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Extinction rates, extinction-prone habitats, and indicator groups in Britain and at larger scales

Clive Hambler *, Peter A. Henderson, Martin R. Speight

Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, UK

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ABSTRACT

We present the first detailed comparison of extinction rates amongst a wide range of nonmarine groups, using data from Britain. For selected taxa, comparisons are made with rates in the United States and the globe. We estimate the overall extinction rate in Britain is 1–5% of the regional species list per century. Most of the groups of organisms assessed have very similar rates, with high rates in some groups which are aquatic, use dead wood or are on their climatic margin. In Britain, the extinction rate probably rose from the 19th to the 20th Century, and is projected to rise in the 21st Century. Habitat loss is the principal driver of extinctions. In Britain, birds are relatively good indicators of extinction rates and extinction-prone habitats, whilst butterflies are not. At larger scales, such as the USA and globally, birds, freshwater fish and amphibians show potential as indicators. Consideration of 'Possibly Extinct' species and monitoring of habitat area may provide more responsive measures of biodiversity loss.

1. Introduction

Extinction rates must be measured if governments are to meet commitments to reduce the rate of loss of biodiversity, yet very few regions have adequate data, and most groups of organism are too poorly studied to detect trends in extinction rates. There is an urgent need for better indicators of biodiversity loss (Nordling, 2009; Butchart et al., 2010).

We present here the first comparison of extinction rates amongst a wide range of nonmarine groups in Britain (England, Scotland and Wales), Scotland alone, the USA, and globally. We give the most accurate estimate of extinction rates available for Britain. We examine patterns of relative endangerment, consider biases due to under-recording, identify habitats with high numbers of extinct species, and compare potential indicator groups at a range of scales.

1.1. Extinction rates

Invertebrate taxa will dominate absolute extinction rates of multicellular species in the current extinction crisis (Myers, 1979; May et al., 1995; Hambler, 2004). Measuring extinction rates requires lists of extinctions in given time-frames, and for most taxa in most regions inadequate recording effort presents major problems (May et al., 1995; Hambler and Speight, 1996; Shaw, 2005; Butchart et al., 2006). There may be under-recording of extinctions where effort is too low to detect decline or former presence, and workers have hesitated to declare extinction in recent decades (May et al., 1995; Shaw, 2005; Butchart et al., 2006; CREO, 2010). There may also be over-recording of extinctions where effort or knowledge is insufficient to find individuals – particularly for groups with inconspicuous stages such as plant seeds or fungi. Further problems include distinguishing recolonisation events after regional extinctions, and rediscovery after reported extinctions. For most marine invertebrates, data on population losses are less comprehensive, and mobility may make regional extinction difficult to define or monitor.

Minimum estimates of global extinction rates of about 1% of the taxon's species per century have been made for birds and mammals (May et al., 1995). Extinctions in these taxa are relatively hard to miss and easy to date, yet even these taxa may show biases in estimates due to hesitation to declare extinction, or premature declaration (Butchart et al., 2006; Roberts, 2006; Elphick et al., 2010).

Comprehensive status surveys find 12% of all known birds, 30% of all known amphibians, and 21% of all known mammals to be in the IUCN threat categories "Critically Endangered", "Endangered" and "Vulnerable" (IUCN, 2009). There is concern that the current global "focus on vertebrates may provide a limited and highly biased view of species extinction risk" (Clausnitzer et al., 2009). Global extinction rates for invertebrates are now being investigated, mostly with representative sampling of the global list, and numerous data deficient species of invertebrates lead to a high range of uncertainty (Vié et al., 2009). Sampling (Vié et al., 2009;

* Corresponding author. Tel.: +44 (0) 1865 271124; fax: +44 (0) 1865 310447.
E-mail address: clive.hambler@zoo.ox.ac.uk (C. Hambler).

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Clausnitzer et al., 2009; IUCN, 2009) suggests 14% (range 9–44%) of Odonata are in IUCN threat categories, whilst some 16–65% of freshwater crabs are in these categories (Cumberlidge et al., 2009).

May et al., 1995; Hambler and Speight (1996, 2004) and May (2007) suggest there is no good reason to believe birds and mammals have atypical extinction rates. However, there is controversy (Thomas et al., 2004; Hambler and Speight, 2004; Thomas and Clarke, 2004) as to whether global and British extinction rates for nonmarine invertebrates are indeed generally similar to those for vertebrates and plants, or whether most invertebrate groups are under-recorded. Thomas et al. (2009) argue that national ''extinction rates of temperate butterflies *and other arthropods* have recently exceeded those of terrestrial vertebrates and vascular plants'' (our italics).

Britain has relatively intensive biodiversity recording and accessible databases, yet even there collating lists of extinct species in different taxa is very challenging (JNCC, undated a; Natural England, 2010). We have previously considered (Hambler and Speight, 1996) those species in the British Red Data Books (RDBs) thought to have become extinct since 1900, and (allowing for recording biases) estimated a rate of extinction of 1–5% of regional species per century amongst British nonmarine invertebrates in general. We reported similar rates for the British vertebrates and flowering plants, which are very well-recorded. Under-recording and hesitation to declare extinctions was evident in major groups such as the flies and parasitic invertebrates (for which there are no conservation status reviews).

