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Selecting the best candidates for resurrecting extinct-in-the-wild plants from herbaria

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Resurrecting extinct species is a fascinating and challenging idea for scientists and the general public. Whereas some theoretical progress has been made for animals, the resurrection of extinct plants (de-extinction sensu lato) is a relatively recently discussed topic. In this context, the term 'de-extinction' is used sensu lato to refer to the resurrection of 'extinct in the wild' species from seeds or tissues preserved in herbaria, as we acknowledge the current impossibility of knowing a priori whether a herbarium seed is alive and can germinate. In plants, this could be achieved by germinating or in vitro tissue-culturing old diaspores such as seeds or spores available in herbarium specimens. This paper reports the first list of plant de-extinction candidates based on the actual availability of seeds in herbarium specimens of globally extinct plants. We reviewed globally extinct seed plants using online resources and additional literature on national red lists, resulting in a list of 361 extinct taxa. We then proposed a method of prioritizing candidates for seed-plant de-extinction from diaspores found in herbarium specimens and complemented this with a phylogenetic approach to identify species that may maximize evolutionarily distinct features. Finally, combining data on seed storage behaviour and longevity, as well as specimen age in the novel 'best de-extinction candidate' score (DEXSCO), we identified 556 herbarium specimens belonging to 161 extinct species with available seeds. We expect that this list of de-extinction candidates and the novel approach to rank them will boost research efforts towards the first-ever plant de-extinction.

Biodiversity extinction rates have increased notably in recent decades and may now be up to 1,000 times the baseline rate[1–3]. This increase is largely due to anthropogenic effects such as land use change, resource use, direct exploitation, pollution, invasive alien species and climate change[4]. For plants, studies estimate that between 20%[5,6] and 39%[7] of all species are at risk of extinction globally, and therefore require urgent conservation action[8]. The International Union for Conservation of Nature (IUCN)[9] distinguishes between the two 'extinct' Red List categories: EX (extinct) and EW (extinct in the wild). EX species are no longer known to occur in wild populations or in cultivation, and so far this category also includes plant species for which we only have herbarium specimens containing seeds. EW species are covered by ex situ conservation programmes of botanic gardens and seed banks, and there have already been several successful translocations of EW plant species into the wild (for example, *Sophora toromiro*, *Nymphaea thermarum*[10]).

With respect to EX species, de-extinction is perhaps the newest and most controversial option in the toolkit of conservation biologists. Defined by the IUCN Species Survival Commission[11] as the creation of a proxy or functional equivalent of an extinct species,

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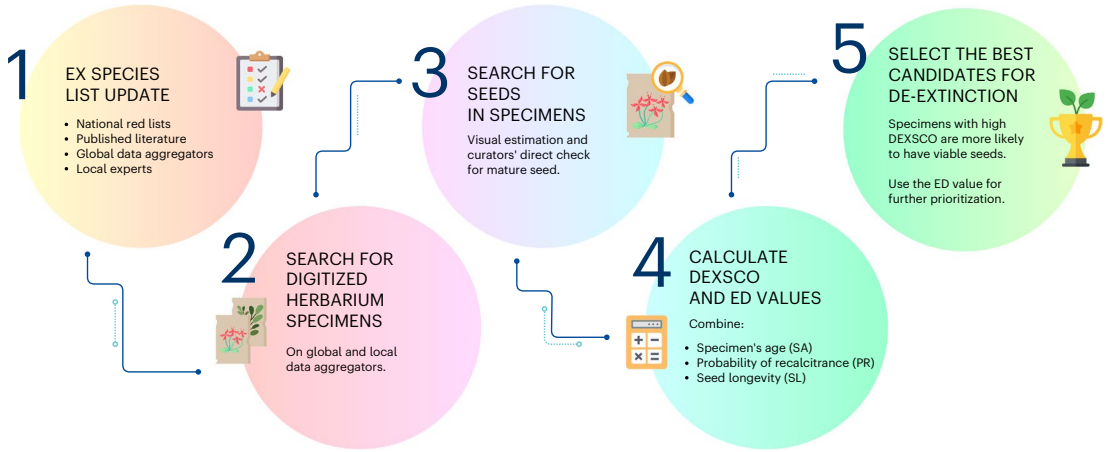

Fig. 1 | Workflow process for selecting the best candidates for de-extinction. Icons created using flaticon.com.

de-extinction as a process is still only theoretical and is the subject of intense debate among conservation biologists[12–14]. Along these lines, it has been hypothesized that animal de-extinction could only be achieved by selective back-breeding, somatic cell nuclear transfer or genome engineering[11]. The above-mentioned techniques would result in the creation of a hybrid engineered living animal, precisely a proxy that fits in a broken lineage of a species. In plants, species no longer occurring in the wild or in cultivation could be recovered by germinating or tissue-culturing old diaspores (that is, seeds/spores) preserved in herbaria. Both methods would result in the recovery of actual species, not proxies[15].

