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Unpacking the extinction crisis: rates, patterns and causes of recent extinctions in plants and animals

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Biodiversity loss is one of the greatest challenges facing Earth today. The most direct information on species losses comes from recent extinctions. However, our understanding of these recent, human-related extinctions is incomplete across life, especially their causes and their rates and patterns among clades, across habitats and over time. Furthermore, prominent studies have extrapolated from these extinctions to suggest a current mass extinction event. Such extrapolations assume that recent extinctions predict current extinction risk and are homogeneous among groups, over time and among environments. Here, we analyse rates and patterns of recent extinctions (last 500 years). Surprisingly, past extinctions did not strongly predict current risk among groups. Extinctions varied strongly among groups, and were most frequent among molluscs and some tetrapods, and relatively rare in plants and arthropods. Extinction rates have increased over the last five centuries, but generally declined in the last 100 years. Recent extinctions were predominantly on islands, whereas the majority of non-island extinctions were in freshwater. Island extinctions were most frequently related to invasive species, but habitat loss was the most important cause (and current threat) in continental regions. Overall, we identify the major patterns in recent extinctions but caution against extrapolating them into the future.

1. Introduction

Biodiversity loss is one of the greatest challenges facing the Earth today [1]. Recent human activities have led to the extinction of hundreds of species of plants and animals [2,3]. However, these recent extinctions remain incompletely studied across living organisms, especially in terms of their causes and their patterns among clades, across habitats and over time. For example, which taxonomic groups and habitats have experienced the most extinctions? Are extinction rates accelerating or decelerating, and how might these rates vary over timescales and among groups? What are the most important causes of recent extinctions, and how do these causes vary among clades, among habitats and over time?

Some prominent studies have suggested that Earth is now experiencing a mass extinction event comparable to those in the fossil record ([4–6], but see [7]). This claim often involves extrapolating extinctions from the past 500 years into the future. We think that a fundamental question has gone largely unaddressed: are these recent human-related extinctions relevant to current and future threats to biodiversity?

Extrapolating from recent extinctions to make conclusions about future biodiversity loss hinges on several assumptions. First, past extinctions should predict current extinction risk among taxonomic groups. Thus, groups with a high frequency of past extinctions should have a high frequency of endangered and threatened species. Second, variation in extinction frequencies and species richness among groups must be considered. It would be problematic to extrapolate extinctions from tetrapods [4,5] or land snails [6,8] across all organisms without establishing that their extinction frequencies also apply to the largest groups (e.g. arthropods, plants). Third, extinctions may depend on where species occur. If past extinctions occurred mostly on islands or in freshwater, then it could be problematic to extrapolate past rates to predict future extinction in terrestrial, mainland species. Fourth, extrapolating past rates into the future requires understanding how past rates vary over time. For example, are extinction rates accelerating over time, as concluded by some authors [5]? Extrapolating past rates forward either requires homogeneous rates or explicit consideration of which time period's rates are being projected. Fifth, the causes of past extinctions should be related to the frequency of current threats. If most past extinctions were caused by one factor (e.g. invasive species) and most currently endangered species were threatened by another (e.g. habitat loss), then past extinctions might not predict future biodiversity loss.

Many important studies have analysed recent extinctions, but few have comprehensively examined these patterns and assumptions. To our knowledge, none examined all of them across living organisms. We give several examples. Ceballos *et al.* [5] examined cumulative species loss in vertebrates for each century over the past 500 years, but not extinction rates over time. McCauley *et al.* [9] suggested that there were more animal extinctions in terrestrial than marine environments and more extinctions in the last 100 years than in previous centuries. Fernández-Palacios *et al.* [10] showed that extinctions were more frequent on islands than on the mainland for many major groups [11–14]. Bellard *et al.* [15] concluded that invasive species were a major cause of vertebrate extinctions, whereas Caro *et al.* [16] concluded that climate change was not a major cause or current threat. Jaureguiberry *et al.* [17] examined causes of biodiversity loss, but not necessarily species extinctions. Christenhusz & Govaerts [18] analysed recent plant extinctions and found these occurred predominantly on islands. Some authors compared extinction rates among groups [2,5,13,19], but generally excluded global fishes, non-avian reptiles, arthropods, mosses, ferns and algae (among others). Thus, they were not comprehensive for animals or plants, and excluded the group containing approximately 77% of animal species (arthropods) and the majority of vertebrates (fishes, reptiles). These are merely examples. Nevertheless, they illustrate that a comprehensive analysis of rates, patterns and causes of recent extinctions across groups is lacking. These studies often used the International Union for the Conservation of Nature (IUCN; [20]) database, either with or without modification.

Here, we examine rates and patterns of recent extinctions across major groups of living organisms to test the five assumptions described above. Specifically, we use IUCN data on extinctions and threats to test if recent extinctions: (i) predict current threat levels among species within a group; (ii) are homogeneous among groups; (iii) are homogeneous across environments; (iv) are homogeneous over time; and (v) have causes that are homogeneous over time and concordant with current threats. More broadly, we examine the rates, patterns and causes of recent extinctions across major groups, possibly for the first time.

2. Material and methods

(a) Data assembly

We downloaded data on all listed plant, animal and fungi species from the IUCN Red List on 27 June 2024 (electronic supplementary material, dataset S1; all datasets available at: https://doi.org/10.6084/m9.figshare.28339850.v1). This included 163 022 assessed species. Throughout, we treat species listed as 'Extinct' and 'Extinct in the Wild' as extinct, totalling 989 species (electronic supplementary material, dataset S2). The IUCN provides assessments for all major macroscopic groups (plants, animals, fungi), but not every species in every group. IUCN strives to use standardized criteria for categorizing species [21]. Nevertheless, there is still some variability in how these criteria are applied. For example, among species listed as extinct, search efforts were mentioned for approximately 45% and the length of time each species was missing was mentioned for approximately 50% [22]. The IUCN database is imperfect, but it may still be the best database spanning macroscopic organisms.

Other authors have assembled a larger list of extinct seed plants [18] that includes additional extinct species listed by an online database, Plants of the World Online (POWO [23]). However, that database does not 'assess' species like IUCN, so it is unclear if species listed as 'not extinct' are actually extant or unassessed. Therefore, the data are not comparable to IUCN. We used IUCN as a (more-or-less) standardized database spanning all major groups (plants, animals, fungi). We also address how our conclusions might change by including these additional extinct plant species (see Discussion).

