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Global dataset shows geography and life form predict modern plant extinction and rediscovery

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Comparison with the IUCN Red List data on modern extinction in seed plants

The nature of Red List data compared to our continuously updated database

Our first step was to compare our species list with the 130 seed plant species listed by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species as globally extinct (EX) or extinct in the wild (EW)¹ (Supplementary Data 2). We focused our analysis on the species level because species are the most widely understood and used unit for measuring biodiversity² and also adopted internationally for conservation policy and environmental legislation³. The Red List is the global authority on the extinction risk of species but its data do not reflect the high rates of current extinction known for some organismal groups⁴⁻⁶ (see also Table 1 in Vellend et al.⁷). It paints an accurate picture for birds and mammals as, indeed, it was developed to do⁸ but coverage remains highly incomplete for other groups of organisms, despite the provision of increasingly detailed guidelines on the application of the criteria to relatively poorly known groups⁹. For example, a previous, detailed analysis of snails led to a doubling of the number of presumed extinct species of molluscs and suggested that an estimated 7% of species may be extinct, compared to the 0.04% suggested by the Red List data alone^{6,10}.

Discrepancies of this sort, and those detailed below, are almost inevitable since botanical and taxonomic research is ongoing while a formal Red List extinction risk assessment presents a snapshot of the state of knowledge at a particular time. Publication of new records or updates to existing ones take time due, in part, to the necessary process of data compilation and peer review. For our study as a whole, taxonomic change accounts for removal of 18% of the species on our original extinction list, while rediscoveries outnumber them by 2:1. These proportions are comparable to the corrections to extinction lists of the Australian flora over a 20-year period: of 228 species listed as extinct 40 were removed for taxonomic reasons while 89 were removed following rediscovery¹¹.

Extinct seed plant species listed by the Red List and in our database

Two-thirds of the 130 species in the Red List (96 species) are also found in our database (Supplementary Data 2). Of these, two are listed under different names, and updating these names does not affect their presumed extinct status. Twelve species have been rediscovered and four have been synonymised with living species. These species should therefore no longer be listed as extinct. A further ten species are known to persist in cultivation and should have their status changed to extinct in the wild (EW) instead of extinct (EX). This highlights 26 species in the Red List whose extinction status is out of date.

Extinct seed plant species listed only by the Red List

Almost a third of the species in the Red List (34 species) are not in our database at all (Supplementary Data 2). Some of these were published by the Red List as endangered (EN) in 1998 and are now listed as extinct (EX), without any associated explanation for their change in status. Others have been published as extinct in the past decade, and these

entries are generally accompanied by full references and extensive explanatory notes. Some of these were added to our database (e.g. *Nymphaea thermarum*; see below). And finally, some species, e.g. several *Brugmansia* species, are thought to be cultivars that have become naturalised and remain widespread in the wild. The extinct status of these species is therefore doubtful.

Of the 34 species on the global Red List but missing from our list, careful vetting resulted in 10 being added to our database. These species (representing 1.8% of our data on plant extinction) had been overlooked during our data compilation because they were published as extinct only recently, because their status was updated without an accompanying literature reference or because recent taxonomic changes have resulted in persisting plants being recognised as distinct species.

The remaining 24 species on the Red List but not added to our list are known to be critically endangered (CR, 1 species), endangered (EN, 1 species), synonyms of species that are not extinct (4 species) or simply not extinct but with no known extinction risk (either rediscovered or should not have been classified as extinct at all; 18 species). In summary, we suggest that 50 species assessments in the Red List need revision. The Red List Unit has been notified.

Final tally of extinct seed plant species in our database

Our database includes a list of 491 presumed extinct species not on the Red List at all (Supplementary Data 1). Our database is therefore the most complete list of recently extinct seed plants published to date and includes 571 species that are presumed to be globally extinct (EX) or extinct in the wild (EW). This is more than 4 times those listed by the Red List and suggests that 0.2% of standing seed plant diversity has become extinct in modern times, while the Red List figure is 0.04%.

Distribution of extinct species among families

The 571 extinct species belong to 102 out of the 428 currently recognised seed plant families. Most records are in globally large and widespread families, for example, 55 species in the coffee family (Rubiaceae), 39 species in the daisy family (Asteraceae) and 30 species in the legume family (Fabaceae; Supplementary Fig. 1). Having a lot of species does not necessarily confer a high number of extinct species however. There are more orchids than any other type of seed plant, and orchids are considered among the world's most threatened plants¹², but there are relatively few documented extinctions of orchids (22 out of ca. 28,000 species).

The top families based on proportions are small and less well known, with at least an order of magnitude fewer species, for example, 4 species of cycads (Zamiaceae; Supplementary Fig. 1). There is a clear mismatch between the families that score high based on species numbers and those that score high based on proportions. Only the bluebells (Campanulaceae) score high on both measures.

