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Supporting Online Material

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Materials and Methods

Fig. S1

Table S1

References

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Comparative Losses of British Butterflies, Birds, and Plants and the Global Extinction Crisis

J. A. Thomas,^{1*} M. G. Telfer,^{2†} D. B. Roy,² C. D. Preston,²
J. J. D. Greenwood,³ J. Asher,⁴ R. Fox,⁴
R. T. Clarke,¹ J. H. Lawton⁵

There is growing concern about increased population, regional, and global extinctions of species. A key question is whether extinction rates for one group of organisms are representative of other taxa. We present a comparison at the national scale of population and regional extinctions of birds, butterflies, and vascular plants from Britain in recent decades. Butterflies experienced the greatest net losses, disappearing on average from 13% of their previously occupied 10-kilometer squares. If insects elsewhere in the world are similarly sensitive, the known global extinction rates of vertebrate and plant species have an unrecorded parallel among the invertebrates, strengthening the hypothesis that the natural world is experiencing the sixth major extinction event in its history.

Large-scale attempts to quantify recent losses of biodiversity are hindered by inconsistencies in the quality of data available for different taxa (1–3). For example, reported rates of global and national extinction in insect species are typically two orders of magnitude lower than those

recorded for birds, large mammals, and certain fish, plant, and snail groups (1, 2). This difference might be merely an artifact of undersampling of the known insect species, exacerbated by the probability that a disproportionate number of the most acutely threatened insects belong to the majority (estimated at 90% globally) of species that have yet to be described (2, 4–6). Models that account for sampling effort do indeed generate more even extinction rates across taxa (6), although others conclude that the available data are inadequate for any comparisons to be made (7). Whatever the validity of these predictions, the assumption that mammals and birds serve as indicator groups for wider species losses remains untested (1, 2, 6, 8, 9). Furthermore, the problem of underrecording of invertebrates is amplified by recent recommendations that biologists focus on population extinctions, albeit at less-than-global scales, as more sensitive measures of decline than species extinctions (8–10).

The repetition of comprehensive surveys of plants, birds, and butterflies over the past 20 to 40 years in Britain generated six very large data sets that allow accurate comparisons (11) of the fate of these three groups at a large (228,073 km²) spatial scale. With colleagues, we organized two surveys of the distributions in Britain of all 1254 native species of vascular plant in 1954 to 1960 (12) and 1987 to 1999 (13); of all 201 native breeding bird species in 1968 to 1972 (14) and 1988 to 1991 (15); and of all 58 native breeding butterfly species in 1970 to 1982 (16) and 1995 to 1999 (17). Each survey achieved 98 to 100% cover of the 2861 10-km (10 km by 10 km) grid squares of England, Wales, and Scotland; in total, >20,000 volunteer recorders submitted >15 million records of species during the six surveys (11), providing the most comprehensive data sets in the world of changing status for each taxon (2, 18).

For every species, change in status was measured as the difference in the total number of 10-km grid squares occupied in each census period [the second butterfly data set being subsampled to equalize recorder effort (11)]. We then ranked species by the percentage change (from the first survey) in their occupancy of squares (Fig. 1). Although this coarse-grained sampling may underemphasize more local changes in status (19), we have previously shown that range changes expressed at this scale are closely correlated with trends in the mean size of individual populations of butterfly (20) and bird (21) species across Britain. Range changes (Fig. 1) are thus a surrogate for abundance, making each survey effectively a population census.

We found (Fig. 1A) that 28% of native plant species have decreased in Britain over the past 40 years, that 54% of native bird species have decreased over 20 years, and

¹Natural Environment Research Council (NERC) Centre for Ecology and Hydrology, Dorset Laboratory, Winfrith Technology Centre, Dorchester DT2 8ZD, UK. ²NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK. ³British Trust for Ornithology, Thetford, Norfolk IP2 2PU, UK. ⁴Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP, UK. ⁵NERC, Polaris House, North Star Avenue, Swindon SN21EU, UK and Centre for Population Biology, Imperial College, Silwood Park, Ascot SL5 7PY, UK.

*To whom correspondence should be addressed. E-mail: jat@ceh.ac.uk

†Present address: Royal Society for the Protection of Birds, The Lodge, Sandy Heath Quarry, Bedfordshire SG19 2DL, UK.