(b) Extinction versus extinction risk

We tested if the proportion of extinct species in a group (among those assessed) was related to the proportion of endangered, threatened and least concern species in that group. We first combined the endangered and critically endangered categories as 'endangered'. We also combined the endangered, critically endangered, vulnerable and near-threatened categories as 'threatened'. We preferred to lump near-threatened species (approx. 5%; electronic supplementary material, dataset S3) with threatened species (rather than 'least concern'). We performed analyses separately for phyla, classes and orders. We eliminated taxa with less than 10 assessed species, given that their proportions might be inaccurate due to limited sampling. We excluded fossil-only taxa and non-accepted species. Data for phyla, classes and orders are given in electronic supplementary material, datasets S3–S5.

We also examined the relationships between the proportion of species that were assessed (by IUCN) in each higher taxon (phyla, classes, orders) and the proportion that were extinct, endangered, threatened or least concern (as defined above). Some studies exclude groups that are incompletely assessed, but it is unclear if this completeness impacts the frequency of extinction or extinction risk. To determine the proportion of species assessed by IUCN, we obtained the number of described species for each group from the Catalogue of Life (CoL [24]) on 10 July 2024. Two classes and 21 orders were included by IUCN but not the CoL. These taxa were excluded from these analyses.

We primarily used standard linear regression in R v. 4.3.1 [25]. A phylogenetic correction is potentially problematic, since these proportions, extinctions and threat levels involve the last 500 years (after these species split), and therefore cannot be shared among species through common ancestry. Nevertheless, we also performed phylogenetic regression analyses. Those methods and results are given in electronic supplementary material, appendix S1. Data are given in electronic supplementary material, dataset S6, and trees in electronic supplementary material, dataset S7.

(c) Estimating extinctions among groups

For each major taxon, we estimated extinction frequencies as the proportion of species that have gone extinct in the last 500 years, either from among all species assessed by IUCN or from among all described, extant species (from the CoL [24]). We primarily focused on extinction among assessed species, and on extinction among kingdoms, animal and plant phyla, and selected higher taxa within animals and within vertebrates. However, estimates based only on assessed species may be biased (underestimated) if extinct species were preferentially assessed (see Discussion).

We considered plants to be the kingdom Plantae (or Archaeplastida), not a subgroup within plants (e.g. Embryophyta). Therefore, plants included Rhodophyta, following the IUCN [20] and CoL [24].

(d) Estimating extinctions over time

The exact year in which a species went extinct is rarely known. Therefore, we generally used the last occurrence date for each species [5]. Although these dates may pre-date the year of extinction, this bias will be shared across species. Furthermore, we analysed the data by the decades and centuries last seen, rather than exact years. Details of assigning species to dates are described in electronic supplementary material, appendix S2.

During this process, we identified 57 species that were recently rediscovered or reclassified as extant. We also found 17 species that were taxonomically invalid. All these excluded species are listed in electronic supplementary material, dataset S2. We also identified three species with older extinctions (pre-1500; *Hippopotamus lemerlei*, *H. madagascariensis, Collisella edmitchelli*), and excluded them. We were able to assign an approximate extinction year for 875 of the 912 valid, extinct species. The remaining 37 species were excluded from the analyses of extinction dates.

We graphed the number of extinctions per century from the 1500s to 1900s (n = 5) within and among major groups. We excluded the 2000s (only 25% elapsed). We regressed the century against the number of extinctions in each century to evaluate whether extinction rates are generally increasing or decreasing (using R).

Similarly, we graphed extinctions among decades from the 1800s to 2010s (n = 22). Extinctions were generally rare before the 1800s. We regressed decade against extinctions per decade, and from the 1900s to 2010s (n = 12), to test if rates are accelerating towards the present.

For these analyses, we did not modify extinction rates based on number of described species at each time period. We also tested the idea that extinctions are constrained by when species were described. We obtained description dates (electronic supplementary material, dataset S2) for each extinct species from the CoL (June 2025); for dates unavailable in the CoL, we used the Global Biodiversity Information Facility (GBIF; gbif.org). We used the date associated with the original species name, regardless of genus-level taxonomy. We found that 391 species went extinct after being described (mean = 63.4 years before), 224 were already extinct when described (mean = 102.9 years after) and 138 were described and last seen in the same decade (including only species with extinction dates in a particular decade). Thus, description dates did not appear to constrain when known species went extinct.

(e) Estimating extinctions among habitats

Within each group, we estimated the proportion of all extinctions that were in each habitat type (terrestrial, marine, freshwater). We then compared these proportions with the overall proportion of known species in each habitat. Habitat data were from IUCN. We performed chi-squared tests in R (two-sided) to evaluate whether extinctions among habitats differed significantly from expectations based on the richness of each group among habitats. Data on habitat-specific richness were obtained from large-scale analyses of animals [26] and plants [27]. We performed statistical tests only for groups with greater than eight species and with observed and expected frequencies differing by greater than or equal to 10%.

Some species occurred in multiple habitats and were counted as occurring partially in each habitat. Thus, a species living in both marine and freshwater habitats was counted as 0.5 species for each.

We also determined whether each extinct species was endemic to islands (i.e. no mainland populations), based on their IUCN account. We considered all land areas surrounded by water to be islands: we preferred not to bias our results by excluding continental islands. We also recorded the specific island groups where extinct species occurred.

We performed chi-squared tests to evaluate whether extinctions occurred disproportionately among island endemics, as suggested previously [10–14,18]. For most groups, the relative richness of island endemics versus continental species is unclear. Nevertheless, the general pattern is thought to be approximately 20% island and approximately 80% mainland [10,12–14], which we used here. We also compared frequencies of extinct freshwater species among island and non-island species using chi-squared tests.

(f) Estimating extinction causes

We analysed the hypothesized cause for each species' extinction. However, these hypothesized causes are often highly conjectural, with many contributing factors often listed for a single species.

We first used the threat classifications for each species from IUCN, which include the estimated causes of species extinctions (https://www.iucnredlist.org/resources/threat-classification-scheme). Threat classifications were downloaded from IUCN on 17 July 2024. Data were available for 565 extinct species.

We obtained causes for an additional 56 species. First, we searched the 'Assessment information in detail' and 'Threats in detail' sections of their IUCN web pages. We also reviewed citations from their IUCN listing and/or NatureServe Explorer page (https://explorer.natureserve.org/). Overall, we compiled extinction causes for 615 species (excluding six extant or invalid species).

We combined several threat categories, given our interest in the broadest categories of threats. Specifically, for 'habitat loss' we combined categories 1 (residential and commercial development), 2 (agriculture and aquaculture), 3 (energy production and mining), 4 (transportation and service corridors) and 7 (natural system modifications).