We reported butterflies and Odonata going extinct in Britain at a higher rate than several other invertebrate groups, and suggested warmth-dependent butterflies have very volatile populations on their climatic margin (consistent with Wenzel et al., 2006; Fleishman and Murphy, 2009). Similarly, for Scotland between 1850 and 1949, Shaw (2005) found very high extinction rates in butterflies compared to other well-recorded invertebrates, vertebrates, vascular plants, bryophytes, and lichens. Some authors (Thomas and Morris, 1994; Thomas et al., 2004) also found butterflies had higher extinction rates than dragonflies, plants or vertebrates in Britain and in a well-recorded British county (Suffolk). Using a much less conservative list of ''native'' species, and less cautious acceptance of extinction, Natural England (2010) compared species they describe as ''lost'' amongst a range of taxa in the last 2000 years (which will bias against most taxa). Natural England (2010) found butterflies to have the highest losses, with high rates in mammals and freshwater taxa such as amphibia, stoneworts and stoneflies.

1.2. Indicator groups

It is not realistic to expect data will ever become available to monitor extinction rates in all invertebrate or microbial groups, globally or regionally. If general invertebrate extinction rates prove to be similar to (or correlated with) easily monitored animal or plant groups in a number of regions it will be possible to make far better estimates of absolute global extinction rates (number of species per unit time). There are no widely agreed indicators for extinction rates, in part because such rates are known for very few groups of organisms in very few regions (May et al., 1995; Thomas et al., 2004; Hambler, 2004; Thomas, 2005; Clausnitzer et al., 2009). Claims that a taxon is a good indicator are frequently made without calibration of the taxon to the other taxa or features of interest (Hambler, 2004; Fleishman and Murphy, 2009).

It has been proposed that butterflies as a group have extinction rates similar to many other invertebrate groups and are good indicators of extinction rates or biodiversity loss (Thomas et al., 2004; Thomas and Clarke, 2004; Thomas, 2005; Wenzel et al., 2006; Stewart and New, 2007; Van Swaay et al., 2008). Birds, amphibians and fish have also been widely proposed as indicators of biodiversity loss (BirdLife International, 2004; Butchart et al., 2010; Amphibian Ark, 2009; US Environmental Protection Agency, 2009). Thomas et al. (2004) state the assumption that mammals and birds serve as indicator groups for wider species losses remains untested. In this paper we use data from three geographical scales (Britain, the USA· and globally) in such a test. The relatively comprehensive British data now permit the first detailed comparison of extinction rates for any region and enable a case-study of challenges in monitoring extinction rates.

2. Methods

In order to capture information from early and recent reviews of a wide range of taxa, in this paper we have to use the terms extinction, endangered and threatened in general ways (*not* referring to IUCN threat categories as used in IUCN (2010)). For Britain, national conservation status reviews of different taxa often pre-date current IUCN criteria for such categories. For regional extinction from Britain we use the term extinction, as do many of our sources. Further clarification of these terms, and details of methods and sources, are given in Appendix B.

2.1. Extinction rates in Britain

We collated a list of reported extinctions in Britain and their approximate dates (Appendix A) using many sources including JNCC (undated b), British RDBs, red lists, official national species status reviews, peer-reviewed journals, the websites and publications of specialist societies and NGOs, and other specialist literature. We also indicate in this list species which are probably extinct in Britain (as discussed in Appendix B).

Endangered species counts were made from the same sources as for extinct species, whenever possible, supplemented by internet searches. We include species listed as endangered and critically endangered. Species which have been listed as extinct and have subsequently been rediscovered are also included as endangered (Appendix A).

The extinction rate is expressed as a percentage of the baseline native British species list becoming extinct in a given time-frame, rescaled to a period of 100 years. The baseline is the approximate minimum number of species we believe it is reasonable to assume were present in 1800. The number of British breeding species in each higher taxon was obtained from the sources in Appendix B. We calculated the British extinction rate in eight non-independent time-frames since 1800. Potential biases in each time-frame are given in Appendix B. Our projected ''Extinct & endangered'' rate for the 21st Century assumes the following are extinct or will have become extinct between 1900 and 2099: all species reported extinct since 1900; ''Critically Endangered'' and ''Endangered'' species in taxon reviews; rediscovered species. Our projected Upper Limit (calculated for less-well-recorded taxa only) also includes possibly endangered species (''Data Deficient'', ''Indeterminate'', and ''Insufficiently Known'' categories in taxon reviews, RDBs and red lists in Appendix B).

The mean rate of extinction across all taxa is calculated for five time-frames to which most extinctions since 1800 can be assigned. The mean is calculated using the total extinctions, endangered species, etc., divided by the sum of known species in the groups assessed (27,423); this sum is an approximation, and the rate is a minimum, given the uncertainties in large groups such as flies and fungi.

2.2. Comparison of rates across geographical scales

Using numbers of regional extinctions and regional species and from sources in Appendix B, we calculated extinction rates in

Scotland, Britain, the USA and globally, and make comparisons with data from continental North America (the USA, Canada and Mexico) for freshwater fish. The USA data (based on Wilcove and Master, 2005) include Hawaii.

To illustrate uncertainty in different regions and taxa, we calculate a minimum rate based on recorded extinctions. Our higher estimate for Britain includes species which are probably extinct (Appendix A), and additional species which may have occurred as native species after 1600 (Appendix B). Our higher estimates of global rates for invertebrates assume all IUCN Red List "Critically Endangered" species (IUCN, 2010) are already extinct. Our higher estimate for fish globally includes Lake Victoria cichlids.