In this framework, the term 'de-extinction' as defined by the IUCN[11] is inappropriate, as it would not include 'true' species recovery. In addition, it must be considered that if a seed of an extinct plant species is alive, the species is technically not extinct, which makes the use of the term 'de-extinction' in this context even more questionable. An inherent problem in this case is that so far, it is impossible to know a priori whether a herbarium seed is alive and can germinate, therefore plants only preserved in herbaria (with seeds) should still be considered as EX despite being actually EW.

In fact, the potentiality of a seed of an extinct species to germinate, in conjunction with the impossibility of knowing whether the seed is alive or if we can germinate it (with current technology), creates a condition of uncertainty such that we might consider our candidates as Schrödinger's species. These species are both dead and alive, extinct and extant, and current technologies and knowledge do not allow this paradox to be solved. These Schrödinger's species could therefore be considered possibly extinct (but differently from the IUCN's 'PE' category conception), potentially extinct or in a state of 'pre-extinction' just one step away from real extinction. Consequently, by germinating these seeds we will not obtain a genuine resurrection but an 'artificial awakening' or the recovery of the life 'stocked' in the seed.

We therefore propose to use the term de-extinction sensu lato referring to the resurrection of EW species from seeds or tissues preserved in herbaria, although we acknowledge all the above-mentioned limitations in the use of this term.

In support of these efforts in plants, there are numerous striking examples of >100-year-old diaspores germinating. These include *Canna compacta* Roscoe (synonym of *Canna indica* L.; canna lily), collected from a >500-year-old tomb in Santa Rosa de Tastil, Argentina[16]; 2,000-year-old seeds of *Phoenix dactylifera* L. (the Date palm)[17]; 1,000-year-old seeds of *Nelumbo nucifera* (Willd.) Pers. (sacred lotus)[18,19] and others[20–22]. These examples of the germination of old diaspores demonstrate that recovering extinct plants may be possible, even though herbaria are not designed for maintaining seed viability and none of the ancient seeds germinated hitherto belonged to an extinct species[21]. Furthermore, seed longevity is a taxon-specific trait and is also highly dependent on favourable seed storage conditions and time.

Although the germination of seeds preserved in herbaria is difficult to achieve[23], with nearly 400 million specimens preserved worldwide[24], herbaria may well be important sources of viable diaspores that could be used for recovering lost genetic variation[25–28]. Albani Rocchetti and colleagues[29] showed that with some exceptions and limitations, there is a general positive consensus among plant scientists on the use of diaspores contained in herbaria to attempt plant conservation. However, several issues remain unresolved concerning the resurrection of extinct plants in practice, namely: (1) the lack of a clear picture of the presence and quality of diaspores in herbarium specimens of extinct plants, (2) the need for methodological guidelines for the selection of the best candidate species, and (3) the lack of specific germination and/or tissue culture protocols for extinct plants. So far, only a few systematic attempts to germinate diaspores from herbaria have been carried out[21,23,30].

Here we explore seed availability in herbarium specimens of extinct species. We propose a method for prioritizing candidates for seed-plant de-extinction sensu lato from diaspores occurring in herbarium specimens, combining data on seed storage behaviour and longevity, as well as specimen age (Fig. 1). These constitute the parameters of the formula for calculating the 'de-extinction score' (DEXSCO), here proposed as a concise, effective tool for prioritization and selection of candidates. Finally, we complement the prioritization of de-extinction candidates with a phylogenetic approach to identify species that may maximize evolutionarily distinct features, using evolutionary distinctiveness (ED hereafter)—a measure of the phylogenetic isolation of a species[31] capturing genomes divergence[32] and hence putatively unique feature diversity[33] (Fig. 1).

Review of the global list of extinct plants

We generated a list of 361 globally extinct species, spanning a wide phylogenetic breadth including 240 genera in 92 angiosperm families (Supplementary Table 2), on the basis of our review of the most recent published literature (up to December 2021; Supplementary Table 1), seed bank accessions and the PlantSearch database of Botanic Gardens Conservation International (BGCI). Among the 2,995 herbarium specimens representing 331 extinct plant species (92% of globally extinct species identified), we identified 556 specimens representing 161 extinct species containing seeds (45% of globally extinct species identified). For 30 extinct species, we were unable to find any digitized specimens or specimens in the herbaria contacted (Supplementary Table 4).