We then summarized these extinction causes by higher taxon, habitat and occurrence on island versus mainland. We also summarized them over time using the inferred extinction years. We regressed time period against the frequency of extinction causes for each time period to evaluate if the most frequent causes changed over time. Each extinction cause was relativized to the number of causes provided for each species (e.g. a species listed for both 'habitat loss' and 'invasive species' was scored as 0.5 for each). When counting causes among habitats, we treated species occurring in two or three habitats as 0.5 or 0.33 of a species for each habitat.

We then compiled current threats for endangered and critically endangered species (endangered hereafter), for comparison with extinction causes. IUCN-assigned threats were available for 26 169 of 28 040 endangered species (93%). Threat classifications were downloaded from IUCN on 4 September 2024. We then tested for significant differences in the relative frequencies of different extinction causes among extinct species and the proportion of different threats among endangered species, using chi-squared tests. We specifically focused on the most frequent extinction causes and threats.

(g) Incorporating potentially extinct species

There can be considerable uncertainty over whether species are extinct or not. Dozens of putatively extinct species have been rediscovered (e.g. 57 here; electronic supplementary material, dataset S2). Alternatively, many species unseen for decades are considered extant, but might be extinct. We performed analyses of species classified as 'possibly extinct' and compared these with our main results based on extinct species. This provided an alternative dataset for addressing the robustness of our results to the particular set of species currently classified as extinct by IUCN.

We first identified species listed by IUCN as 'possibly extinct' or 'possibly extinct in the wild'. Furthermore, eight additional species had verbal descriptions stating that they were assigned as 'possibly extinct'. These included gastropods (*Opisthostoma thersites*, *Pseudobithynia euboeensis*), fish (*Trichomycterus venulosus*), amphibians (*Atelopus sernai*, *Incilius peripatetes*, *Pristimantis albericoi*) and plants (*Viguiera media*, *Coffea charrieriana*). We did not consider subspecies.

We also recorded the year that these species were last seen and assigned these years to centuries and decades. We qualitatively examined patterns over time, among habitats, and on islands versus mainland to compare them with the extinct species. We also examined the hypothesized causes of extinction among these species.

3. Results

(a) Documenting extinctions

We identified 915 valid, extinct species (electronic supplementary material, dataset S2). We excluded three species inferred to have gone extinct long before 1500, and subsequent analyses were based on the remaining 912 (electronic supplementary material, dataset S2).

(b) Past extinctions do not strongly predict current extinction risk among groups

We tested for a relationship between the proportion of species in a phylum, class or order that were considered extinct and the proportion that were classified as endangered, threatened and least concern. We found no significant relationships for any variables for phyla and classes (n = 15 and n = 45; electronic supplementary material, table S1 and datasets S3–S4), but among orders (electronic supplementary material, dataset S5), there were weak relationships between the proportions of extinct species and endangered, threatened and least-concern species (n = 261; r^2 = 0.023–0.027; p = 0.008–0.016). Thus, past extinction levels within these major groups did not strongly predict current threat levels, and so may be unrelated to future extinctions. Results were similar using phylogenetic regression (electronic supplementary material, table S2).

We also examined the relationship between the proportion of species assessed (by IUCN) in each higher taxon (phyla, classes, orders) and the proportion that were extinct, endangered, threatened or least concern (electronic supplementary material, table S3). We generally found no significant relationships. Thus, extinction frequencies did not appear to be influenced by the completeness of the group's sampling by IUCN (suggesting little justification for excluding incompletely assessed groups). However, among classes (n = 43) and orders (n = 240), groups with the highest proportion of assessed species had the highest proportion of least-concern species (r^2 = 0.324 and 0.251, respectively, p < 0.0001). Conversely, among orders, there were significant, negative relationships between the proportions of assessed species and those that were endangered and threatened (n = 240; r^2 = 0.115–0.181; p < 0.0001). Results were similar using phylogenetic regression (electronic supplementary material, table S4), but relationships between assessed species and those that were endangered, threatened and least concern were weaker in the phylogenetic analyses among orders (r^2 = 0.02–0.04).

(c) Extinctions vary among groups

We found considerable heterogeneity in extinction frequencies among higher taxa (figure 1; electronic supplementary material, table S5 and dataset S2). Among all 163 022 assessed species, 0.6% were extinct, with higher frequencies in animals (0.8%) than plants (0.2%). There were no extinct fungi documented, although some fungi were assessed by IUCN (n = 794 species). In animals, frequencies were higher in molluscs (2.9% of assessed species) than chordates (0.7%), tetrapods (0.7%) or arthropods (0.4%). Among arthropods, frequencies were similar in insects (0.4%) and non-insect arthropods (0.5%). For chordates, frequencies were higher in turtles (2.9%), birds (1.5%) and mammals (1.4%) than in amphibians (0.5%), ray-finned fishes (0.4%) and squamates (0.2%; lizards and snakes). In plants, frequencies were higher in assessed bryophytes (1.9%; mosses) and rhodophytes (1.3%; red algae) than tracheophytes (0.2%; vascular plants: including extinct angiosperms, cycads and ferns).

Only a small percentage (7.5%) of plant, animal and fungal species have been assessed by IUCN (electronic supplementary material, table S5). Therefore, when considering the proportion of extinct species relative to all species in each group, overall extinction frequencies were much lower, by approximately 10-fold (or 100-fold for insects). The main exceptions were in chordates, in which most species were assessed. Therefore, considering all species, extinction frequencies were highest in turtles, birds and mammals. Frequencies in molluscs were much higher than in arthropods and plants, but lower than in chordates.

(d) Extinctions vary over time

We focused on when species were last seen as a proxy for when they went extinct (electronic supplementary material, dataset S8). We first examined these patterns among centuries (figure 2*a*; electronic supplementary material, dataset S9). Across all species, extinction rates (extinctions/century) were low in the 1500s, 1600s and 1700s, increased dramatically in the 1800s, and then approximately doubled in the 1900s. Regressing the rate of extinction per century and the century showed an overall significant, positive relationship (r^2 = 0.78; p = 0.0458; n = 5; electronic supplementary material, table S6). This was the overall pattern in plants, animals, arthropods, molluscs, ray-finned fishes and amphibians (with significant results in animals, plants, tetrapods and birds; electronic supplementary material, table S6). Ray-finned fishes showed a much stronger, 13-fold increase between the 1800s and 1900s. In contrast, tetrapods collectively showed little increase between the 1800s and 1900s. Amphibians and mammals had their highest extinction rates in the 1900s, but in birds the 1800s and 1900s had equal extinction rates, and in turtles and squamates, extinction rates were higher in the 1800s than 1900s.