2.3. Habitats of each species in Britain

Habitats for each species were subjectively assessed by one author (C.H.) from the same range of sources as extinct species, whenever possible, supplemented by internet searches. Habitat types are mostly not exclusive. A "woodland" species may have occurred in "dead wood" habitats, but (to emphasise the requirement for mature forest) the reverse is not known to be true. Dead wood includes old trees, hollow trees and branches, and standing and fallen coarse woody debris.

3. Results and discussion

3.1. Extinction rates for Britain

We found 400 native breeding species were reported to have become extinct in Britain since 1800, and inclusion of probable extinctions takes the total to 437 species (listed in Appendix A). The total number of British species in the groups assessed was about 27,500, of which most of the roughly 7000 species of fungi and roughly 6000 species of fly were not assessed in detail. Almost all of the species extinct in Britain survive elsewhere.

Recorded and projected British extinction rates for selected taxa and groups of taxa are illustrated in Fig. 1. Extinction rates for all assessed groups are given in Appendix C. It should be noted that these rates are in part an artefact of the subjective taxonomic composition of the groups.

The mean rate of all recorded extinctions in Britain in three time-frames, and projected mean rate, is given in Fig. 2a. The rate since 1800 is roughly 1% per century (of c. 27,500 species). This is a minimum estimate, given inadequate data for some large groups (especially flies and fungi).

Based on the total of recorded extinctions, the extinction rate rises from the 19th Century to the 20th Century (Fig. 2a), and the rates for 1900–1949 and 1900–1999 are similar (1.0% and 0.8%). The slopes of graphs of extinctions versus group size (Appendix D) provide another measure of extinction rates, but one which is dependent on group composition. Rates in flies and fungi – the groups which have been incompletely assessed - are outliers. There is no significant difference in the slopes of the graph in the 19th Century and 1900–1949 time-frames ($p = 0.15$, excluding outliers). The slope of the graph for 1800–1899 is significantly higher than for 1900–1999 ($p < 0.05$, excluding outliers), which probably reflects bias against declaring extinctions in very recent decades.

Four independent time-frames capture most of the recorded extinctions, and these also suggest a stable or rising rate for all species combined (Fig. 2b). We find 952 species to be endangered, an unknown fraction of which are already extinct (Fig. 2a). We therefore do not concur with Natural England (2010) who, extrapolating from South East England, reported losses of invertebrates have "apparently" declined after 1910: such appearance is probably due to reporting bias. The number of reported extinctions per decade is plotted (Appendix E) for the 340 species which can be assigned a likely decade of extinction. This figure illustrates the problems of considering short time-intervals, with evidently poor data for the early 1800s, the World War II years (1940s) and for recent decades.

Recorded extinction rates for most groups are within our previously estimated overall range of 1–5% per century since 1900. Plots of extinctions versus group size in various time-frames (Appendix D) confirm there is remarkable consistency in extinction rates between these groups in Britain, with rate being highly correlated with group size (excluding flies and fungi). We give linear regressions for the 19th Century ($R^2 = 0.86$, $p \ll 0.0001$), 20th Century ($R^2 = 0.33$, $p < 0.001$, and 1900–1949 ($R^2 = 0.33$, $p < 0.001$) time-frames.

The number of endangered species in a group is also very highly correlated with group size (Appendix D, $R^2 = 0.93$, $p \ll 0.0001$), suggesting highly consistent rates of endangerment and projected future extinctions in these groups. The 19th Century extinction rate for a group is very highly correlated ($R^2 = 0.79$, $p \ll 0.0001$) with the number of endangered species in the group (Appendix D). The projected extinction rates underestimate extinctions amongst species not yet considered endangered. They also assume the endangered species go extinct within this century. Some endangered species will transpire to be 20th Century extinctions, but if endangered status is used accurately, the projections suggest rates will rise without increased conservation efforts.

The similarity in rates in several time-frames suggests recording biases against early extinctions of specialists in some groups are not as problematic as Thomas and Clarke (2004) argue. Shaw's (2005) method explicitly avoids such bias by using groups well known in 1850–1949, and generally gives rates close to ours for those large groups which both studies consider (birds and plants, Appendix C). Using a similar method for 1850–1949, we find broadly similar patterns to other time-frames (Appendix C) and this is also true for the 1850–1899 time-frame. Imperfect base-line recording (especially of rare and vulnerable specialist species) is probably an insurmountable problem in precise assessment of past and present extinction rates in other regions and globally, for almost all groups of organism. There is a risk of overlooking former breeders due to shifting baselines. For example, the Atlantic sturgeon (*Acipenser sturio*) might have been breeding, feeding or vagrant in British rivers, and assuming breeding substantially increases the extinction rate for British fish.

Under-recording of extinctions is evident from comparison with previous data on flies and moths (Hambler and Speight, 1996). Improved data have brought extinction rates for the well-recorded families of these groups near or within the range of 1–5% per century. Considering species listed as "Endangered" but probably extinct in relatively well-recorded fly families, we estimate 20th Century extinction rates for tipulid flies at 3% (c. 10 of 300 species), tabanid flies at 3% (1 of 30 species), and hoverflies at 0.4% (1 of 250 species). A high ratio of endangered to extinct flies suggests many flies listed as "Endangered" in reviews may now be extinct. Low rates in most flies and fungi are not reliable on current evidence. With the exception of molluscs, groups with no recorded extinctions (Appendices A and C) are either small, or less-well recorded (e.g. Homoptera).