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Table 1 | Top 50 plant taxa that are the best candidates for de-extinction

Rank	Family	Taxon	DEXSCO	SA	SL	PR	ED
1	Ericaceae	*Leucopogon cryptanthus* Benth.	1.270	42	3	0.0021	6.121
2	Fabaceae	*Astragalus endopterus* (Barneby) Barneby	1.238	49	3	0.0013	14.693
3	Fabaceae	*Streblorrhiza speciosa* Endl.	1.232	47	3	0.0126	7.934
4	Fabaceae	*Aspalathus cordicarpa* R.Dahlgren	1.177	71	3	0.0014	10.887
5	Malvaceae	*Byttneria ivorensis* N. Hallé	1.172	73	3	0.0022	23.522
6	Solanaceae	*Solanum bauerianum* Endl.	1.168	72	3	0.0070	17.819
7	Fabaceae	*Dalea sabinalis* (S.Watson) Shinners	1.165	78	3	0.0015	28.052
8	Malvaceae	*Sphaeralcea procera* Ced.Porter	1.162	80	3	0.0011	5.741
9	Piperaceae	*Peperomia degeneri* Yunck.	1.144	93	3	0.0021	53.262
10	Fabaceae	*Vicia dennesiana* H.C.Watson	1.137	99	3	0.0022	16.063
11	Asteraceae	*Tetramolopium conyzoides* Hillebr.	1.135	102	3	0.0017	1.980
12	Juncaceae	*Juncus pervetus* Fernald	1.132	105	3	0.0020	44.766
13	Asteraceae	*Lipochaeta degeneri* Sherff	1.132	93	3	0.0125	1.902
14	Amaranthaceae	*Achyranthes atollensis* H.St. John	1.128	98	3	0.0114	7.530
15	Amaranthaceae	*Achyranthes mangarevica* Suess.	1.126	87	3	0.0234	7.530
16	Asteraceae	*Tetramolopium tenerrimum* Nees	1.122	118	3	0.0014	1.980
17	Asteraceae	*Centaurea tuntasia* Heldr. ex Halácsy	1.118	124	3	0.0011	7.024
18	Aizoaceae	*Cephalophyllum parvulum* (Schltr.) H.E.K.Hartmann	1.117	125	3	0.0017	4.376
19	Fabaceae	*Orbexilum stipulatum* (Torrey & A. Gray) Rydb.	1.114	118	3	0.0083	7.548
20	Eriocaulaceae	*Eriocaulon johnstonii* Ruhland	1.112	133	3	0.0017	56.130
21	Orchidaceae	*Bulbophyllum pusillum* Thou.	1.104	12	1	0.0101	28.404
22	Solanaceae	*Solanum nava* Webb & Berthel.	1.102	131	3	0.0125	17.819
23	Proteaceae	*Persoonia laxa* L.A.S.Johnson & P.H.Weston	1.099	113	3	0.0252	24.979
24	Caryophyllaceae	*Schiedea amplexicaulis* H.Mann	1.096	170	3	0.0017	15.930
25	Cyperaceae	*Eleocharis brachycarpa* Svenson	1.092	187	3	0.0007	22.154
26	Fabaceae	*Crudia zeylanica* Benth.	1.087	153	3	0.0159	17.769
27	Malvaceae	*Hibiscadelphus wilderianus* Rock	1.083	111	3	0.0407	14.209
28	Malvaceae	*Ruizia rosea* (Lindl.) Dorr	1.047	191	3	0.0407	7.861
29	Malvaceae	*Corchorus thozetii* Halford	1.039	N/A	3	0.0009	22.506
30	Fabaceae	*Aspalathus variegata* Eckl. & Zeyh.	1.039	N/A	3	0.0009	10.887
31	Fabaceae	*Liparia graminifolia* L.	1.038	N/A	3	0.0017	11.971
32	Aizoaceae	*Trianthema cypseleoides* Benth.	1.038	N/A	3	0.0017	45.866
33	Caprifoliaceae	*Valerianella affinis* Balf.f.	1.038	N/A	3	0.0017	26.727
34	Proteaceae	*Leucadendron spirale* (Salisb. ex Knight) I.Williams	1.038	N/A	3	0.0019	17.605
35	Malvaceae	*Pavonia papilionacea* Cav.	1.038	N/A	3	0.0021	10.407
36	Campanulaceae	*Delissea niihauensis* H.St.John	1.027	N/A	3	0.0125	9.565
37	Campanulaceae	*Delissea parviflora* Hillebr.	1.027	N/A	3	0.0125	9.565
38	Rubiaceae	*Kadua foliosa* Hillebr.	1.025	N/A	3	0.0143	10.162
39	Euphorbiaceae	*Acalypha wilderi* Merr.	1.016	92	3	0.1141	23.405
40	Campanulaceae	*Delissea fallax* Hillebr.	1.001	N/A	3	0.0368	9.565
41	Malvaceae	*Hibiscadelphus bombycinus* C.N.Forbes	0.997	N/A	3	0.0407	14.209
42	Rhamnaceae	*Nesiota elliptica* Hook.f.	0.992	N/A	3	0.0461	21.415
43	Plantaginaceae	*Veronicastrum liukiuense* (Ohwi) T.Yamaz.	0.984	32	2	0.0125	16.389
44	Apiaceae	*Ducrosia ismaelis* Asch.	0.899	45	2	0.0125	8.229
45	Amaranthaceae	*Ptilotus senarius* A.R.Bean	0.874	54	2	0.0010	18.408
46	Brassicaceae	*Lepidium obtusatum* Kirk	0.832	70	2	0.0020	20.423
47	Rosaceae	*Potentilla uliginosa* B.C.Johnst. & Ertter	0.823	75	2	0.0020	75.797