We then examined extinction rates among recent decades, 1800s–2010s (figure 2*b*; electronic supplementary material, dataset S10). Apart from tetrapods, most groups had few extinctions in the 1500s, 1600s and 1700s. Across all species, there were peaks in the 1870s, 1930s, 1970s and 1980s. Animals showed a similar pattern. Plants had their highest extinction rates in the 1920s. Arthropods peaked in the early 1900s. Mollusc extinctions were highest in the 1870s and 1990s. Ray-finned fishes peaked in the 1970s whereas tetrapods peaked in the 1890s. Extinction rates in amphibians were highest in the 1970s, 1980s and 1990s (presumably due to chytrid fungus). Mammals peaked in the 1930s and birds in the 1890s and 1900s. Except molluscs and amphibians, all groups had their highest extinction rates 50 years ago or more, and many important groups had their highest extinction rates 100 years ago or more (plants, arthropods, tetrapods). Nevertheless, there were significant, positive relationships between decade (1800s–2010s) and the extinction rate of extinction per decade across all groups (r^2 = 0.30; p = 0.0081; n = 22) and in animals, plants, ray-finned fishes and amphibians (electronic supplementary material, table S6).

Finally, we examined extinction rates in the last approximately 100 years (1900s–2010s; figure 2*b*). No groups showed a significant, positive relationship between rates and decades (electronic supplementary material, table S6), as predicted if extinction rates were accelerating towards the present. Many groups showed a non-significant, negative relationship, including all species combined, animals, tetrapods, birds and mammals. These negative relationships were significant in arthropods (r^2 = 0.58; p = 0.0038; n = 12) and plants (r^2 = 0.44; p = 0.0196; n = 12). Overall, these results do not suggest that documented extinctions have been accelerating in recent decades, but instead have declined in the largest group of animals and in plants.

(e) Extinctions vary among environments

We first tested whether extinctions varied among major habitat types, relative to the overall proportional species richness of each group in each habitat. Extinctions among habitats often differed significantly from expectations based on the species richness of habitats (figure 3; electronic supplementary material, table S7 and dataset S11). Across animals (n = 746 extinct

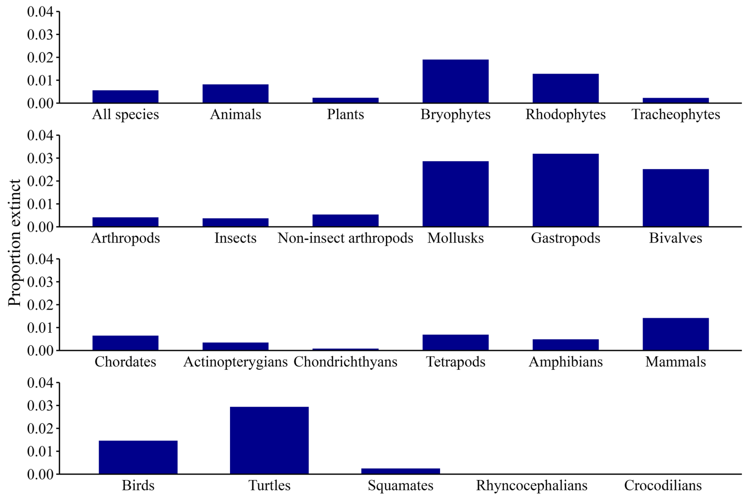

Figure 1. The proportion of extinct species in each major group. The number of extinct species in each major group is divided by the total number of species in that group that were assessed by the IUCN. Data for all groups are given in electronic supplementary material, table S5.

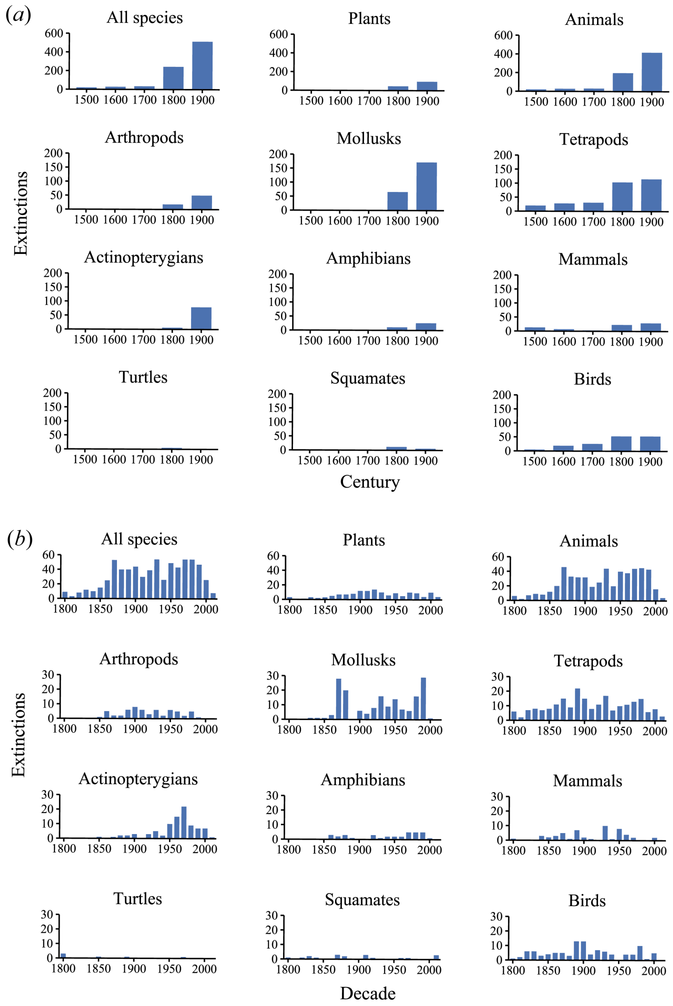

Figure 2. Extinctions over time. The number of extinctions are shown for each century since 1500 (*a*) and for each decade since 1800 (*b*). For each time period, we give the number of species that were inferred to have gone extinct in that time period, based primarily on the dates when each species was last seen. Extinction dates for each species are given in electronic supplementary material, dataset S8. Data for each century for each group are given in electronic supplementary material, dataset S9, and for each decade in electronic supplementary material, dataset S10.

species; electronic supplementary material, table S7), marine extinctions were rarer (1% observed versus 12% expected; $p < 0.0001$), freshwater extinctions were more common (30% versus 11%; $p < 0.0001$) and terrestrial extinctions were less frequent than expected (68% versus 77%; $p = 0.0002$).

Across arthropods ($n = 70$ extinct species; electronic supplementary material, table S7 and dataset S11), freshwater extinctions were over-represented, but otherwise patterns were not significant. However, among crustaceans ($n = 11$), freshwater extinctions were significantly more common than expected (observed = 100% of extinctions versus expected = 17%; $p < 0.0001$), and marine extinctions were significantly rarer (observed = 0%, expected = 78%). For insects and arachnids, observed and expected frequencies were similar.