Phylogenetic signal of modern extinction in seed plants

Using a phylogenetic tree with family-level resolution¹³ (Fig. 2, main article) including 371 seed plant families, we employed three commonly used measures for analysing the phylogenetic distribution of traits, to test whether there is phylogenetic signal to modern extinction in plants at the family level: Pagel's λ and Blomberg's K for proportion extinct species per family and the D-statistic for treating extinction as a binary variable (presence/absence of extinct species within a family)¹⁴⁻¹⁷. We used both λ and K because, although they both test for phylogenetic signal, they treat data (e.g. tip branches) slightly differently, and their performance is known to differ under some circumstances¹⁸. The D statistic is a similar test but for discrete data, rather than continuous. The subjective nature of taxonomic categories makes summarising extinction and rediscovery by family somewhat artificial; therefore, the data were analysed both as proportions and numbers. Pagel's λ was calculated using the 'transformPhylo.ML' function in the R¹⁹ package *motmot*²⁰, Blomberg's K using 'phylosig' in *phytools*²¹ and the D-statistic using 'phylo.d' in *caper*²².

All tests provided strong support for the phylogenetic independence of extinction: $\lambda = 0$ ($\Delta AICc = 31.1$ compared to Brownian motion, which is equivalent to $\lambda = 1$, where differences among the families are proportional to the phylogenetic distances among them); $K = 0.43$ ($P = 0.07$ compared to a phylogenetically random distribution); and $D = 0.96$ ($P = 0$ compared to the distribution generated by a process that approximates Brownian motion, equivalent to $D = 0$, and $P = 0.40$ compared to a random distribution, equivalent to $D = 1$). Thus, phylogeny is not predictive of which families contain species documented to have become extinct in recent centuries.

Rediscovery of species misreported as extinct

Distribution of rediscovered species among families

The rediscovered species belong to 82 families (Supplementary Figure 1). For some plant groups, e.g. orchids, over half of the species declared extinct have been rediscovered (30 of 52 species), compared to none for the coffee relative *Psychotria* (0 of 23 species, most of which inhabited islands; Supplementary Data 1). All but one of the families with the most extinct species also had the most rediscovered species. As for extinction, there is no overlap between families that have a high number of rediscovered species and those that have high proportions of rediscovered species.

Only three families have high proportions of both extinct and rediscovered species (Bruniaceae, Frankeniaceae and Portulacaceae). There is thus much less overlap among these smaller families but, importantly, there is overlap, suggesting that a high proportion of declared extinct species in certain families is unlikely to be due to a lack of knowledge about these families. Furthermore, it is inevitable that some of the species presumed extinct today will soon be rediscovered again.

Phylogenetic signal of rediscovery

All tests showed the same results as for extinction: rediscovery has been phylogenetically random: $\lambda = 0$ ($\Delta\text{AIC} = 27.3$ compared to Brownian motion); $K = 0.36$ ($P = 0.39$ compared to a random distribution); and $D = 0.92$ ($P = 0.32$ compared to a phylogenetically random distribution, $P = 0.001$ compared to Brownian motion).