Table 1 (continued) | Top 50 plant taxa that are the best candidates for de-extinction

Rank	Family	Taxon	DEXSCO	SA	SL	PR	ED
48	Boraginaceae	*Cryptantha hooveri* I.M.Johnst.	0.807	83	2	0.0070	11.959
49	Amaranthaceae	*Atriplex tularensis* Coville	0.791	100	2	0.0009	9.153
50	Boraginaceae	*Plagiobothrys lamprocarpus* (Piper) I.M.Johnst.	0.791	100	2	0,0012	11,878

Table 1 Taxa are presented in descending order of DEXSCO, with SA, SL, PR and ED. Missing data for specimen age are indicated with 'N/A'.

Best candidates for plant de-extinction

The DEXSCO of the 556 identified specimens ranged from 0.28 to 1.27, with a median value of 0.467 (Supplementary Table 5). The highest 50 de-extinction candidates are shown in Table 1, and the full list of species ranked according to the best DEXSCO is given in Supplementary Table 6. In both lists, for species with more than one herbarium specimen, we used the one with the highest score. The highest 50 scores ranged from 1.270 to 0.791, with a median of 1.090. Specimen age (SA) and probability of recalcitrance (PR) ranged from 12 to 191 years old (median = 93) and 0.001–0.114 (median = 0.002), respectively. With respect to seed longevity (SL) rank, 82% of the highest 50 candidates produce long-lived seeds, 16% medium-lived seeds and 2% short-lived seeds.

Of these highest 50 candidate species, 52% belong to just five families: Fabaceae (18%), Malvaceae (14%), Asteraceae (8%), Amaranthaceae (6%) and Campanulaceae (6%), with the remaining 48% spread across 20 families (Table 1). The ED index of the 240 genera listed is 1.08–85.43 (median = 16.06; s.d. = 16.32; Supplementary Table 3). The subset of taxa with confirmed specimens bearing mature seeds or fruits includes 113 genera, with an ED index of 1.90–75.80 (median = 12.56; s.d. = 13.92; Supplementary Table 6). Higher values of ED indicate species with a high phylogenetic distinctiveness, potentially exhibiting unique evolutionary and functional features. The introduction of ED into the de-extinction candidate ranking aims to provide an additional, phylogenetic approach that could be used to select de-extinction candidates, as it may be more important and acceptable to focus on the recovery of unique lineages that might otherwise be lost. The ED was not included in the formula because it is unrelated to feasibility, but instead allows prioritization of de-extinction candidates that putatively maximize evolutionarily distinct features after identification of those species with available, potentially alive diaspores. Finally, we found a weak, positive correlation between DEXSCO and ED at the specimen level (Spearman's rank correlation coefficient = 0.219; d.f. = 554; $n = 556$; $P < 0.001$).

Discussion

Reviving extinct species is a fascinating idea for scientists and the general public[34,35]. Whereas some theoretical progress has been made on the animal side along these lines[36,37], the de-extinction of plants has only been discussed relatively recently[38]. A major goal of de-extinction is to restore ecological functions lost with a species' extinction, through replacement with a living, functionally equivalent organism, achievable by back breeding, cloning or genomic engineering[39], and to enrich extant ecosystems through the translocation of the resurrected species[37]. A list of animal de-extinction candidates (including the dodo, thylacine and woolly mammoth) has already been proposed[37]; this is the first attempt to develop a similar list for plants.

It has been hypothesized that plant de-extinction could be achieved by germinating old propagules, seeds or spores from herbarium specimens of extinct plant species[15,28]. This idea is particularly interesting for two main reasons. First, plant de-extinction from herbaria could reverse losses of plant diversity and also shed light on the aging and death mechanisms in seeds[40]. Second, as explained above, the resurrection of an extinct species from seeds from herbaria would challenge the concept of extinction itself. Extinction in plants would not happen when the last living individual dies[9], but rather when the last seed does.