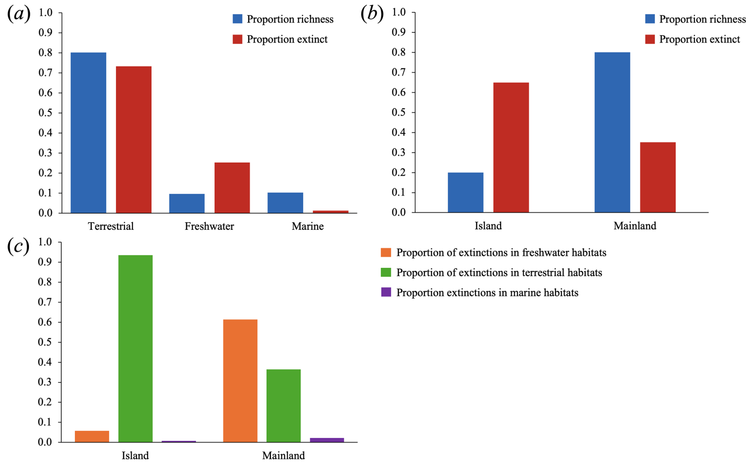

Figure 3. Patterns of extinction among environments relative to their species richness. (*a*) The proportion of extinct species in each habitat (red), compared with the proportion of overall species richness of plants and animals in each habitat (blue). Extinctions of freshwater species are relatively frequent, whereas marine extinctions are relatively rare, relative to overall species richness among habitats. (*b*) The proportion of extinct species that are island endemics versus continental species, compared with the proportion of all species on islands versus the mainland. The majority of extinct species are island endemics, but island endemics are only approximately 20% of global species richness. (*c*) The proportion of extinctions in freshwater (orange), terrestrial (green) and marine (purple) habitats for island versus continental species. Island extinctions were mostly of terrestrial species, whereas mainland extinctions were predominantly in freshwater.

In chordates, almost half of all known species are ray-finned fishes (actinopterygians), and this group contains similar numbers of freshwater and marine species (electronic supplementary material, dataset S11). However, almost all their extinctions were in freshwater (99%; $n = 93$; $p < 0.0001$). Surprisingly, in amphibians and turtles, terrestrial extinctions were more common than expected (75% and 94%; $p = 0.0002$ and $p = 0.0098$), and freshwater extinctions were less common. Observed and expected frequencies were similar among habitats in birds, mammals and squamates.

Across molluscs ($n = 261$ extinct species), marine extinctions were significantly less common than expected (0.4% observed versus 60% expected; $p < 0.0001$), and freshwater extinctions were more common (33% versus 7%; $p < 0.0001$) as were terrestrial extinctions (67% versus 33%; $p < 0.0001$). In bivalves ($n = 21$), all extinctions were freshwater and not marine (whereas 89% are marine and 11% freshwater; $p < 0.0001$). Gastropods ($n = 240$) reflected the overall pattern across molluscs with fewer than expected marine extinctions (0.4% versus 54%; $p < 0.0001$), and more common extinctions in freshwater (27% versus 6%; $p < 0.0001$) and on land (72% versus 39%; $p < 0.0001$).

In summary, freshwater extinctions were over-represented relative to marine extinctions in crustaceans, ray-finned fish, bivalves and gastropods. Terrestrial extinctions were more common than expected in amphibians, turtles and gastropods.

We next tested whether extinctions were more common among island endemics than continental species (figure 3*b*; electronic supplementary material, table S8 and dataset S12). The relative richness of island endemics versus mainland species is thought to be approximately 20% island and approximately 80% mainland. Yet, across all groups, 65% of past extinctions were of island endemics (chi-square test; $p < 0.0001$; $n = 912$ species). This same bias occurred across most groups (all $p < 0.0001$ unless noted; electronic supplementary material, table S8 and dataset S12), including plants (69% island; $n = 166$), animals (64%; $n = 748$), arthropods (59%; $n = 70$), molluscs (69%; $n = 261$), chordates (61%; $n = 412$) and most major tetrapod groups (birds, mammals, squamates, turtles [$p = 0.0098$]). However, there were exceptions, including crustaceans (25% island; $n = 12$; $p = 1.000$), ray-finned fishes (6%; $n = 93$; significantly fewer island extinctions than expected, $p = 0.0045$), amphibians (45%; $n = 38$; $p = 0.0508$) and bivalves (14%; $n = 21$; $p = 1.000$). Among these exceptions (excluding amphibians), most were freshwater.

Across all taxa (electronic supplementary material, dataset S12), the most extinctions of island endemics were on the Hawaiian Islands (23%; 133/591 extinct island species), French Polynesia (13%; 74/591) and the Mascarene Islands (11%; 62/591; e.g. Mauritius), especially among plants, arthropods, molluscs and birds. The West Indies (8%; 49/591) and Saint Helena (6%; 37/591) were the next most important. The highest proportion of island plant extinctions was on the Hawaiian Islands (35%; 40/115), followed by Saint Helena (9%; 10/115), the West Indies (8%; 9/115) and French Polynesia (6%; 7/115). Almost all were tracheophytes, but the two extinct island moss species were from Madeira. Most arthropod island extinctions were on the Hawaiian Islands (34%; 14/41) and Seychelles (32%; 13/41). For insects, the majority were on the Hawaiian Islands (54%; 14/26). Most mollusc island extinctions were on the Hawaiian Islands (29%; 52/179) and French Polynesia (29%; 52/179). Island bird extinctions were most frequent on the Mascarenes (21%; 32/152), Hawaiian Islands (18%; 27/152) and New Zealand (12%; 18/152). Almost half of island mammal extinctions occurred in the West Indies (46%; 22/48), whereas other important islands included the Galápagos (6%; 3/48) and Christmas Islands (6%; 3/48). Most reptile island extinctions occurred on the Mascarenes (42%; 13/31) and West Indies (29%; 9/31). All 17 extinctions of island amphibians occurred in Sri Lanka. Overall, most island extinctions occurred on oceanic islands (e.g. Hawaii, French Polynesia, Mascarene Islands).

We also examined the intersection of habitat and islands (figure 3*c*; electronic supplementary material, table S9 and dataset S12). Across all organisms, most island extinctions were among terrestrial species (94%; $n = 591$ species), whereas most non-island extinctions were among freshwater species (61%; $n = 321$ total non-island species). This pattern was driven primarily by animals (72% of continental extinctions among freshwater species; $n = 270$ continental extinct species), including arthropods (47% freshwater; $n = 29$), chordates (63% freshwater; $n = 159$) and especially molluscs (99% freshwater; $n = 81$). For example, 97% of extinct, non-island gastropods were freshwater ($n = 64$), whereas 98% of extinct island gastropods were terrestrial ($n = 176$).