Geographic patterns of rediscovery

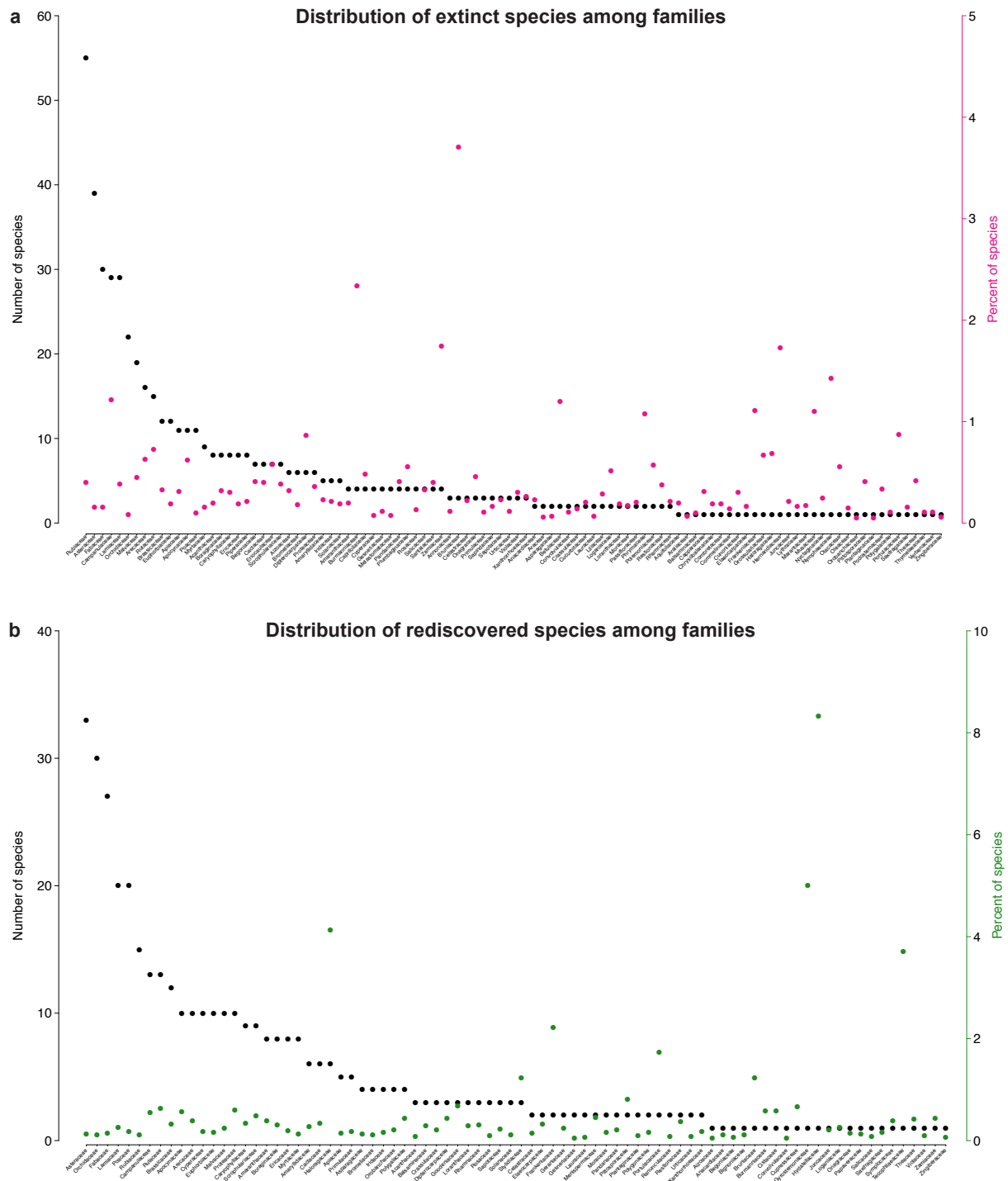
Rediscovered species are from 128 country-level regions²³, compared to 123 for extinct species. Western Australia stands out as having the highest number of rediscovered species (75 species), followed by Hawaii (36 species), California (32 species), India (27 species) and the Cape Provinces of South Africa (25 species). About half of the regions with most presumed extinct species also have the most rediscovered species, including tropical islands (Hawaii, Mauritius and Madagascar) and regions with a Mediterranean-like climate (the Cape region in South Africa, India, Western Australia and California). Overall, however, rediscovery is much lower on islands than on continents (130 and 404 species, respectively) but more likely for species that are geographically more widespread (87% of rediscovered species occur in a single TDWG level 3 region, compared to 98% of extinct species). At a continental scale, rediscovery is high in Australasia and North America but low in South America and Africa. Australia, India, California, Hawaii and South Africa are examples of areas that are home to long-term professional botanical surveys. Some of the geographical differences in the balance between extinction and rediscovery might therefore indicate a bias in our knowledge of modern extinction in plants, driven by global inequality in botanical survey work.

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Supplementary Figures and Figure Legends



Supplementary Fig. 1 | Distribution of extinct and rediscovered species among seed plant families. **a**, Recently extinct (Red List categories EX and EW) and **b**, rediscovered species. Numbers are shown in black and proportions in pink (extinct species) and green (rediscovered species). It is clear that those families that have a high number of extinct/rediscovered species are not same as those that have high proportions of extinct/rediscovered species. Families are sorted by decreasing number of extinct/rediscovered species.

Supplementary Tables

Supplementary Table 1 | Extinction risk of rediscovered species

Extinction risk, according to Red List criteria¹	Number of species²
Critically endangered, CR	234
Endangered, EN	69
Vulnerable, VU	79
Near threatened, NT	1
Least concern, LC	11
Data deficient, DD	37

¹Species in the top three extinction risk categories, marked in bold, are considered to be threatened with extinction.

²Overall, 88.6% of species are threatened with extinction (CR, EN and VU), 2.8% are not considered to be threatened (NT, LC) and 8.6% are data deficient (DD).

Supplementary Data

Supplementary Dataset 1 | The database of modern extinction in seed plants

Available as a supplementary file (Excel table) linked to the online version of the paper at www.nature.com/nature.

Supplementary Dataset 2 | The IUCN Red List of extinct seed plant species

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