Metrics, adaptations and strategies to consider for de-extinction

By combining information on herbarium specimen age, storage behaviour and the respective species' seed longevity, our study suggests that there are species that may be in a good position to be revived from suitable herbarium specimens. In particular, the Fabaceae, Malvaceae and Ericaceae taxa are prominent among the most promising 50 candidates (Table 1), reflecting their widely demonstrated seed longevity[41–43]. For instance, *Leucopogon cryptanthus* Benth. and *Streblorrhiza speciosa* Endl. can be considered suitable extinct angiosperm species for attempting de-extinction from herbarium diaspores due to their considerable seed longevity and being represented by comparatively young herbarium specimens (42 and 47 years old, respectively; Table 1). Moreover, several species with lower DEXSCO may still be considered good candidates due to the existence of several specimens, increasing the chance of finding at least one mature and viable seed (for example, *Solanum bauerianum* Endl., *Psychotria obscurinervia* Merr. and *Haplostachys linearifolia* (Drake) Sherff, all with more than 15 specimens each). Success will certainly vary widely depending on the species (when all other factors are held constant) and seed abundance. Among the many species-specific characteristics that should be considered, seed freezing adaptation is of particular importance when considering herbaria. The customary, relatively recent herbarium management practice is to freeze specimens at −20 °C for 3–7 days before accession into collections[44] to prevent damage from pests. Therefore, taxa that have evolved freeze adaptations (that is, physical seed dormancy, freezing avoidance and freezing tolerance[45]) could be considered better candidates in de-extinction taxa selection. However, the effect of freezing cycles on seeds housed in herbaria is poorly known[27]. Another barrier to de-extinction from propagules available in herbaria is the widespread past use of DNA-altering chemicals that may have reduced seed viability in older specimens[46,47]. To have high confidence, DEXSCO should be tested by germinating seeds that have been scored. We see the development of ad hoc germination or in vitro culture protocols for plant de-extinction candidate species as the next priority in this field: the longer we wait, the lower the chances for successful germination.

At present, the main challenge to plant de-extinction is the lack of optimized germination or in vitro culture protocols for related congenerics and, more crucially, diaspore viability of the respective herbarium specimens. Diaspores preserved in herbarium specimens of extinct species are precious and cannot be wasted. Therefore, species that are phylogenetically related to extinct ones, such as those within the same genus, should be used to develop such protocols[48]. An issue especially when testing long-lived seeds is finding the most suitable dormancy-breaking technique. In the case of the most represented families of the highest 50 candidates (for example, Fabaceae and Malvaceae; Table 1), these typically produce seeds with a hard, impermeable coat, requiring the use of specific treatments (for example, scarification) to overcome physical seed dormancy[49]. Moreover, seed vigour (that is, 'the sum of those properties that determine the activity and performance of seed lots of acceptable germination in a wide range of environments'[50]) could be improved in old seeds by using a range of priming techniques (that is, technologies designed to improve germination performance under adverse environmental conditions[51]).

Constraints and potential of ED

We consider feasibility a necessary and priority condition to other characteristics and indexes that may contribute to species' selection. A phylogenetic approach to the selection of de-extinction candidates is taken here as an example of other metrics that can be coupled with DEXSCO and should be regarded as a complementary approach, rather than a fundamental component of the prioritization. Nevertheless, this approach remains highly interesting because ED can be considered as an additional criterion alongside DEXSCO. In the case of species with similar scores, the ED becomes a key index for species prioritization. In this study, several taxa, including for instance, *Leucopogon cryptanthus* Benth. and *Streblorrhiza speciosa* Endl., showed a high DEXSCO but very low ED (<10). This suggests that although the de-extinction of these taxa appears most feasible, from a phylogenetic point of view, the impact would be low. Exceptions to this include *Peperomia degeneri* Yunck., *Eriocaulon johnstonii* Ruhland and *Juncus pervetus* Fernald, all of which show relatively high DEXSCO and ED index values. Further research is needed to assess the possibility of including functional diversity (FD[52]) or other metrics important for the translocation of a recovered taxon into the wild[13] (for example, original habitat intactness).

Upstream and downstream of DEXSCO

The role of herbaria as a source of information for species conservation status assessment[28] has become very clear during our systematic search for specimens of extinct species and evaluation of seed presence. We found that 13% of the taxa listed as extinct in Humphreys et al.[3] should be removed from this list due to rediscoveries and taxonomic changes that can be tracked via herbarium vouchers[53]. For example, *Campomanesia lundiana* (Kiaersk.) Mattos was declared extinct some 20 years ago[54], but its status is controversial due to the presence of an herbarium specimen collected in 2018. In this, as in other similar cases, it is too early to formally declare a species as extinct beyond any reasonable doubt[9] and consequently, we did not include these ambiguous cases in our de-extinction candidate list. However, it should be noted that herbaria are neither strictly ex situ conservation facilities nor propagation centres, and seeds preserved in herbarium specimens lose their viability much faster than in seed banks[55] where seeds are kept in controlled, optimal storage conditions of humidity and temperature for viability. Therefore, as a precautionary measure, it may also be worth attempting germination of these species as soon as possible, because waiting for a formal declaration of extinction could result in a total loss of seed viability.