It is very unlikely that in Britain many hundreds of species are going extinct per century without being noticed, even amongst the flies, wasps, beetles and fungi. Our estimated upper limits for the 20th Century often do not greatly exceed 5% per century (Appendix C). High numbers of poorly-known species may explain the high projected extinction rates in lichens and micro-moths. The high British extinction rate for butterflies is not a recording artefact (as Thomas et al., 2004 suggest), being above our upper limit of extinction rates for many groups in the 20th and the 21st Centuries.

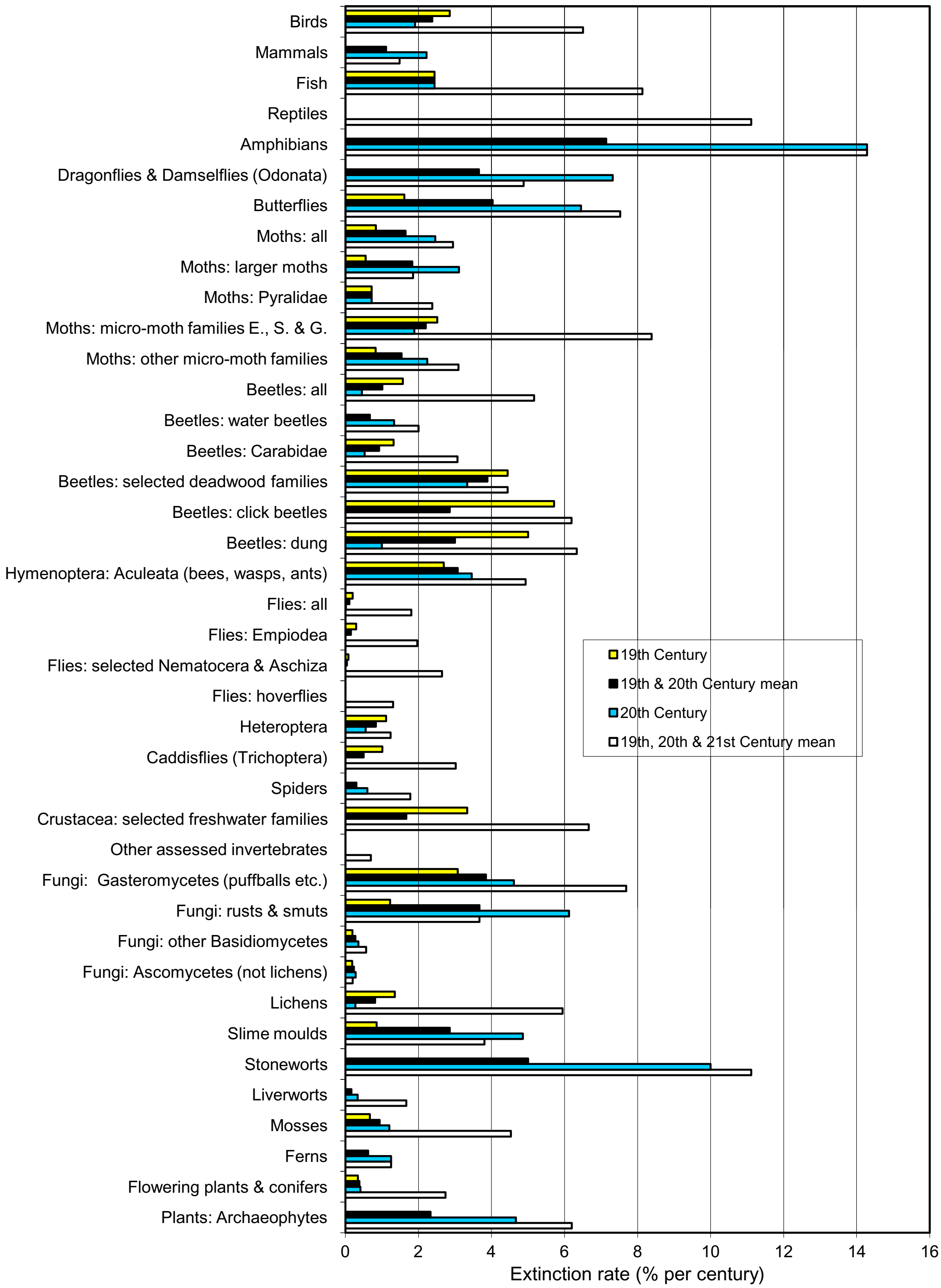

Fig. 1. Recorded and projected extinction rates in Britain, by group. Rates expressed as a percentage of the resident species in the group becoming regionally extinct per century, in four non-independent time-frames. Composition of groups as in Appendix B.

Low extinction rates are probably reliable in some groups with active recording protocols. Whilst previous estimates of plant extinction rates have included Archaeophytes (Hambler and Speight, 1996), *native* flowering plants were found here to have relatively low rates. Spiders also have a low extinction rate (maximum 4 of 620 species = 0.6% since 1900). It might be relevant that spiders often occur in more than one habitat type (such as grassland and heathland) provided the microclimate and architecture is suitable, and that temperate regions are not marginal for a high fraction of the many species in the family Linyphiidae. The apparent lack of extinctions amongst molluscs is notable. Asexual reproduction and dormancy might reduce extinction risk in some plants and molluscs, if they can survive isolation and temporary disturbance of habitats.