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that a majority of butterfly species (71% over ~20 years) has declined. Across the spectrum of changing distributions (Fig. 1B), butterflies have also fared worse than birds or plants: Two (3.4%) butterfly species became extinct in Britain between censuses compared with six (0.4%) native vascular plants over 70 years and no breeding bird species, and the most rapidly declining 10% of butterfly species experienced a $\geq 49\%$ net loss in their occupancy of 10-km squares compared to birds ($\geq 29\%$) and plants ($\geq 22\%$). Similarly, the most rapidly increasing 10% of butterfly species showed net increases of only 21 to 164% in 10-km square occupancy compared to native birds (141 to 2900%) and plants (59 to 2583%). Population extinctions were recorded in all the main ecosystems of Britain, and were distributed with remarkable evenness across the nation, rather than concentrated in a few degraded regions (fig. S1).

The greater loss among British butterfly species may foreshadow similar declines in birds and plants, because insect populations typically respond more rapidly to adverse environmental change than longer-lived organisms or those with dormant propagules (22). On the other hand, we found even greater disparities over longer periods in smaller areas—single sites, the English county of Suffolk (3838 km²), and the Netherlands (33,238 km²)—where the proportions of res-

ident butterfly species that became locally extinct over 100 to 150 years exceeded those of plants and vertebrates by one to two orders of magnitude (3). Comparatively crude assessments of other British insects (aculeate Hymenoptera, other Lepidoptera, some Diptera) suggest rates of decline similar to that of butterflies (3, 23), supporting the use of butterflies as realistic, as well as practical, indicators of change (2, 6, 24, 25). Beyond Europe, invertebrate declines may be seriously underestimated compared to declines among plants and vertebrates, owing to artefacts from low sampling levels (6), and at present even the more comprehensive attempts provide a mixed picture. Thus, large higher-trophic animals are reported as being more sensitive to human perturbation than are invertebrates in <10,000-ha study areas of Amazonian rainforest, yet in Brazil's heavily degraded Atlantic rainforests, the reported extinction of butterfly species (four) marginally outnumbered that of vertebrates (two parrots) (24). In the United States, Species Reports Cards suggest that certain invertebrate groups (butterflies, Tiger beetles, dragonflies) have experienced fewer national extinctions than vertebrates in recent years, although a higher proportion of the former's known species are listed as "at risk"; on the other hand, freshwater inver-

tebrates (mussels, crayfish) have much the highest recorded extinction rates among all listed taxa (25). The extinction of marine invertebrate species may also have been grossly underrecorded worldwide (26).

Despite the low diversity of Britain's biota, we suspect that the relative changes reported here are not atypical. Certainly, the main drivers of change in British plant, bird, and butterfly populations (13, 14, 20) are the same processes responsible for species' declines worldwide (27, 28). Their impacts in Britain were perhaps muted during our inter-census period because (i) the major clearances of primary vegetation occurred in an earlier age, leaving degradation and fragmentation as the main adverse habitat changes (and the main driver of population extinctions in Britain); (ii) climate warming, to date, has enhanced the net capacity of British ecosystems to support butterfly and perhaps plant and bird species (20, 29); (iii) few exotics have colonized British ecosystems with the damaging impacts found in many less robust communities elsewhere [we found that 0, 6, and 48%, respectively, of established butterfly, bird, and plant species are aliens, despite a history in Britain of frequent introductions during the past 100, 200 (15), and 2000 (13) years, with very few alien plants dominant in ecosystems]; and (iv) targeted conservation measures, including regulation of collecting