In conclusion, with DEXSCO, we provide a methodological tool for assessing the feasibility of de-extinction beyond the list of taxa presented here. The germination potential of diaspores, including spores and pollen, and therefore the application of DEXSCO may be extended to ferns and other plants preserved in herbaria and other natural history collections (for example, carpological and ethnobotanical collections). We anticipate that this approach will boost national and international research efforts in recovering EW plants preserved as seeds in herbaria.

Methods

Review of the global list of extinct plants

On the basis of the list by Humphreys et al.[3], we reviewed globally extinct seed plants using online resources (that is, global data aggregators[56–58]; up to December 2021) and additional literature for North America[59], Mexico[60], Cuba[61], Europe[53], South Africa[62], India[63], Australia[64–67], New Zealand[68] and Hawaii[69] (see Supplementary Table 1 for a full list of references used; Fig. 1).

We specifically excluded those taxa with verified ex situ populations in botanic gardens and seed banks (EW taxa following IUCN[9]) according to the PlantSearch Database by BGCI (https://www.bgci.org/), the Millennium Seed Bank Seed List (http://apps.kew.org/seedlist/SeedlistServlet) and the ENSCONET database (http://enscobase.maich.gr/), as these species are more likely to qualify as Extinct in the Wild rather than Extinct according to IUCN Red List categories.

Search for seed-bearing specimens of extinct plants in worldwide herbaria

A search for mature fruits and seeds in herbarium specimens of extinct seed-plant species was performed by examining digitized herbarium specimens across the largest global data aggregators (for example, GBIF, https://www.gbif.org/; JACQ, https://www.jacq.org/#database; Tropicos, https://www.tropicos.org/home; Supplementary Table 1) that include major herbaria (for example, Paris, Meise, Kew, Harvard and so on), plus more regionalized aggregators (for example, Calflora, https://www.calflora.org/; the Chinese Virtual Herbarium, https://www.cvh.ac.cn/index.php; Supplementary Table 1 and Fig. 1). The names of each extinct taxon (recent accepted name and synonyms) are reported according to the World Plants list (https://www.worldplants.de/world-plants-complete-list/complete-plant-list). We visually estimated the presence or absence of fruits, seeds and envelopes that might contain seeds for each specimen. Since this visual estimation from digitized specimens was difficult in some cases, we also contacted curatorial staff of the host herbaria to check directly for the presence of mature fruits or seeds. In total, we contacted 102 herbaria (Supplementary Table 1), of which 61 (60%) replied to our information request. All data were collected in a spreadsheet file using Microsoft Excel.

Score and prioritization of de-extinction candidates

For each taxon with at least one herbarium specimen bearing mature fruits or seeds, we obtained the seed storage behaviour at the genus or family level as the PR, using the Seed Storage Predictor tool (https://seedcollections.shinyapps.io/seed_storage_predictor/ (ref. [70])). The PR ranges from 0 (orthodox) to 1 (recalcitrant), with results close to 0.5 being considered less reliable than more extreme values. Results presented here refer to orthodox taxa (PR < 0.5) only.

For each taxon with orthodox seed behaviour (that is, PR close to 0), we assigned an SL category in ambient conditions as follows: 1 = short-lived (P50 < 4.85 years; P50 expresses the time to lose 50% of the initial viability); 2 = medium-lived (4.85 < P50 < 9.7); 3 = long-lived (P50 > 9.7), according to Colville and Pritchard[41]. Each extinct taxon was assigned to one of these categories at the genus or family level on the basis of published literature (Supplementary Table 1 and Fig. 1). Taxa with no available data on seed longevity were assigned as short-lived (Supplementary Table 2).

We then combined the above-mentioned numerical metrics with the age of each specimen into the DEXSCO formula at the specimen and species levels (Fig. 1). Our candidate scores were calculated according to a modified version of the Evolutionarily Distinct and Globally Endangered index (EDGE index[71]), which was developed to prioritize species-based conservation activities and is computed as follows:

$$\underbrace{\left(\frac{10}{1+SA}}_{\text{A}}+\underbrace{SL*\frac{\ln(2)}{2}}_{\text{B}}\right)*\underbrace{(1-PR)}_{\text{C}}$$

Term A is designed such that a specimen collected in the current year has the maximum score of 10 (recent specimen, higher chances of viability). Term B is designed such that seed longevity has a low weight in the score, as this characteristic is poorly known for most taxa. Term C is the additive inverse of the PR, so a fully recalcitrant species has a score of 0. We assigned families with missing or variable longevity data to the lowest SL category (that is, 1). Missing data for SA or PR does not contribute to the score. The score ranges from 0 (PR = 1, that is, fully recalcitrant species) to 11.04 (SA = 0, SL = 3 and PR = 0). The higher the score, the greater the theoretical probability of de-extinction.

