“pests”) have been the subject of numerous studies, and the information available for these species fills the body of knowledge relatively well, but many taxa have not yet been studied. On the other hand, only a small fraction of rare and threatened beetles have been adequately studied, and common species with neutral roles in forestry are still neglected in molecular studies, despite their critical importance to forest ecosystem functioning. The recommended directions for future molecular studies of saproxylic beetles would not only expand basic scientific knowledge, but would also be critical for the appropriate protection of rare and threatened taxa or for effective management of “pest” populations. In this regard, the database presented in this article (Supplementary Table S1) should be an excellent starting point for future scientific endeavors.

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Authors have rights to all materials used in the article (all figures had been prepared originally for this article and all photographs used are property of one of the two Authors: Jerzy M. Gutowski and Radoslaw Plewa).

This study did not involve any experiments on animals or did not involve the use of human subjects. The research was carried out in accordance with accepted scientific standards.

**Data availability statement**

A list of the data sources is found in Supplementary Table S1 available at DOI [https://doi.org/10.17605/OSF.IO/JK6V3](https://doi.org/10.17605/OSF.IO/JK6V3).

**Supplementary material**

Supplemental data for this article can be accessed here.
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