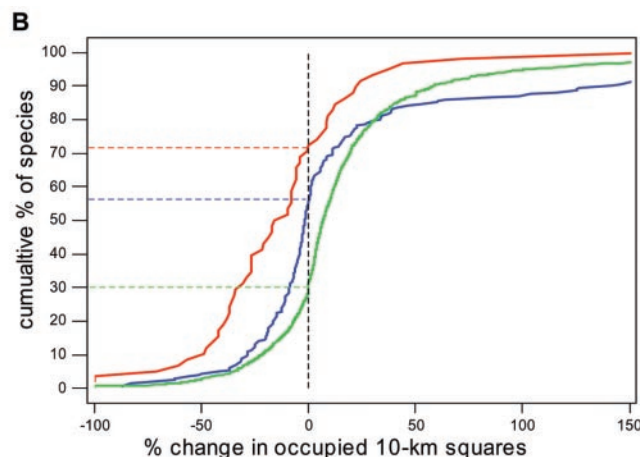
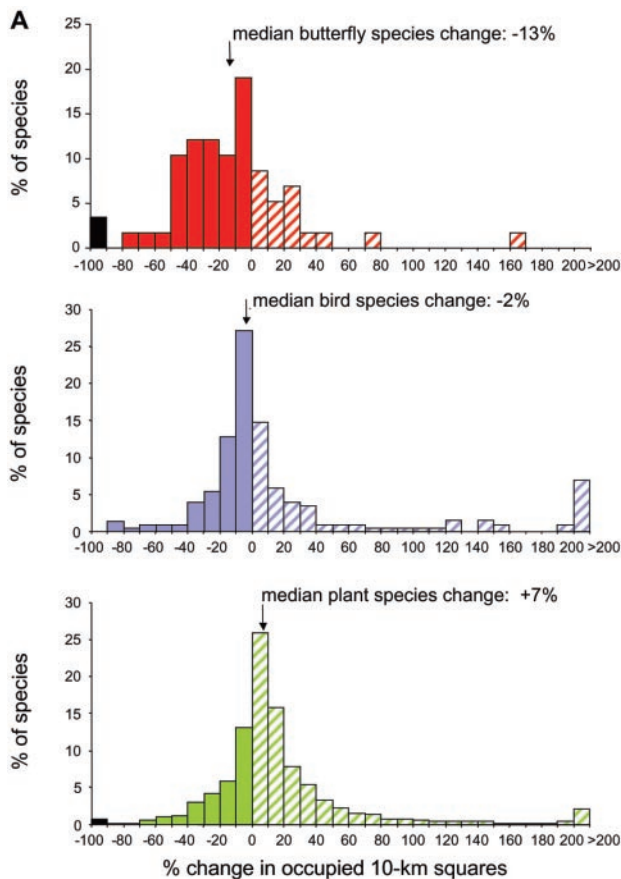


Fig. 1. Changes in the number of 10-km (10 km by 10 km) squares in Britain occupied by native butterfly, bird, and plant species between the two censuses of each taxon. **(A)** Frequency distributions: median butterfly species (red, $n = 58$) < median bird species (blue, $n = 201$, $P < 0.001$) < median plant native species (green, $n = 1253$, $P < 0.001$). Black, extinct species; solid color, declining species; hatched color, increasing species. **(B)** Cumulative frequency distributions [butterfly declines (red) > bird declines (blue) > plant declines (green); Kolmogorov-Smirnov tests, $P < 0.001$].

and hunting, have reversed the former declines of several species. Nevertheless, exactly one-third of all the species we surveyed had declined, which is more than 50% greater than the proportion of mammal species estimated to have declined in a century across six subsets of continents (8). That this scale of population extinctions has yet to translate into species' extinctions (8) is explained by the fact that Britain contains few declining species that are not widespread across Europe or indeed the Palearctic or Holarctic. In contrast, the Hawaiian islands, with a land area just 7% that of Britain, contain a comparable number of insect, plant, and land bird species to that of Britain (about 10,000, 1100, and 135, respectively), but 89 to 100% of them are endemics. Cookie-cutter models, in which endemic-species packing is a key parameter, explain well the observed geographical variation in bird species' extinctions in response to environmental change across this whole spectrum from biodiversity hot-spots to cold-spots (1). However, birds are imperfect model organisms because they represent just 0.6% of the world's described species; no equivalent global data exist for insect extinctions (54% of described species).

Our data sets may also be unrepresentative of the wider world. Nevertheless, the important result here (Fig. 1) is that the only insect taxon to have been rigorously compared with plants or birds at this temporal or spatial scale experienced at least as many regional extinctions when exposed to the same range of environmental changes that afflict plants and vertebrates worldwide (27, 28). If insects elsewhere are similarly sensitive, we tentatively agree with the suggestion (6) that the known global

extinction rates of vertebrate and plant species may have an unrecorded parallel among the insects, strengthening the hypothesis (1, 2, 4), derived from plant, vertebrate, and certain mollusk declines, that the biological world is approaching the sixth major extinction event in its history.

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