Seed longevity is a key trait for the selection of de-extinction candidates, as long-lived seeds have higher chances of remaining viable over time and germinating. However, the intrinsic uncertainty related to intraspecific variation, lack of data at the species level (and in most cases at the genus level; Supplementary Table 2) for extinct species

and the heterogeneity of the method used for longevity assessment (Supplementary Table 1) demand the prudent use of this parameter. Therefore, we lowered the weighting of SL in the formula, treating specimen age and seed behaviour as the leading parameters.

Calculation of ED

To identify de-extinction candidates that putatively maximize evolutionarily distinct features, we complemented the above information with a phylogenetic approach to account for the evolutionary histories of the taxa. To this end, we calculated the ED for each genus (Fig. 1). This analysis is based on the genus-level version of the most comprehensive time-calibrated vascular plant phylogenies available[72,73].

For each species, we calculated the genus-wise ED using the function evol_distinct() from the R phyloregion package[74], utilizing the option 'fair.proportion'. We chose to calculate ED at the genus level because neither molecular data were available at the species level, nor was it possible to sample the total diversity of all genera to estimate the distinctiveness of each species within each genus. Nevertheless, 52% of the genera in our dataset were represented by a single species. It should be noted that our goal was to prioritize each extinct species against other extinct species, not against the whole global flora. Not all genera were represented in our reference tree: 34 genera were missing and for these we used the most closely related genera to calculate ED (Supplementary Tables 1 and 3). After calculating ED for extinct plant taxa, we performed a Spearman correlation analysis (data were not normally distributed) between ED and the average DEXSCO at the species level, using SPSS 21.0 (https://www.ibm.com/products/spss-statistics). Although at present there is no biological evidence suggesting that there might be a link between ED and the de-extinction score, a positive correlation between these indices would imply the possibility of resurrecting species of high phylogenetic interest and the recovery of unique genetic variability.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data in Materials and Methods are included in the paper and/or the Supplementary Materials. Additional data related to this paper are available from the corresponding author on reasonable request, as some original data were provided under a confidentiality clause.

The following databases were consulted for the revision of extinct plant species:

BGCI | Botanic Gardens Conservation International (https://www.bgci.org/)

ENSCOBASE (http://enscobase.maich.gr/)

IUCN, The IUCN Red List of Threatened Species. V. 2021-3 (2022) (https://www.iucnredlist.org/)

Millennium Seed Bank—Seed List (http://apps.kew.org/seedlist/SeedlistServlet)

Threatened Species Programme | SANBI Red List of South African Plants (http://redlist.sanbi.org/index.php)

A Database of the World's Recently Extinct Species: Plants, Animals and Fungi – The Recently Extinct Plants and Animals Database (https://recentlyextinctspecies.com/)

Virtual herbaria specimens were researched using:

Biodiversity Center of Japan (https://www.biodic.go.jp/index_e.html)

Calflora - Information on wild California plants (https://www.calflora.org/)

Chinese Virtual Herbarium - 中国数字植物标本馆 (CVH) - 国家植物标本资源库在线共享平台 (https://www.cvh.ac.cn/index.php)

GBIF (https://www.gbif.org/)

JACQ - Virtual Herbaria (https://www.jacq.org/#database)

e-ReColNat Infrastructure (https://www.recolnat.org/en/)

RM Herbarium Specimen Search (http://rmh.uwyo.edu/data/browse_scientific.php)

AVH - The Australasian Virtual Herbarium (https://avh.chah.org.au/)

Tropicos - Home (https://www.tropicos.org/home)

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Author contributions

G.A.R., T.A. and A.C. conceptualized the project. G.A.R., T.A. and A.C. developed the methodology. G.A.R. and T.A. conducted the investigations. G.A.R. performed visualization. T.A. administered the project. T.A., G.C. and C.C.D. supervised the project. G.A.R. and T.A. wrote the original draft. A.C., A.M., S.G., C.C.D., G.C., M.A.A., K.A., R. Bijmoer, R. Borosova, C.B., E.B., M.B., S.B., L.H.C., N.G.D.S., A.H.D., R.M.D., J.B.D., M.F., A. Fleischmann, A. Franks, G.H., G.K., C.K., U.L., L.M., L.G.R., R.J.S., I.S., P.S., H.V., A.W., J.J.W. and E.Z. reviewed and edited the manuscript. G.A.R., T.A., A.C., A.M., S.G., C.C.D., M.A.A., K.A., R. Bijmoer, R. Borosova, C.B., E.B., M.B., S.B., L.H.C., N.G.D.S., A.H.D., R.M.D., J.B.D., M.F., A. Fleischmann, A. Franks, G.H., G.K., C.K., U.L., L.M., L.G.R., R.J.S., I.S., P.S., H.V., A.W., J.J.W. and E.Z. contributed data.