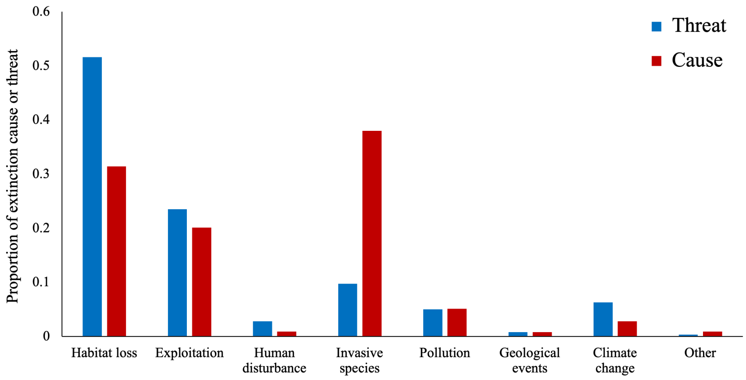

Figure 4. Comparing the frequency of different causes of extinction with the frequency of different threats among extant species. The proportion of species extinctions associated with different causes are shown in red, whereas the proportion of threats among endangered species are shown in blue. Data on causes are summarized in electronic supplementary material, table S10, and data on threats are summarized in electronic supplementary material, table S12. Statistical comparisons are in electronic supplementary material, table S13. The frequencies of habitat loss and invasive species are significantly different between extinct species and endangered species.

Table 1. Causes of recent extinction in different environments. The first column of values shows the total number of extinct species having hypothesized causes for their extinction and their distribution among environments. The next four columns show the most frequent extinction causes and the proportion of species in which that factor was hypothesized to drive their extinction, for different habitats and islands versus mainland. Data for each taxonomic group on extinction in different habitats and on islands versus mainland are shown in electronic supplementary material, tables S7 and S8.

environment	number of extinct species	habitat loss	exploitation	invasives	pollution
total	615	0.314	0.201	0.380	0.051
terrestrial	429.3	0.242	0.217	0.471	0.007
freshwater	175.8	0.501	0.140	0.168	0.161
marine	9.8	0.127	0.627	0.195	0.034
island	370	0.183	0.232	0.522	0.010
mainland	245	0.511	0.155	0.165	0.114

All these differences in the frequencies of extinct freshwater species between island and non-island habitats were significant (electronic supplementary material, table S9). The pattern was weaker in plants (only 7% of extinct, non-island species were freshwater; $n = 51$), although almost all island endemics were terrestrial (99.6%; $n = 115$). The pattern was also weaker in insects (26% of non-island species freshwater; $n = 21$), birds (21% freshwater; $n = 12$) and mammals (3%; $n = 35$).

(f) Extinction causes and current threats

We quantified the hypothesized causes of extinction, but these causes are often uncertain, and multiple potential causes were given for many species. Among the 615 species with hypothesized causes (figure 4 and table 1; electronic supplementary material, dataset S13), the most frequent were invasive species (38%), habitat loss (31%), exploitation (20%) and pollution (5%). Invasive species were also most important across animals, arthropods and chordates (electronic supplementary material, table S10). Habitat loss was more important for annelids, molluscs and plants (electronic supplementary material, table S10).

These patterns also varied by environments (table 1; electronic supplementary material, dataset S13). For terrestrial habitats, invasive species were the most frequent cause of extinctions (47%; $n = 429$ species), habitat loss was most common for freshwater species (50%; $n = 176$) and exploitation was the most important for marine species (63%; $n = 10$). On islands ($n = 370$ species), the most frequent cause was invasive species (52%), whereas in continental regions ($n = 245$), habitat loss was most frequent (51%).

These causes also varied over time (figure 5; electronic supplementary material, dataset S13). We examined 601 species in which both the century of extinction and the cause were hypothesized (figure 5*a*). Earlier extinctions (1500s–1700s) were caused predominantly by invasive species and exploitation. More recent extinctions (1800s–2000s) were caused most often by invasive species and habitat loss. The contributions of pollution, human disturbance, geological events and climate change to modern extinctions also increased towards the present. Regressing causes against time (electronic supplementary material, table S11) showed that extinctions from habitat loss and climate change significantly increased over time (habitat loss: $r^2 = 0.73$, $p = 0.0294$; climate change: $r^2 = 0.87$; $p = 0.0062$; $n = 6$), whereas the relative frequency of extinction from invasive species and exploitation decreased (but not significantly).

We also examined the frequency of extinction causes across decades for 482 species that went extinct between 1800 and 2010 with a hypothesized cause (figure 5*b*; electronic supplementary material, table S11 and dataset S13). Extinctions from habitat loss and invasive species dominated. Extinction frequencies from habitat loss increased significantly over time ($r^2 = 0.21$; $p = 0.0327$; $n = 22$) and those from exploitation significantly decreased ($r^2 = 0.39$; $p = 0.0019$; $n = 22$). Extinctions from invasive species and (surprisingly) climate change did not change significantly over time ($p = 0.34$–0.39).

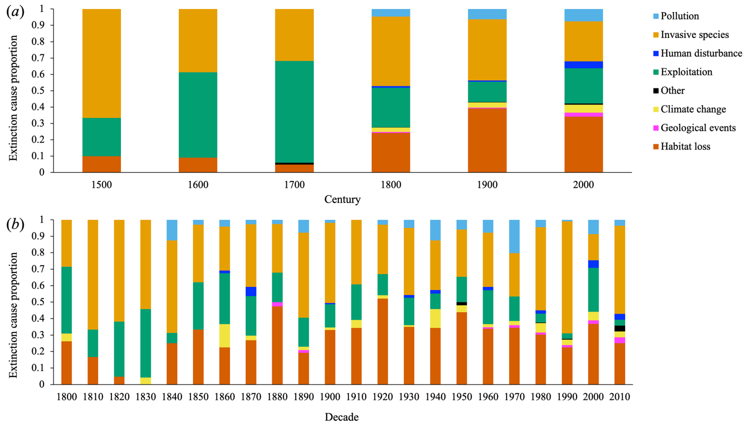

Figure 5. Extinction causes over time. Extinction causes were plotted by (*a*) extinction century since 1500 and (*b*) extinction decade since 1800. These trends are analysed statistically in electronic supplementary material, table S11.

The causes of recent extinctions sometimes differed substantially from current threats (figure 4). We summarize the most important current threats to endangered species in electronic supplementary material, table S12, with full details in electronic supplementary material, dataset S14. Among recently extinct species, the most frequent cause was invasive species (38%), whereas invasive species are a current threat to only 10% of endangered species. Conversely, among endangered species, the most important threat is habitat loss (52%), whereas this caused extinction of only 31% of extinct species. These differences in frequencies (between extinction causes and current threats) were statistically significant for both invasive species and habitat loss (chi-squared test; $p < 0.0001$; electronic supplementary material, table S13). Exploitation was a similar threat for extinct and endangered species (20% versus 24%, respectively), whereas other threats were similarly infrequent (e.g. pollution, climate change, human disturbance, geological events, all less than 10%).

(g) Potentially extinct species

There were 1384 species categorized as possibly extinct (electronic supplementary material, table S14 and dataset S15). These included more plants, arthropods, amphibians and squamates than the extinct species dataset. Among assessed species, extinction frequencies for these possibly extinct species were similar among plants, animals, arthropods and chordates (0.7–0.9%). Frequencies for amphibians were very high (2.3%) relative to other tetrapod groups (0.2–0.5%). Frequencies were also high in molluscs (1.8%).

Almost all possibly extinct species were last seen in the 1800s, 1900s and 2000s, with a strong increase in the 1900s in all major groups (electronic supplementary material, dataset S16). Among decades (electronic supplementary material, dataset S17), the maximum extinction rate across organisms was in the 1980s, driven by animals and especially amphibians and ray-finned fishes. Plant extinctions peaked in the 1920s. Arthropod extinctions peaked in the 1970s, and molluscs in the 1930s and 1990s. Most groups showed declining extinction rates after peaking in the 1980s (or before).

Patterns among environments (electronic supplementary material, table S15 and dataset S18) were similar to those for extinct species. Marine extinctions were rare (1%), and freshwater extinctions were common (27%). This bias was strongest in largely aquatic groups (crustaceans, molluscs, ray-finned fishes). There was also a strong bias towards island extinctions among largely terrestrial groups (greater than 50% of possibly extinct species; electronic supplementary material, table S16 and dataset S19), including plants, arthropods and all tetrapods except amphibians (with significant bias against island extinctions).

The causes of putative extinction among possibly extinct species (electronic supplementary material, tables S17–S18 and dataset S20) differed from extinct species. Specifically, habitat loss was most important among possibly extinct species (49%, followed by invasive species at 18%), whereas invasive species were more important among extinct species (38%, with habitat loss at 31%). The pattern for possibly extinct species was more similar to that for threats among endangered species.

4. Discussion

Biodiversity loss through the global extinction of species is among the greatest challenges facing humanity today. The most direct information on species loss comes from extinctions that have already happened. However, it has been unclear whether these past extinctions predict current threats to living species, and whether these past extinctions are biased among groups, habitats and over time. These issues are crucial to the question of whether past extinctions can be extrapolated to predict future extinctions globally and across groups. More broadly, there have been few analyses of rates and patterns in recent extinctions spanning living organisms.

Our results suggest that these past extinctions may not reflect current threats to global biodiversity. We found that recent extinctions are largely decoupled from current threat levels among groups, are highly biased among groups and among habitats, and have causes that vary over time and differ significantly from current threats. Extinction frequencies (among assessed species; figure 1) were highest in molluscs (2.9%), turtles (2.9%), birds (1.5%) and mammals (1.4%), but relatively low among the largest groups of animals and plants (arthropods, 0.4% and tracheophytes, 0.2%; among assessed species). Thus, extrapolating extinction rates from these tetrapod groups or molluscs to all living organisms to predict global mass extinction [4–6,8] may be problematic. Importantly, extinctions were also uncommon among amphibians (0.5%), squamates (0.2%) and ray-finned fishes (0.4%), similar to arthropods and plants. These three tetrapod groups together make up most vertebrates and have been well assessed by IUCN (electronic supplementary material, table S5). Therefore, their lower extinction rates cannot be dismissed as artefacts of incomplete assessment. Indeed, we found no relationship between extinction frequencies and how thoroughly assessed a group was (electronic supplementary material, table S3). Recent extinctions were rare among marine species and common among freshwater species (figure 3*a*), and the majority of recent extinctions were of island endemics (figure 3*b*; see also [10–14]). The majority of non-island extinctions were among freshwater species (61%), whereas most island extinctions were among terrestrial species (94%; figure 3*c*; electronic supplementary material, table S9). The most frequent inferred cause of past extinctions was invasive species (especially on islands), whereas the most common current threat is habitat loss (figure 4). In summary, most known biodiversity consists of mainland, terrestrial species (mostly arthropods and plants; approx. 90% [24,26,27]) that are most often threatened by habitat loss, whereas recent extinctions have been dominated by tetrapods and molluscs on islands and have most often been related to invasive species. Thus, these past extinctions should not necessarily be seen as a preview of future extinctions across all organisms.

These past extinctions also do not support the idea that biodiversity loss is presently accelerating (even if it actually is). Extinction rates have generally increased across centuries in the last 500 years (figure 2*a*). Data on recent tetrapod extinctions (cumulative extinctions per century) have been used to suggest that extinction rates are presently accelerating [5]. However, we found that extinction rates in tetrapods were similar between the 1800s and 1900s, have not significantly increased over the last 200 years, and showed a downward trend over the last 100 years (figure 2). We also found that decadal extinction rates over the last approximately 100 years (figure 2) significantly declined in the two groups of organisms encompassing most known global biodiversity (arthropods and plants). These trends may reflect increasing conservation efforts [28,29], loss of the most vulnerable species (leaving more resilient species still extant), delays in assessing species and in adding extinct species to the IUCN database or other factors. Importantly, treating 'possibly extinct' species as extinct suggests more recent peaks in extinction rates for many groups. Yet, even for these possibly extinct species, the maximum extinction rates were often approximately 40 years ago, and approximately 100 years ago for plants. We do not suggest that these declining extinction rates mean that there is no current biodiversity crisis. Instead, these past extinctions may fail to reflect the current crisis. Furthermore, presenting cumulative numbers of extinct species for each century [5] may not accurately reflect recent trends in extinction rates among decades over the last century.

We also emphasize that these past extinctions might not reflect future threats. For example, past extinctions strongly suggest that climate change is not an important threat to biodiversity [16]. Remarkably, we found here that species-level extinctions related to climate change have not significantly increased over the last approximately 200 years. However, many studies concur that approximately 20–30% of all plant and animal species may be lost to climate change in future decades under pessimistic climate scenarios [30,31]. Note that IUCN classifies climate-related extinctions broadly (e.g. including extreme weather events), which presumably explains climate-related extinctions before the Industrial Revolution and recent warming. However, even given this broad definition, one would still expect an increase in climate-related extinctions in recent decades. Again, these past extinctions might not reflect future threats.

We found that invasive species were the most important cause of extinctions among insular species, and most recent extinctions were of island endemics [12]. There has been debate about whether introduced species are a major cause of extinctions [15,32]. We found that they were the most important cause of recent extinctions (table 1). There is often considerable uncertainty about these causes, but this uncertainty also applies to alternative explanations besides invasive species. We make two important but contrasting points here: (i) invasive species appear to have been the most frequent driver of recent extinctions, making them important for that reason alone; and (ii) the circumstances under which invasive species cause widespread extinctions may be limited (i.e. on islands).

Our goal here was to analyse patterns of extinction among groups, habitats, regions and time. We did not focus on explaining these patterns, which would require many additional analyses. Nevertheless, several patterns should be explored further. The highest extinction frequencies were among turtles and molluscs. Turtle extinctions generally involved large tortoises on small islands (Galápagos, Mascarene), and were related to human exploitation. Large tortoises may suffer from overexploitation because of low replacement rates and their long time to reach sexual maturity [33], approximately 30−40 years for wild Galápagos tortoises [34]. Among molluscs, most extinctions were of terrestrial gastropods on islands [35]. Terrestrial molluscs can have very small range sizes, which may make them especially vulnerable [35]. Across all organisms, we found increased extinction on islands [10,12–15]. Various factors may explain the vulnerability of island species, including small population sizes, low clutch sizes and loss of predator-defence traits [10]. We also found that extinctions were disproportionately common among freshwater species and rare among marine species. This difference may be related to range size, given that freshwater species tend to be narrowly distributed [36] and marine species more widely distributed [9,37]. For example, North American freshwater fishes with smaller range sizes are more likely to be endangered, and freshwater fishes have smaller range sizes than terrestrial vertebrates [36]. Furthermore, many freshwater extinctions have been caused by dams, such as the many narrowly endemic molluscs driven to extinction by the damming of Alabama's Coosa River in the 1900s [38].

We acknowledge several limitations of our study. First, our study was based on IUCN data. These data are widely used in studies of recent extinctions (see Introduction), but they might give a biased picture of these extinctions. For groups that have few species assessed relative to their species richness (e.g. arthropods, molluscs, plants), it is not always clear why some species were assessed and others were not. We also found some differences in our results using extinct versus possibly extinct species. Importantly, our analyses showed that the proportion of assessed species in a group was not strongly correlated with the proportion of extinct or threatened species. Therefore, it may be more problematic to exclude incompletely assessed groups than to include them. Furthermore, our analyses suggest that the biases in extinction patterns favouring island and freshwater species (and against marine species) are similar between well-sampled groups (i.e. chordates) and more poorly sampled ones (i.e. plants, arthropods, molluscs), using both extinct and possibly extinct species.

We also note that results for insects are based on a limited number of assessed species, but the IUCN data for insects seem to be biased towards including extinct species. For example, there are 42 insect genera with one or more extinct species in the IUCN database (electronic supplementary material, dataset S2). These genera span most of the largest orders (Coleoptera, Diptera, Hemiptera, Lepidoptera, Orthoptera), along with several smaller orders (Blattodea, Dermaptera, Ephemeroptera, Mantodea, Odonata, Phasmida, Plecoptera, Trichoptera). The majority ($n = 24$) of these 42 genera are represented in IUCN only by extinct species, even though they contain other extant species (electronic supplementary material, dataset S21). Similarly, there are 26 insect families with extinct species in IUCN, and for eight families, the only species included in IUCN are listed as extinct, even though they each contain many non-extinct species (electronic supplementary material, dataset S21). Thus, extinction frequencies among assessed insect species may be overestimated, not underestimated. In summary, there may be many additional extinctions among unassessed insects, but IUCN's assessment of insects appears to be taxonomically broad and biased towards extinct species.

Second, there can be errors in assigning species to categories. Many species may have gone extinct that are not yet assigned to this IUCN category [35], and many putatively extinct species have been rediscovered [13,39,40]. Thus, there are alternative lists of extinct species in some groups, such as plants [13,18] and molluscs [40]. We dealt with this uncertainty (at least in part) by also assessing patterns among 'possibly extinct' species. These latter patterns were generally similar to those from extinct species (e.g. more common extinctions on islands and in freshwater), but potential extinctions were generally more recent and more often related to habitat loss, and more frequent in some groups (amphibians, arthropods, plants). A larger list of putatively extinct plant species ($n = 962$) also suggests that plant extinctions peaked in the 1920s [18], as do our analyses (figure 2). These additional species would increase the extinction proportion of plants relative to animals, but since these additional species can be outside those assessed by IUCN, it may be more appropriate to calculate the extinction proportion relative to all plant species. This yields 0.25% extinction, very similar to that among assessed plant species (0.23%; electronic supplementary material, table S5).

Third, we acknowledge that there may be many 'dark' or 'Centinelan' extinctions: species that have gone extinct without being formally described [41–44]. Hypothetically, these dark extinctions might increase the number of extinct species, and might lead to taxonomic and ecological patterns of extinctions different from those described here among documented extinctions. However, we are not aware of taxonomically and geographically comprehensive projections that have inferred such patterns. This is an important area for future research. We also focused exclusively on extinctions after 1500. We assume that older extinctions would be even less relevant to predicting future extinctions.

5. Conclusions

A key aspect of the current biodiversity crisis is the loss of hundreds of species of plants and animals over the last 500 years. However, the rates, patterns and causes of these recent extinctions have remained incompletely understood. Furthermore, it is unclear whether these recent extinctions predict current threats and future biodiversity loss. Our results show that these recent extinctions are highly biased among groups and habitats, and do not necessarily reflect current threats or threat levels. Most known species are mainland, terrestrial species of arthropods and plants, and the majority of species that are endangered are threatened by habitat loss. In contrast, recent extinctions have been dominated by tetrapods and molluscs on islands (and freshwater species), and have most frequently been related to invasive species. Finally, these past extinctions do not show biodiversity loss as rapidly accelerating, but instead show extinction rates that generally peaked many decades ago, and that declined over time in some important groups (arthropods, plants). Overall, we do not downplay the current extinction crisis or future risks to biodiversity. Instead, we suggest that both might be very different from these patterns of past extinctions over the last 500 years.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data (electronic supplementary material, datasets S1–S21) and R code (electronic supplementary material, dataset S22) are freely and permanently available on Figshare: [45].

Supplementary material is available online [46].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. K.E.S.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; J.J.W.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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