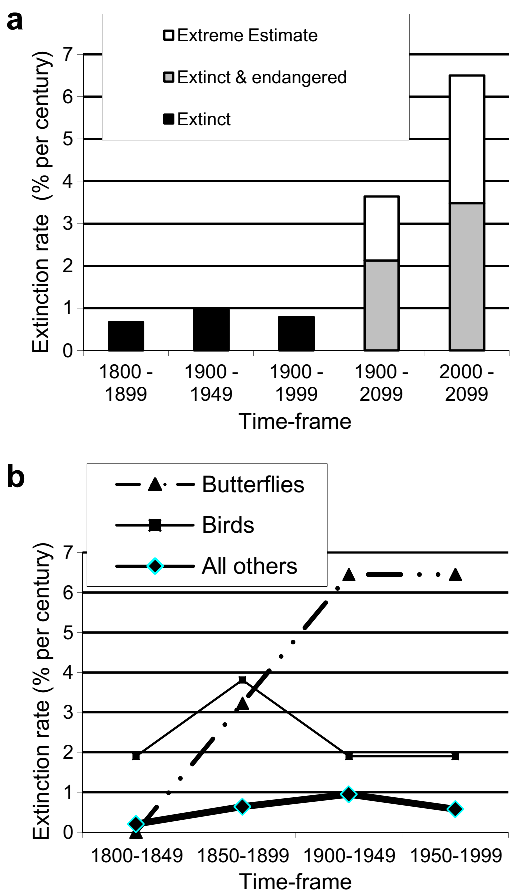

Fig. 2. British extinction rates since 1800. (a) Mean extinction rates for all assessed species in Britain. High estimate includes possibly endangered species such as "Data Deficient" species. 1900–1949 data are a subset of the 1900–1999 data, with a higher confidence of extinction. (b) Comparison of recorded British extinction rates in birds, butterflies and all other taxa. (Rates without birds, or without butterflies, are indistinguishable on this scale.)

3.2. Comparison of Britain with larger scales

Rates for well-recorded groups in Britain are generally at least an order of magnitude higher than for the same well-recorded groups of organism globally, and are higher in all cases than in the USA (Table 1). This may reflect the effects of isolation, small island populations and climatic range margins in Britain.

Vascular plants have relatively low recorded extinction rates on all scales (although the global rates are probably seriously underrecorded). Low recent extinction rates are also apparent in the reptiles on all scales; this taxon may have been relatively robust to forest and wetland loss, but now faces threats to drier habitats.

Butterflies have atypically high extinction rates in Britain (Fig. 1) and Scotland (Shaw, 2005), yet negligible rates of recorded extinction in Europe (Van Swaay and Warren, 1999) on the continental USA and globally (where range margins are not an issue). Only four species of butterflies are listed as globally extinct by IUCN (2010). Very low global rates of extinction and endangerment may reflect lack of recording effort and the substantial methodological challenges of recording butterflies (Fleishman and Murphy, 2009) but may also reflect the number of warmth-dependent butterfly species which benefit from habitat degradation such as anthropogenic canopy loss and grazing (Hambler, 2004).

Dung beetles have apparently declining rates of extinction in Britain, unlike most taxa, which may reflect the early loss of large mammals. Globally dung beetles have low recorded rates, with no recorded extinctions (IUCN, 2010) and this group is relatively well known (ScarabNet, 2010).

3.3. Habitats used by extinct species, and causes of extinction, in Britain

At least one habitat type was evident for 381 of the 437 species (Appendix A). The proportions of extinct (including probably extinct) species in Britain which were known to use particular habitats are given for selected groups in Fig. 3. It is not possible to compare extinction rates per species or per unit area in these habitats, due to the lack of data on species richness and area of each habitat.

In Britain, woodland, dead wood, wetland and short-grassland habitats had the most extinctions. Woodland was used by about 40% of species which have become extinct since 1800, of which about 40% needed mature trees and dead timber. 40% is significantly higher than expected if extinctions were randomly distributed in Britain, of which about 10% is wooded ($p < 0.001$, χ^2, 1 d.f.), and may reflect a combination of a high total species number in woodland, loss of area and degradation.

The most extinction-prone habitat varies substantially between groups. This would be expected in part because the groups included here have different specialisms (such as aquatic life stages). Some groups such as aculeate Hymenoptera, butterflies and Archaeophytes (which are often arable weeds) have high proportions of species requiring warm early successional microclimates in the north of their global range, and some insects have declined rapidly through succession after myxomatosis reduced grazing by feral rabbits (*Oryctolagus cunninculus*) in Britain (Thomas and Morris, 1994).

Low extinction rates have been recorded for most exclusively freshwater aquatic groups in Britain in the 19th Century (such as caddisflies, water beetles and stoneflies). However, aquatic species occur in many other groups, and in general are currently highly threatened (comprising about 35% of the invertebrate species in the RDBs, Hambler and Speight, 1995). In freshwater in Britain, fish, amphibians and stoneworts (charophytes) have higher 20th Century and/or projected rates than many other groups, possibly reflecting their low numbers of species.

Information for the Holocene as a whole is less reliable. However, patterns in the taxa with the best subfossil and/or historical evidence (mammals and birds, Fig. 3) also show substantial proportions lost from woodland and wetland. At least four woodland birds and at least nine wetland birds have probably been lost between 200 and 10,000 years ago. About a third of the c. 120 known Holocene beetle extinctions were dead wood species, about a half were woodland species and about a fifth used wetlands.

The broad consistency in the ranking of rates of extinction and endangerment in a variety of higher taxa in Britain would be expected only if loss of habitat area and quality is the principal driving agent of extinctions, acting through the Species-Area relationship (May et al., 1995). It is less parsimonious to ascribe such similar rates to co-incidence (with hunting, pollution or climate shifts influencing groups differently). However, the sources for our extinction list suggest that for mammals and birds, persecution and/or hunting have been major influences during the Holocene. These factors contributed to about 30% of bird extinctions after 1800, but did not cause extinctions of mammals after 1800. After 1800 some groups (Fig. 1) experienced relatively high early losses (e.g. some beetle families) and others have high rates somewhat later (e.g. butterflies), possibly reflecting habitats such as dead wood and short grassland being lost at different rates in different time-frames.

Table 1
Recorded extinction rates. Average percent per century of a group becoming extinct in specified time-frames. Numbers in brackets are number of species used in the calculation for the region. Rates for the USA include Hawaii. Upper global rates include possibly extinct species. Insufficient data denoted by "?". Sources in Appendix B.

Group of organism	Global		Britain			Scotland	USA including Hawaii
	1500–2008	1800–1999	1600–1999	1800–1999	1900–1999	1850–1949	1800–2005
Birds	0.3% (138–153 of 9990)	0.3–0.5% (69–103 of 9946)	1.4–2.0 (12–17 of c. 21)	2.4–3.3% (10–14 of 210)	1.9–2.9% (4–6 of 210)	0.9% (2 of 230)	1.3–1.9% (20–29 of 783)
Mammals	0.3–0.4% (78–107 of 5488)	0.5% (48 of 4630)	1.1 (2–3 of 45 or 46)	1.1% (1 of 45 or 46)	2.2% (1 of 45 or 46)	3.2% (1 of 31)	0.1–0.2% (1–2 of 421)
Reptiles	0.05% (22 of 8734)	0.1% (14 of 7400)	0% (0 of 6)	0% (0 of 6)	0% (0 of 6)	0% (0 of 3)	0% (0 of 295)
Amphibia	0.1–0.5% (39–159 of 6347)	0.04–1% (5- c. 122 of c. 5750)	3.6–6.3% (1–2 of 7 or 8)	7.1–12.5% (1–2 of 7 or 8)	14.3–25% (1–2 of 7 or 8)	0% (0 of 6)	0.2–0.4% (1–2 of 258)
Freshwater fish	0.1–0.4%[a] (70–172 of c. 12,000)	0.3–0.7% (70–172 of c. 12,000)	1.2–1.8% (2–3 of c. 41)	2.4–3.7% (2–3 of 41)	2.4% (2 of 41)	?	1.0–1.3% (16–20 of 798) 2.6%[c] (61 of 1187[c])
Vascular plants	0.04–0.07%[a] (380–750 of >270,000[a])	?	0.2% (14 of c. 1530)	0.5% (14 of 1530 or[b] 16 of c. 1800)	1.3% (19 of 1530, or[b] 23 of c. 1800)	1.8% (18 of 987)	0.03–0.4% (10–143 of 16,230)
Butterflies	?	0.01–0.03% (4–11 of c. 17,500)	?	4.0% (5 of 62)	6.5% (4 of 62)	12.8–15.4% (5–6 of 39)	0%[d] (0 of 621[d])
Dragonflies and Damselfies (Odonata)	?	0.02–0.5% (2–58 of 5680)	?	3.7% (3 of 41)	7.3% (3 of 41)	0% (0 of 21)	0–0.4% (0–4 of 465)
Mayflies and stoneflies	?	?	?	0.6% (0–1 of 80)	1.2% (0–1 of 80)	?	0.2–1.1% (4–26 of 1186)
Dung beetles (Scarabaeinae)	?	0% (0–1 of c. 6000)	?	3% (6 of 100)	1% (1 of 100)	?	?

[a] 1600–2006.
[b] Includes *Hieracium* "species".
[c] Continental North America.
[d] Excludes disputed *Xerces* species/subspecies.

It is also apparent from species' accounts in the taxon reviews (Appendix B) that the majority of British extinctions are due to habitat loss (including degradation), with threats (such as removal of dead wood, or loss of wetland) often stated. The same conclusion is reached by Natural England (2010). Between 1945 and 1984 Britain suffered loss or damage to 30–50% of its "ancient" woodland, 80% of its lowland calcareous grasslands, 50% of its fens and 94% of its lowland raised bogs (NCC, 1984). Such loss of area has not yet translated into *recorded* extinctions in many taxa, but may have generated extinctions and an extinction debt. For some taxa (such as some lichens and some freshwater species including charophytes) pollution is reported as relevant.

Some natural extinctions and turnover will be expected, particularly for species on the northern margin of their range. Possible examples include *Stictopleurus* spp. bugs and *Ampedus* spp. bees, some moths, and Savi's warbler (*Locustella luscinioides*). Loss and subsequent recolonisation by a species is recorded as extinction, and therefore well recorded and mobile species such as birds will potentially have over-estimation of extinctions. Few if any of the reported extinctions of birds in Britain can be attributed to climate shifts, with the possible exception of snowy owl (*Bubo scandiacus*) on its southern margin. Species with possibly or definitely artificially extended northern limits (such as the large blue butterfly *Phengaris arion* and several Archaeophytes which were arable weeds) have become extinct partly as a result of land-use change and modern cultivation methods. If habitat loss is the principal driver, then presently under-recorded species-rich taxa (such as nematodes, mites or parasitic hymenoptera, Shaw and Hochberg, 2001) may well have extinction rates within the typical range of 1–5%.

3.4. Indicator groups

The typical habitat requirements of higher taxa doubtless vary substantially in resource type, level and scale. No single group will be able to capture all the features of interest in biodiversity loss in all groups, and no single group should be relied on for monitoring (Hambler, 2004). However, a calibrated indicator could save substantial survey and monitoring effort, with essential caveats. Our results provide such a calibration.

We find the group which best satisfies the requirements of an indicator of overall extinction rates is the birds. For this group, the data for the period post 1800 have relatively little uncertainty at all geographical scales, because breeding birds are relatively easy to detect (although still presenting challenges, Elphick et al., 2010). Birds show potential to monitor extinction rates on Scottish, British, USA and global scales; on large scales the extinction rate of birds can be compared with few other taxa, but is not extremely high or low (Table 1).

In Britain birds have extinction rates similar to most other well-recorded taxa, lying very close to trend lines in regressions of group size against recorded extinction (Appendix D). Their 20th Century rate (c. 2%) is roughly in the middle of the range of 1–5% in which many other taxa of diverse life-forms fall (Fig. 1). The mean rate for British birds since 1800 is relatively stable, as is

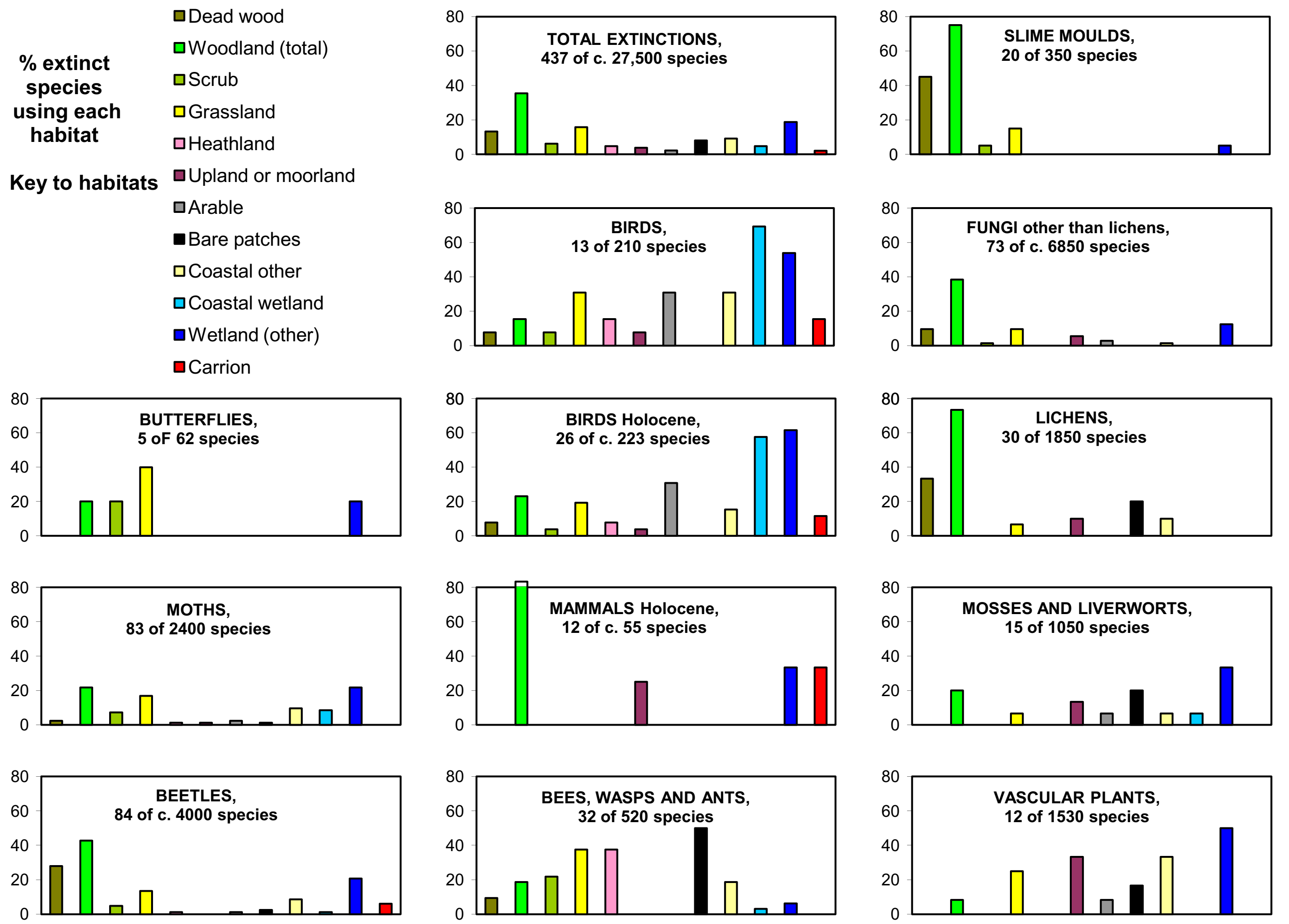

Fig. 3. Habitats used by species which have become extinct in Britain. Percentage of the extinct and probably extinct species known to use particular habitats within Britain. Data in Appendix A.

the mean for all 27 500 species (Figs. 1 and 2b). Large taxa (or groups of taxa) such as birds are less likely to exhibit the (possibly stochastic) volatility in apparent extinction rates in 50- or 100-year intervals evident in groups with very small numbers of species (such as other British vertebrates and butterflies).

No single taxon can be used to predict all the habitats in which extinctions are occurring in Britain, nor does any taxon have extinctions in the same proportions as the total extinctions in each habitat type. Birds, beetles and moths have each been lost from almost the full range of the habitat types we include. For most taxa in Fig. 3 (excluding Holocene birds and mammals), the distribution of extinctions across habitat types differs significantly from the distribution of all other extinctions ($p < 0.05$, χ^2, 11 d.f.). For moths, butterflies and bryophytes, distributions of extinctions are not significantly different to those of all other taxa (which in the latter two groups probably reflects low numbers of extinctions). For moths, larger moths, beetles and fungi, extinctions in a habitat are correlated with the extinctions from all other taxa in that habitat (all $p < 0.05$, Appendix F); in Britain, these large groups could in theory be used to predict some of the habitats with high total numbers of extinctions.

However, indicators must not only be representative, but must be tractable in terms of sampling, identification and knowledge of habitat specialism. For most regions, groups such as moths, larger moths, beetles and fungi are not viable indicators of extinction-prone habitats. The birds are the only group which, in Britain at least, could indicate the wide spread of habitat types from which extinctions are occurring, although (at current rates) they could not indicate the habitats with most extinctions. Birds have been lost from habitats in Britain known to be highly threatened regionally and globally, such as wetland and mature forest, although birds do not highlight the very small patches of bare earth needed by some invertebrate and other species. About 90% of the birds extinct in Britain since 1800 used wetlands of some type, and about 20% used woodland, but several (being high in trophic pyramids) were habitat generalists. All of Britain's 12 "Critically Endangered" birds (Eaton et al., 2005) require wetland (58%) or woodland (42%), and these habitats host many other threatened species (Hambler and Speight, 1995, 1996).

Freshwater fish and amphibians also show some potential for monitoring rates on scales using large numbers of species, but require more calibration against other taxa. Globally, freshwater fish appear to have similar rates to vertebrates other than reptiles, and in Britain rates are typical of other groups. In the USA, rates of extinction and imperilment for fish and amphibians are similar to those for freshwater insects and shrimps, but much lower than those for mussels and crayfish (Wilcove and Master, 2005).

Butterflies are not indicators of extinction rates, having extremely high or extremely low rates on different geographical scales (Table 1) and time-frames (Fig. 2b). On all scales, the very few extinct species were lost from a very narrow range of habitats; for example, in Britain they do not (and could not) represent the important mature forest and dead wood habitat.

Birds, fish, amphibians (and other easily monitored groups) should be further calibrated against other groups in other regions. If similar results are obtained, then global losses of these vertebrates can be used with relatively high confidence to indicate progress towards conservation targets.

4. Conclusions

There is still no reason to believe terrestrial and freshwater invertebrate extinction rates are substantially different from those for vertebrates. Extinctions of birds, freshwater fish and amphibians in a region suggest numerous other species in the same habitats are being lost. For every bird species lost from Britain since 1800 at least 35 species from other taxa have been lost. Continuing high levels of global endangerment and extinction in birds (Butchart et al., 2010) provide further evidence that the global 2010 target for a significant reduction in the rate of loss of biodiversity has not been met. Monitoring of birds alone (whilst far from ideal) would have detected an extinction risk in a wide range of nonmarine habitat types in Britain. If such results are found to be more general, it will considerably aid monitoring in regions with very poor inventories of invertebrates, fungi and other groups.

Many British species were listed as "Endangered" in recent reviews (and despite recent conservation initiatives such as Biodiversity Action Plans). There are roughly 30 regionally endangered birds in Britain (Eaton et al., 2005). We therefore argue it is very likely that extinction rates in Britain will rise this century without greatly increased conservation effort (including restoration of woodlands and wetlands). The continuing loss of ancient habitat and slow recovery of other habitat will drive further extinctions.

In a large data set of this type, it is inevitable there are errors from a range of sources, as described in Appendix B. We believe our errors will not be seriously biased with respect to taxa or time interval, or obscure or generate strong general patterns. Based on the many difficulties encountered, we suggest improved reporting methods (Appendix B) which would make more of the data easily available, minimise variation in methods and permit a more rapid re-calculation of extinction rates. In particular, we encourage use of a 'Possibly Extinct' tag in all lists of threatened and extinct species (Butchart et al., 2006; Roberts, 2006; Vié et al., 2009). This would facilitate rapid searching for the most endangered species, and would permit greater sensitivity in comparing rates in different time-frames, taxa and habitats.

Given that data quality is likely to remain low for many taxa indefinitely, it is unrealistic to seek direct measurements of rapid changes in overall rates of extinction for use in short-term policy targets. We suggest an approach focussing on habitat degradation and the Species-Area relationship (May et al., 1995) will be required as a surrogate for species loss. However, it is likely that changes in extinction rates detectable using some well-recorded taxa will help reveal the wider results of conservation efforts.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.09.004.

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