Competing interests

The authors declare no competing interests.

Additional information

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Microsoft Excel, Microsoft Corporation, 2018.
Data analysis	R 4.1, function evol_distinct() from the R phyloregion package, option “fair.proportion”. SPSS Statistics 21.0, IBM.

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All studies must disclose on these points even when the disclosure is negative.

Study description	This paper reports the first list of plant de-extinction candidates based on the actual availability of seeds in herbarium specimens of globally extinct plants. We reviewed globally extinct seed plants, with online resources (i.e. data aggregators) and additional literature on National red list, resulting in a list of 361 extinct taxa. We then proposed a method for prioritizing candidates for seed-plant de-extinction from diaspores occurring in herbarium specimens and complemented the prioritization of candidates with a phylogenetic approach to identify species that may maximize evolutionarily distinct features. Combining data on seed storage behaviour and longevity, as well as specimen age in the novel "best de-extinction candidate" score (DEXSCO), we identified 556 herbarium specimens belonging to 161 extinct species with available seeds. Finally, we provided the first top-50 list of candidates for de-extinction and evaluate the Evolutionary Distinctiveness (ED) of the extinct plant taxa, capturing genomes divergence and hence putatively unique feature diversity.
Research sample	Review of extinct plants using published literature and Web sources: BGCI | Botanic Gardens Conservation International, (available at https://www.bgci.org/). ENSCOBASE, (available at http://enscobase.maich.gr/). IUCN, The IUCN Red List of Threatened Species. vERSIONE 2021-3 (2022), (available at https://www.iucnredlist.org/). Millennium Seed Bank — Seed List, (available at http://apps.kew.org/seedlist/SeedlistServlet). Threatened Species Programme | SANBI Red List of South African Plants, (available at http://redlist.sanbi.org/index.php). A Database of the World's Recently Extinct Species: Plants, Animals and Fungi - The Recently Extinct Plants and Animals Database, (available at https://recentlyextinctspecies.com/). Virtual herbaria specimens research using: Biodiversity Center of Japan, (available at https://www.biodic.go.jp/index_e.html). Calflora - Information on wild California plants, (available at https://www.calflora.org/). Chinese Virtual Herbarium - **中国数字植物**标本馆（CVH）-**国家植物**标本资源库在线共享平台, (available at https://www.cvh.ac.cn/index.php). GBIF, (available at https://www.gbif.org/). JACQ - Virtual Herbaria, (available at https://www.jacq.org/#database). e-ReColNat Infrastructure, (available at https://www.recolnat.org/en/). RM Herbarium Specimen Search, (available at http://rmh.uwyo.edu/data/browse_scientific.php). AVH - The Australasian Virtual Herbarium, (available at https://avh.chah.org.au/). Tropicos - Home, (available at https://www.tropicos.org/home).
Sampling strategy	no sample size pre-calculation was performed. Initial dataset used is published by Humphreys, A. M., Govaerts, R., Ficinski, S. Z., Nic Lughadha, E. & Vorontsova, M. S. Global dataset shows geography and life form predict modern plant extinction and rediscovery. Nat. Ecol. Evol. 3, 1043–1047 (2019).
Data collection	Review of globally extinct plants using puiblished literature and web sources; evaluation of the presence of seeds in herbarium specimens by visual estimation across the largest global data aggregators, plus more regionalised aggregators, and check by curatorial staff of the host herbaria; seed storage behaviour at genus or family level reported as the probability of recalcitrance (PR), using the Seed Storage Predictor tool (https://seedcollections.shinyapps.io/seed_storage_predictor/)
Timing and spatial scale	Data collection from January 2020 to September 2021.
Data exclusions	We excluded those taxa with verified ex-situ populations in botanic gardens and seed banks (EW taxa following IUCN), according to

Data exclusions	the PlantSearch Database by Botanic Gardens Conservation International (BGCI), the Millennium Seed Bank Seed List, and the ENSCONET database, as these species are more likely to qualify as Extinct in the Wild rather than Extinct according to IUCN Red List categories.
Reproducibility	Data collected from published literature, methodology fully reproducible and applied formula provided.
Randomization	Not relevant. Data was not grouped, the analyses did not require randomization.
Blinding	Blinding not relevant, no test performed.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging