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Policy analysis

The European palaeoecological record of Swedish red-listed beetles

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ABSTRACT

Recent global changes have triggered a biodiversity crisis. However, climate fluctuations have always influenced biodiversity and humans have affected species distributions since prehistoric times. Conservation palaeobiology is a developing field that aims to understand the long-term dynamics of such interactions by studying the geohistorical records in a conservation perspective. Case studies exist for vertebrates and plants, but insects have largely been overlooked so far. Here, we analysed the current red-listed beetle species (Coleoptera) in Sweden and investigated their occurrence and representation in the European Quaternary fossil record. Fossil data currently exist for one third of the Swedish red-listed beetle species. All the red-list conservation classes are represented in the fossil record, which may allow for comparative studies. We found significantly different representations in the fossil records among taxonomic groups and ecological traits, which may depend on the fossil depositional and sampling environments and variation in how difficult species are to identify. Species that are today associated with modern urban environments were mostly found in Quaternary sites with archaeological human settlements, reflecting early human-driven environmental change. Combining modern and fossil insect species data for biodiversity conservation needs to be undertaken with care, and attention paid to biases in both modern and palaeo-data. Nevertheless, this approach opens new opportunities for conservation biology by providing a millennial-scale perspective on biodiversity change, including consideration of the long-term dynamics of species range shifts, species invasions and regional extinctions under changing climates.

1. Introduction

Recent global change is causing species range shifts and contractions, species extinctions, decline in species abundances and biotic homogenization (Dirzo et al., 2014; Parmesan, 2006). Insects appear to be particularly affected (Reichholf, 2018; Simmons et al., 2019; Thomas et al., 2004), yet they represent a significant knowledge gap in conservation science and practice (Cardoso et al., 2020). Indeed, although there is much national variation, the IUCN has assessed an extremely small proportion of insect species ($n = 7490$) to date, many of which (~34%) have been classified as extinct, critically endangered, endangered, vulnerable, conservation dependent or near threatened (www.iucnredlist.org, accessed on 03.02.2021).

Changes in insect biodiversity have so far been almost exclusively analysed within the time frame of one or a few decades (e.g. Baranov et al., 2020; Hallmann et al., 2017; Thomas, 2016) although studies spanning about a century also exist (Jeppsson et al., 2010; Kerr et al., 2015; Maes and Van Dyck, 2001; McDermott, 2021). Here, we apply a much longer perspective, using a palaeoecological approach, to the current insect biodiversity crisis (Cardoso et al., 2020; Wagner, 2020). Palaeoecology provides unique tools that can aid conservation biology by analysing previous periods of environmental and climate stress, putting the magnitude and dynamics of current biodiversity trends in context and elucidating the legacy of past changes (Barnosky et al., 2017; Dietl and Flessa, 2017; Fordham et al., 2020). For example, a palaeoecological study on molluscs found that species with declining long-term distributional trends are those with highest current risk of extinction (Foote et al., 2007). Fossil data have also been used to improve ecological niche models, and thus better predict the effects of future climates on, for example, the jaguar (*Panthera onca*; Lima-Ribeiro et al., 2017) and to support the apparent resilience of the North cod fisheries (Eide, 2017).

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Since the pioneering work of Coope (1967), Quaternary insect fossil records have frequently been used for reconstructing past climates and environments (e.g. Buckland et al., 2018; Elias, 2013) and for studying long-term biogeography (e.g. Abellán et al., 2011; Schafstall et al., 2020). More recently, fossil data have been used as points of reference in phylogenetic studies (Abellán et al., 2011; Opgenoorth et al., 2020) and for reconstructing baselines in rewilding studies (Hodder et al., 2005; Perino et al., 2019). However, while the use of historical museum collections has been suggested for increasing the reliability of conservation assessments (Connolly and Ward, 2020), insect fossil records have rarely been analysed for biodiversity conservation (cf. Abellán et al., 2011; Lindbladh et al., 2013; Sandom et al., 2014; Whitehouse, 2006; Whitehouse et al., 2008). This study showcases the potential of insect palaeoecological data for biodiversity conservation purposes and discusses the advantages and possible caveats of this approach, the ultimate aim being to increase awareness of such methods among entomologists and conservationists. As a case study, we analysed the beetle species (Coleoptera) currently red-listed in Sweden and investigated their occurrence in the European Quaternary fossil record. The relatively frequent preservation of beetles in archaeological and geological contexts makes them ideal candidates for insect palaeoecological analyses (Coope, 2004). Present day distributions are a product of both current and past environmental conditions, and the capacity of each species to survive in situ when conditions change or to move to new sites that have become suitable. A full understanding of the ecological traits, as well as the available distribution data for any species, is therefore essential for assessing potential bias in the fossil record towards specific groups of species, ecological niches, or geographical distributions. Therefore, by combining modern and fossil data, we asked: (1) How are red-listed beetles represented in the fossil record? (2) How are species within different conservation classes, taxonomic groups, geographical distributions, and ecological traits represented in the fossil record? (3) In broad terms, what were their past and present distributions? We expected a higher representation in the fossil record for species (a) with lower current extinction risk, because they may have had higher abundances and larger geographical distribution also in the past; (b) associated with landscapes typical of post-glacial Scandinavia, i.e. woodlands, wetlands; (c) associated with habitats that generate ideal sediments for the preservation of insect fossils, e.g. bogs. Furthermore, we (d) expected no difference in the representation of species from different geographical regions of Sweden in the fossil record, due to the large range of environments and climates experienced in Europe in the past millennia.

2. Methods

2.1. Species' conservation status and traits

We extracted the red-list category, and a set of ecological traits (landscape, habitat, trophic group and substrate/food association) of Swedish beetle species from the database ArtFakta (https://artfakta.se; accessed in April 2020; SLU Artdatabanken, 2020). The full list of trait categories is reported in Appendix Table A1. Species-trait associations are classified as strong or weak, and individual species can be associated to more than one category within a trait group. In our analyses, we only used strong associations. Another source of traits for beetles, specific for palaeoecological studies, is available in the BugsCEP database (www.bugscep.com; Buckland, 2014; Buckland and Buckland, 2006; partly based on Koch, 1992, 1989). We analysed the trait data from ArtFakta to compare species with and without fossil records, and the BugsCEP's trait system to discuss the palaeoecological inferences. We consider red-listed species those that are classified as regionally extinct (RE), critically endangered (CR), endangered (EN), vulnerable (VU), and near threatened (NT) according to the IUCN classification system (data deficient species are excluded). In addition to the ecological traits, we also gathered information on the current (1950–2020) geographical distribution of species in Sweden from www.artportalen.se. We classified each species as a northern species if only occurring from the provinces Värmland and Dalarna northwards, southern species if only occurring from these provinces southwards, or “other” if occurring in Värmland, Dalarna, or in both north and south (see Appendix Fig. A1 for map). This classification approximates to the Limes Norrlandicus, the border between the boreal and the boreonemoral biogeographic regions in Sweden (Gustafsson and Ahlen, 1996).

2.2. Fossil record

We gathered fossil beetle data from the Strategic Environmental Archaeology Database (SEAD, www.sead.se, date accessed: 01.08.2019; Buckland et al., 2018). SEAD is an open access database that contains a wealth of palaeoenvironmental and archaeological data, including the past distribution of insects from over 1300, primarily European, archaeological and Quaternary geological sites. It is continually updated and derives its insect data from the BugsCEP database. Archaeological sites are places where the insect fauna is expected to have been influenced by past human activities, mainly from or near the location of archaeological excavations. These data can provide information on human-driven environmental impacts, and on anthropogenic environments. Quaternary geological sites (hereinafter “natural deposits”) consist of samples from peatbogs and lake and riverine sediments some distance (or time) from known archaeological sites and provide records away from direct human impact. Each site contains at least one dataset of beetle counts from at least one sediment sample, most often more. These data have been collated from over 1400 published palaeoentomological studies in both scientific journals and consultancy reports, references to which are available through BugsCEP and SEAD. Approximately 57% of datasets include full quantification of Coleopteran taxa (i.e. minimum number of individuals per taxon per sample), the rest consisting of either partial abundances or presence only. Sixty-nine percent of the occurrences in the database are species, 27% are genera (or species aggregates) and 4% are families. Here, we only used taxa identified to species.

As part of the Swedish LifeWatch project (Wremp, 2017), we matched the list of Swedish beetle species (taxonomy from: www.dyntaxa.se, accessed in April 2020) with the taxonomic list of the SEAD database, and extracted the fossil record for the matching species (Appendix Table A2). We analysed the fossil records of Swedish red-listed species at the European scale, as the full extent of the past distribution of the species can provide valuable information on both the palaeoecological context and origins of the modern fauna. The number of samples and sites where species of different red-list categories were found and their abundances are reported in Appendix Tables A2 and A3.

2.3. Modern European distribution

As with the fossil record, we gathered the current (1950–2020) European distribution of Swedish red-listed species with fossil records from GBIF (GBIF: The Global Biodiversity Information Facility; www.gbif.org), using the R package *rgbif* (Chamberlain and Boettiger, 2017). We applied a quality control procedure to the GBIF records and removed data points: with equal latitude and longitude (1), zero coordinates (2), coordinates in the sea (3), corresponding to country centroids and capital cities (4) or to zoos, botanical gardens or museums (5), using the R package *CoordinateCleaner* (Zizka et al., 2019).

2.4. Data analysis

To answer our first research question, we analysed the fossil record of the red-listed species to investigate patterns in their occurrence. For each species, we computed the total number of fossil samples as well as the proportion of archaeological sites (vs natural deposits) where it occurred. For the subset of species for which abundance data were available (220 species out of 232), we also computed the total abundance of each species in the fossil record. We tested whether the species associated with the different landscape types occurred in a similar number of archaeological sites and natural deposits using paired *t*-tests (*t.test* function of R package *stat*; R Core Team, 2019). A paired t-test was run for each landscape type, comparing the number of archaeological sites and natural deposits where each species of that landscape type occurred in the fossil record. We ran paired t-tests on log - transformed data, to meet the test's assumption of approximate normality.

To answer our second research question, we ran a series of χ^2 tests, using the *chisq.test* function of R package *stat* (R Core Team, 2019), to investigate whether the proportion of the species with and without fossil records differed across conservation classes, taxonomic groups, geographical distribution and ecological trait categories. Under the null hypothesis, the expected proportion of the species with and without fossil records is equal across the different categories. A χ^2 test was run for conservation classes, taxonomic groups and for each trait (geography, landscape, habitat, trophic group and substrate/food association), which resulted in a total of seven χ^2 tests.

To answer our third research question, we plotted the modern and fossil distribution of Swedish red-listed species in Europe, based on the two databases (GBIF and SEAD) described above. For this, we computed and plotted the number of Swedish red-listed species and their total abundance in each 0.5° × 0.5° grid cell of a raster covering Europe.

3. Results

ArtFakta reports 5710 known species of Coleoptera in Sweden. Out of these, 3440 are classified as least-concern (LC) and 842 as red-listed species, specifically: 391 as threatened (CR, EN, VU), 403 as near threatened (NT), and 48 as regionally extinct (RE; Appendix Fig. A2). In addition, 91 species are classified as data deficient and 1337 are not classified. We did not include the two latter groups in any analyses.

3.1. *Description of the fossil record*

Fossils have been recorded for 41% (n = 2357) of the Coleoptera species reported for Sweden. Out of these, 1804 are classified as species of least-concern, 291 are red-listed (including 16 data deficient species), and the remaining 262 have not being assessed. In the fossil record, most of the red-listed species are present in low numbers (<10 individuals) and occur in few samples only, which results in a species abundance distribution with more rare species than predicted by a typical log-normal model (Appendix Fig. A3). The highest total abundances were recorded for *Thanatophilus dispar* (NT), *Anotylus nitidulus* (NT) and *Aglenus brunneus* (VU), with 515, 1292 and 1681 individuals respectively. Four threatened species (all classified as vulnerable: *Lyctus linearis*, *Tournotaris (Notaris* in SEAD*) bimaculata*, *Onthophagus joannae* and *Aglenus brunneus*) and five near-threatened species (*Micropeplus porcatus*, *Otiorhynchus rugifrons*, *Thanatophilus dispar*, *Grynobius planus* and *Anotylus nitidulus*) were recorded in more than 100 samples (Appendix table A2). Most of these abundant or frequent species typically require decaying plant or animal matter; *L. linearis* and *G. planus* live in the deadwood of broadleaved trees. *Thanatophilus dispar*, with most records from littoral carrion (Lane et al., 2021), is common in the fossil record of cold periods, such as the Late Glacial, and *A. brunneus*, blind and subterranean, has been linked to the artificially warmed litter layers of past human and animal stall floors (Buckland et al., 2009).

The red-listed species that are associated with modern urban landscapes occurred more frequently at archaeological sites, compared to natural deposits (paired *t*-test, $t = 2.811$, df = 25, $p < 0.001$). In contrast, the species associated with woodlands, wetlands and freshwaters occurred more frequently in natural deposits (woodland: $t = 3.661$, df = 95, $p < 0.001$; wetland: $t = 5.561$, df = 53, $p < 0.001$; freshwater: $t = 5.635$, df = 20, $p < 0.001$; Appendix Fig. A4).

3.2. *Comparison between species with and without fossil records*

Fifty-two percent of all species of least-concern in Sweden are represented in the fossil record, while the representation ranges between 28% and 46% among the threatened and near threatened red-list categories (RE, CR, EN, VU, NT). The representation in the fossil record does not differ significantly among the five red-listed categories ($\chi^2 = 6.569$, df = 4, $p = 0.165$, Fig. 1a–b).

The superfamilies with the highest number of red-listed species are Staphylinoidea, Curculionoidea, Chrysomeloidea and Tenebrionoidea, while the highest number of red-listed species in the fossil record are found for Curculionoidea, Caraboidea and Staphylinoidea (Fig. 1c–d). The distribution of species among superfamilies differs between the species with and without fossil records ($\chi^2 = 77.31$, df = 15, $p < 0.001$), with Caraboidea and Scarabaeoidea having a higher proportion of species with a fossil record ($p < 0.05$).

Most of Sweden's red-listed beetle species are found only in the south (Fig. 1e–f). The fossil record mirrors that pattern, and the three geographical distribution-groups do not differ significantly in their proportion of species in the fossil record ($\chi^2 = 4.17$, df = 2, $p = 0.124$).

The most common landscape types for red-listed beetle species are agricultural and woodland, followed by wetlands, seashores, urban and freshwater landscapes. The red-listed species with fossil records mirror this pattern, with the exception of the association with freshwaters being significantly more common and the association with woodlands being less common among species with fossil records ($\chi 2 = 57.55$, df = 7, $p < 0.001$; Fig. 1g–h).

Most red-listed species are associated with the habitats: human disturbed/created lands, bare ground, dry grassland, open mires and open grassland. We record a similar pattern for the species with fossil records, although open-mire species are significantly under-represented in the fossil record ($\chi^2 = 47.80$, df = 17, $p < 0.001$; Fig. 1i–j).

The red-listed species are most commonly herbivores, predators and detritivores. The species with fossil records mirror this pattern ($\chi^2 = 9.63$, df = 6, $p = 0.141$; Fig. 1k–l).

The most common substrate/food source for red-listed species are dead trees, and wood and bark. Species using animal remains, living animals, and/or non-woody plant matter have significantly higher proportions of red-listed species with a fossil record than other substrate/food sources ($\chi^2 = 67.99$, df = 13, $p < 0.001$; Fig. 1m–n).

3.3. *Spatial and temporal distribution of the fossil record*

Swedish red-listed species are today present mostly in western, central and northern Europe (Fig. 2). They were recorded in 2222 fossil samples at 589 sites (305 archaeological, 284 natural deposits, Appendix table A3), mostly in Great Britain, which is also the region with the highest number of fossil samples. In Scandinavia, fossil occurrences are confined to the southern part of the region (Fig. 2).

The majority (55%; $n = 1231$) of the fossil samples with Swedish red-listed species are from the Holocene (the last 11,500 years) and 80% are younger than 16,300 years before present (BP). The oldest sample is between 5.3 and 2.5 million years old, and the youngest sample extends into the last centuries.

4. Discussion

4.1. *The European palaeoecological record of beetle species on the Swedish red list*

Extending the temporal scope of ecological studies into the centennial and millennial scale has the potential to reveal long-term natural dynamics of species distributions and the impact of human society on biodiversity through history. A prerequisite for combining contemporary and palaeo-data analyses for species conservation is a full understanding of the available data, i.e. their resolution, spatial and temporal

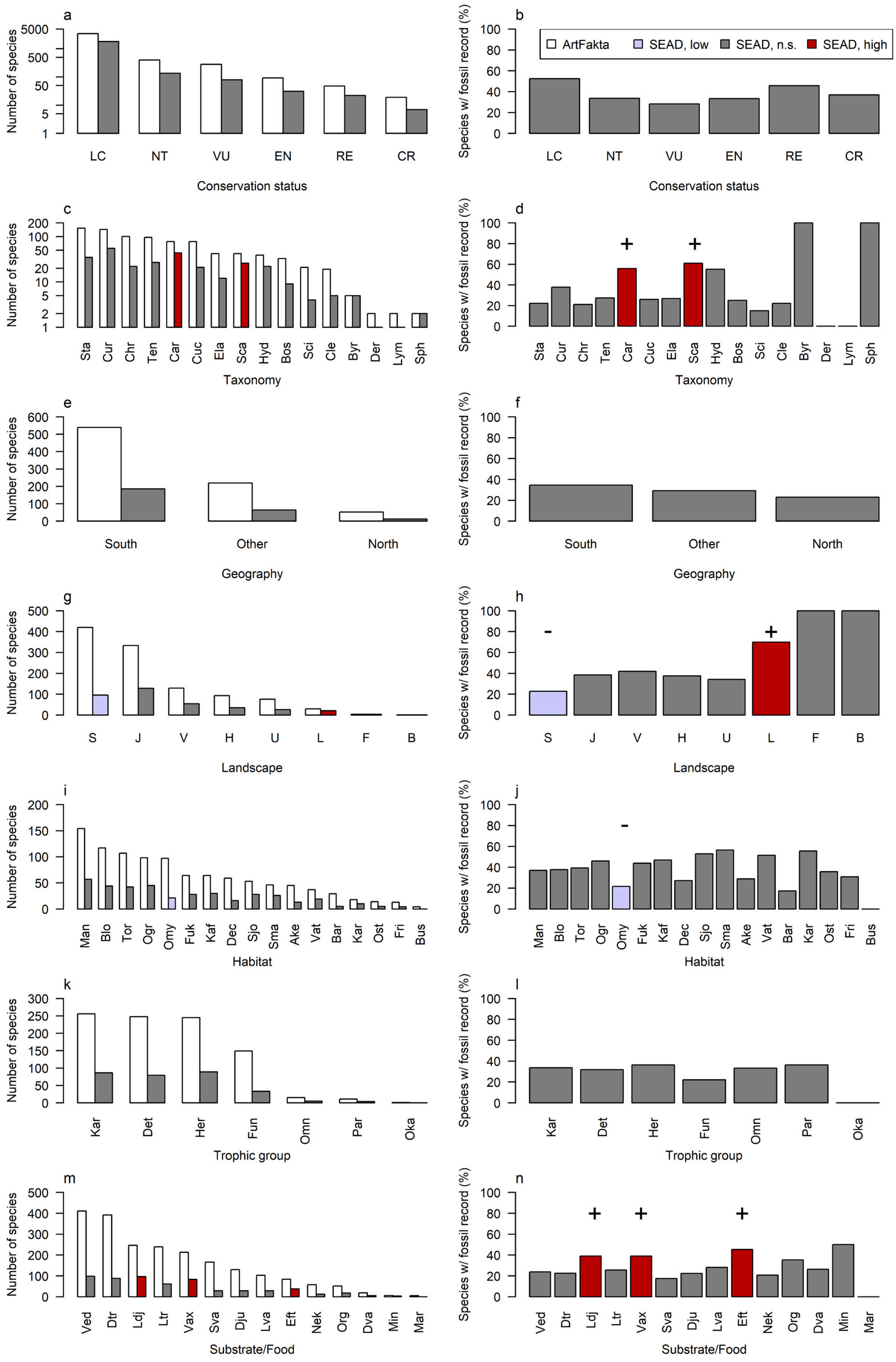

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Fig. 1. Number of beetle species with fossil record (in light blue, grey and red) compared to the full checklist of beetle species (white) in Sweden. All plots besides the ones showing the conservation status (first row) are restricted to red-listed species (CR, EN, VU, NT and RE). Values are shown as absolute numbers (left panels: a, c, e, g, I, k, and m) and as proportions of all species in the groups (right panels: b, d, f, h, j, l, and n). Note that the two upper left panels have a logarithmic y-axis. + and - denote groups with significantly higher (red) and lower (light blue) proportion in the fossil record (see text), not-significant groups are in grey. Conservation status: LC = least concern, NT = near-threatened, VU = vulnerable, EN = endangered, CR = critically endangered, RE = regional extinct. Taxonomy: Bos = Bostrichoidea, Byr = Byrrhoidea, Car = Caraboidea, Chr = Chrysomeloidea, Cle = Cleroidea, Cuc = Cucujoidea, Cur = Curculionoidea, Der = Derodontoidea, Ela = Elateroidea, Hyd = Hydrophiloidea, Lym = Lymexyloidea, Sca = Scarabaeoidea, Sci = Scirtoidea, Sph = Sphaeriusidae (family, suborder Myxophaga), Sta = Staphylinoidea, Ten = Tenebrionoidea. Geography: North = north Sweden only, South = south Sweden only, Other = both north and south Sweden, or in the provinces of Värmland and/or Dalarna. Landscape: S = woodland, J = agricultural, V = wetland, H = seashore, U = urban areas, L = freshwater, F = alpine and subalpine zone, B = brackish water. Habitat: Man = human disturbed/created land, Blo = bare ground, Tor = dry grassland, Ogr = open grassland, Omy = open mires, Fuk = moist to wet grassland, Kaf = acidic mires, Dec = deciduous woodland, Sjo = lake, Sma = small water bodies, Ake = arable land, Vat = running water, Bar = coniferous forest, Kar = calcareous fen, Ost = open shoreline habitats, Fri = mesic grassland, Bus = bushes. Trophic groups: Kar = predator, Det = saprotroph/detritivore, Her = herbivore, Fun = fungivore, Omn = omnivore, Par = parasitoid, Oka = unknown. Substrate/food: Ved = wood and bark, Dtr = dead trees, Ldj = living animals, Ltr = living trees, Vax = plant matter, not wood, Sva = fungi and lichens, Dju = animals, Lva = non-woody living plant parts, Eft = animal remains, Nek = nectar/pollen, Org = organogenic soils/sediments, Dva = non-woody dead plant parts, Min = mineral soils/minerogenic sediments, Mar = bare ground/sediment as substrate. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coverage and distribution, and their inherent taphonomic biases (from the influence of different depositional environments and in-situ decay processes, through field sampling and sample processing, to identification issues).

Our results show that Swedish red-listed beetle species are relatively well represented across conservation classes in the fossil record (range 28–46%). This good representation of the different groups can allow for comparative analyses. Comparative methods in conservation biology (Fisher and Owens, 2004) have been used to identify the traits that cause higher risks of extinction (e.g. Chichorro et al., 2019). In the palaeoecological context, comparative studies could investigate spatial and temporal species distribution across conservation classes to elucidate the legacy of past distributional dynamics, human impacts, and climate change on species extinction risk (Foote et al., 2007).

Species with different traits are differently represented in the fossil record, partly for taphonomic reasons and partly because of the directed nature of archaeological and palaeoecological research. Insects are better preserved in waterlogged sediments than other depositional environments (Buckland et al., 2018), and peats and organic-rich silts account for the majority of samples from natural deposits. The high proportion of red-listed aquatic species having a fossil record may therefore reflect the dominance of these deposits and sampling environments. Due to their broad phylogenetic, geographical and ecological diversity (Jäch and Balke, 2008; Short, 2018), water beetles have been the subject of a large variety of ecological and evolutionary studies (Bilton et al., 2019) and have been used as indicators for freshwater biodiversity and environmental assessments (Bilton et al., 2006; García-Criado and Fernández-Aláez, 2001). Similarly, changes in the distribution of fossil water beetles could reveal alteration of aquatic ecosystems through time (Abellán et al., 2011; Foster and Greenwood, 2016). An example of this is the decline in riffle beetles (Dryopidae: Elminae) in lowland rivers as a result of increased silt load from forest clearance and farming since the mid-Holocene (Smith and Howard, 2004).

The red-listed species that are associated with modern urban landscapes are more frequently found at archaeological sites than natural deposits, reflecting well-established synanthropic associations (Panagiotakopulu and Buckland, 2018; Smith et al., 2020). Most of the species with extensive geographical distributions in the fossil record are

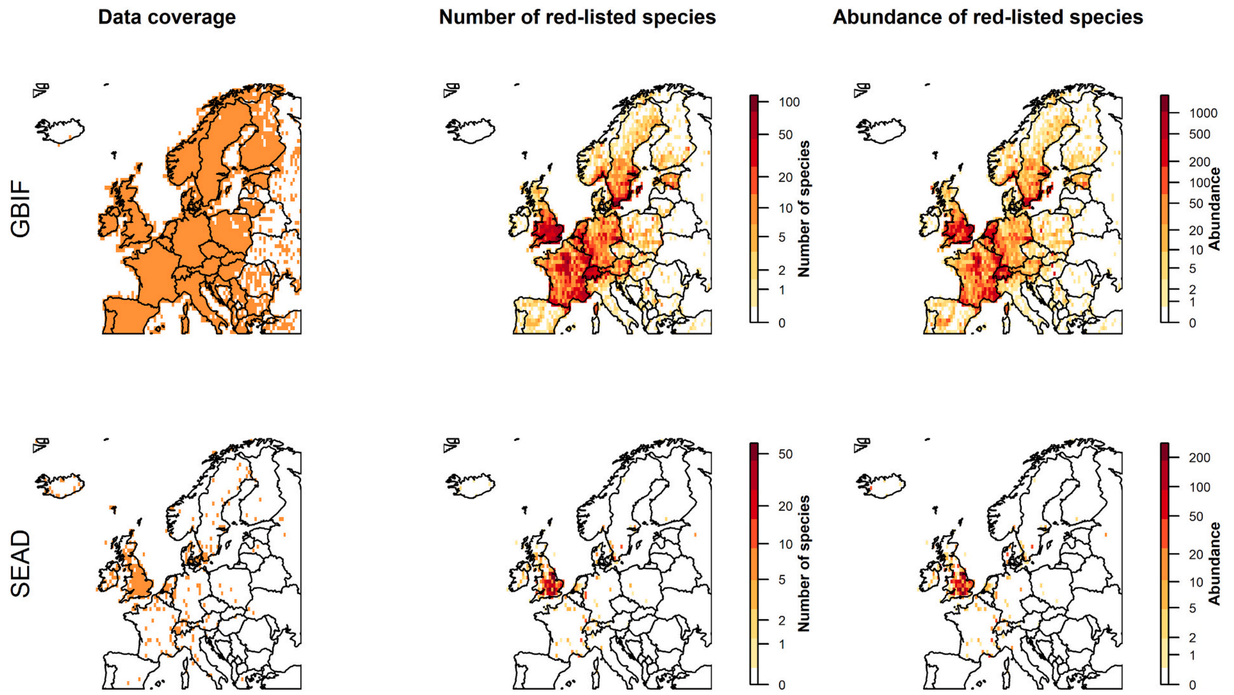

Fig. 2. Distribution of Swedish red-listed species in the modern (GBIF, upper panels) and fossil (SEAD, lower panels) records. The first column shows the geographical coverage of the two databases: orange grid cells have at least one beetle occurrence (independent from the conservation status). The second and third columns show the number of Swedish red-listed species and their total abundance in each grid cell (0.5° × 0.5°, WGS 84) based on the two databases. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

associated with agricultural landscapes (*A. nitidulus*, *T. dispar*, *A. brunneus*, *L. linearis*, *M. porcatus*, and *O. rugifrons*). However, the use of modern landscape classifications in the interpretation of fossils can be misleading if the ecology and habitat details of individual species are not considered. A landscape type assigned through remote sensing or survey, and then mapped to an insect observation, may differ considerably from what is important to the insects at a smaller scale. Often, the food sources and substrates of these species suggest agricultural or pastoral activities, with a strong component of the decaying organic matter which is also the signature for much of humanity's past (Smith et al., 2020). For example, *Aglenus brunneus* is now associated with entirely man-made landscapes, and while its natural habitat is probably damp continuous leaf litter in forests, it has adopted a synanthropic habitat (Girling, 1984) in the dark, warm, mouldy and foul environments of grain stores, cellars and stables (Buckland et al., 2009). While these structures may be components of an agricultural landscape, such a description is equally relevant to the urban landscapes of Medieval London (Smith, 2012) or Roman Amiens (Matterne et al., 1998).

Woodland landscapes have the highest number of red-listed species ($n = 96$) in the fossil record, after agricultural landscapes ($n = 128$). However, the number of species without a fossil record is proportionally higher for woodlands than for the other landscapes. Potential explanations for this include low natural population densities but also fewer samples from (fossil) woodland environments, and from Northern Sweden. Although there are claimed Early Holocene analogues for boreal woodlands in the British Isles (Worrell, 1996), more samples from where boreal woodlands have been chronologically continuous would increase the probability of finding more and rarer woodland species. The disappearance of pine-dominated woodland from lowland Britain led to extirpations and severe declines in frequency and distribution in the Holocene fossil record relate to such woods, although several species, such as the longhorn *Arhopalus rusticus* (Alexander, 2002) and weevil *Rhyncolus ater* (Aubrook, 1972), have re-expanded their range in the expanses of alien conifers. A baseline for Swedish deciduous forest is provided by Palm's extensive work (Palm, 1951, 1959); many of the species he logged as widespread before the modernisation of forestry are now rare. Geographical biases may also explain the low representation of the Swedish red-listed species that are associated with open bog habitats. Although most fossil samples from natural deposits have been collected in peatbogs, the shortage of fossil data from Northern Sweden most likely imposes biogeographical constraints on species detection.

The majority of the fossil samples where Swedish red-listed species were found are from the Holocene, i.e. younger than 11,700 years BP, and thus after the Last Glacial Maximum in Sweden. By focusing on the Holocene, post-glacial species dynamics can be revealed in the context of climatic changes and growing human populations and impacts (Kalis et al., 2003).

4.2. Challenges in combining modern and palaeo biodiversity data for conservation

In the previous section, we indicated possible uses of the fossil record for the study and conservation of red-listed species. Combining modern and palaeo data, however, presents some challenges deriving from the nature of the data and from current knowledge gaps in both. An effort in linking biodiversity databases of different nature (including Quaternary data) is ongoing in the Swedish Biodiversity Data Infrastructure (https://biodiversitydata.se), and similar initiatives are connected to GBIF internationally for different time periods, organism groups and research contexts (LeFebvre et al., 2019). A significant issue in these developments has been the inclusion of fossil sample dates into databases designed to handle present-day (or historical) observations of species occurrences. Fossil dates are based on a variety of methods, including radiometric (e.g. radiocarbon), statistical (e.g. age-depth models), stratigraphic and archaeological methods (e.g. co-occurrence with datable artefacts or relation to excavated contexts). The result is a broad variety of age ranges, accuracy and uncertainty, far from the temporal resolution of modern biodiversity data.

Another issue is the taxonomic mismatch between modern and palaeoecological databases. If only small fragments of sclerotized body parts are available, the identification of fossil insects is often possible only at a coarse taxonomic level, which may limit the use of such data. In this context, the high relative representation of Caraboidea and Scarabaeoidea in the fossil record could be related to these families being generally less difficult to identify to species level, partly thanks to the abundant reference literature available. However, preservation conditions and varying representation of habitats in the fossil samples are likely to be the main factors driving species occurrences in the fossil records and may override any taxonomic resolution biases.

As anticipated above, most of the European records of fossil insects are from Great Britain. Geographical biases in data availability, however, are not restricted to the fossil record, as assessments of the modern distribution and conservation status of species are often incomplete (Meyer et al., 2015). Distribution and conservation status coverage varies considerably between and within different biotic groups (Troudet et al., 2017). While comprehensive information is available for birds and mammals (e.g. Spooner et al., 2018), the current distribution and conservation status of invertebrates are still largely understudied (Cardoso et al., 2011; Girardello et al., 2019). For example, our analysis shows that the majority of European GBIF beetle biodiversity data concentrate in western Europe and Scandinavia, while considerable gaps persist in eastern Europe, despite the abundance of entomological collections there (Wetzel et al., 2018). At a global scale, the major geographic knowledge gaps for invertebrates are in the tropics (Wagner, 2020). The Living Planet Index (Collen et al., 2009) assesses the population trends of about 4000 animal species; invertebrates are not included in the dataset yet, and major geographic gaps persist for Central, West and North Africa, Asia and South America (WWF, 2018).

As demonstrated above, there is a need to evaluate the modern habitat information that is not only used to interpret the fossils in terms of environmental reconstructions, but also fundamental to conservation strategies (e.g. Pilskog et al., 2020). Alexander (2012) has criticised palaeoecologists for confusing the requirements of insects with the landscapes with which their substrates are associated, e.g. the interpretation of proxy indications of *wood* for indications of *woodland* (e.g. Sandom et al., 2014). Similarly, the use of dung beetles as indicators of animals also has its pitfalls, with many species being equally at home in eutrophic mud, grass cuttings and other foul deposits, and their environmental preference being more tied to the degree of exposure and substrate upon which the dung has been deposited than any particular animal type (Roslin et al., 2014). Such contention is not only limited to discussions between ecologists and palaeoecologists, and archaeologists can disagree on the interpretation of a site when analysed through different methods. An archaeologically explained watering hole may turn into a dung pit, viewed with palaeoentomological data (Buckland and Buckland, 2019). It is thus equally important that the ecologist understands the issues associated with the use of archaeological interpretations when combining modern and palaeo data.

5. Conclusions and opportunities

We have demonstrated that Swedish Red-listed species have a significant fossil record, which would allow for their study with a long-term perspective. In addition to the red-listed species, the fossil record includes 278 species that are today listed as data deficient or not-classified. Fossil information on these species could eventually be used once their conservation status is assessed. Assessments like ours could be repeated in other regions, to evaluate the opportunities of incorporating fossil data in conservation efforts under different geographical settings. In regions with high spatiotemporal data resolution, occupancy models could be applied to fossil insect data to improve the estimates of past species abundances after taking into account potential detection bias.

Different frameworks of occupancy models could be used and validated with simulated datasets, such as a multi-species models that includes species' ranges and site sampling histories (Guzman et al., 2021), or single-species models with site-level environmental covariates, as recently done for fossil pollen data (Lawing et al., 2021). In regions with lower data resolution, climate models can be combined with fossil data to compare known and predicted faunas, as Vickers and Buckland (2015) have done for the North Atlantic beetle fauna. Palaeodata can also be used to assess and refine species distribution models (Inman et al., 2018), and thus more accurately assess the susceptibility of species to future climate change (Jarvie et al., 2021).

Species and habitat conservation will benefit from increased interdisciplinary synergies between conservation biology, palaeoecology and environmental archaeology, especially in understanding the long-term impacts of humans and climate change. While it is fundamentally important that insects be incorporated into the ongoing conservation palaeobiology discussions, it is also critical that a more integrated, ecosystem orientated approach, using multiple lines of evidence (proxies), is used to understand the long-term component of our modern biodiversity. This is not only relevant for natural environments, as the use of data from archaeological sites can provide insights into the constantly changing relationships between human societies and the environment, and thus help provide an insect's perspective on the Anthropocene.

We encourage conservation biologists to make use of the wealth of fossil beetle data. In particular the data on red-listed species is useful in conservation internationally, and up to now this potential may have been underestimated. Study of the fossil record provides a long-term perspective on biodiversity and increases our capacity to understand how species and environments change over time. For example, the fossil record can reveal if invasive species really are invasive, or if they were already present in the studied region in the past, and it can help predict species vulnerability to future climate change. Modern population trends could be compared with trends in the fossil record to assess if the modern trends have equivalents in the past. The extensive fossil beetle record of the British Isles (Buckland, 2014) includes over 200 species which are now regarded as extinct in the region (Duff, 2018), most of which can be found living in other areas of Europe. As the climate warms, some of these and other species will change their distributions, whereas some restricted to a few refugial mountain tops will have nowhere to go. Studying their fossil distributions could help in predicting their adaptability, vulnerability and future potential distributions.

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CRediT authorship contribution statement

F.P.: Conceptualization; Data curation; Formal analysis; Writing - original draft, review & editing. M.D.: Conceptualization; Writing - review & editing. G.L.: Writing - review & editing, P.C.B.: Writing - review & editing. P.I.B.: Conceptualization; Data curation; Writing - original draft, review & editing; Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109203.

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