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**Extinct in the Wild: The precarious state of Earth’s most threatened group of species**

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29 **Teaser:** The perilous state of Extinct in the Wild species demands urgent attention and  
30 action.

31

32 **Abstract:** Extinct in the Wild (EW) species are placed at the highest risk of extinction under  
33 the International Union for Conservation of Nature Red List, but the extent and variation in  
34 this risk has never been evaluated. Harnessing global databases of *ex situ* animal and plant  
35 holdings, we report on the perilous state of EW species. Most EW animal species, already  
36 compromised by their small number of founders, are maintained at population sizes far below  
37 the thresholds necessary to ensure demographic security. Most EW plant species depend on  
38 live propagation by a small number of botanic gardens, with a minority secured at seed bank  
39 institutions. Both extinctions and recoveries are possible fates for EW species. We urgently  
40 call for international effort to enable the latter.

41

42 **EXTINCT IN THE WILD: AN OVERLOOKED CATEGORY OF SPECIES AT RISK**

43 A crisis of species loss unprecedented in human history continues to deepen (1, 2). Over the  
44 last century, extinctions in well-understood groups such as vertebrates have far exceeded  
45 what would be considered to be a normal background rate based on the fossil record (3). The  
46 wave of extinctions lies largely ahead: the proportion of species threatened with extinction  
47 amongst the most comprehensively assessed speciose groups ranges from 13% in birds to  
48 42% in gymnosperms (4), and patterns of decline and extinction in poorly known taxa may be  
49 even more severe (5, 6). However—despite the failure to meet similar commitments in the  
50 2010 Aichi Biodiversity Targets (7)—the 2022 Kunming-Montreal Global biodiversity  
51 targets to halt extinctions and recover species (8) should be regarded as achievable. This is  
52 because the field of conservation biology is continuing to demonstrate that the status of  
53 threatened species can be improved, and extinctions in the wild prevented and even reversed.  
54 The conservation status of the world’s vertebrates, though deteriorating, would be  
55 significantly worse were it not for conservation interventions (9). Indeed, 28-48 extant bird  
56 and mammal species would have gone extinct between 1993 and 2020 were it not for actions  
57 such as habitat protection, translocation, and *ex situ* conservation using breeding facilities and  
58 zoos (10). *Ex situ* conservation using botanic gardens and seed banks has also been used to  
59 support the restoration of at least eight plant species and populations that had disappeared  
60 from their indigenous range (11). Amongst these endeavours sits a category of species  
61 representing a striking nexus of responsibility, vulnerability, and opportunity: those that—  
62 having been entirely extirpated in the wild—exist solely in zoos, aquariums, botanical  
63 gardens, or seed banks, i.e., those that qualify for the International Union for Conservation of  
64 Nature Red List of Threatened Species (Red List) category of Extinct in the Wild (EW) (4).  
65 This category is applied to any species “known only to survive in cultivation, in captivity or  
66 as a naturalized population (or populations) well outside the past range” (12).

67 Species that have found themselves restricted to *ex situ* care arrived there through a variety of  
68 means. In some cases, individuals were collected from highly threatened populations with the  
69 specific aim of species conservation. The lizard fauna native to Christmas Island in the Indian  
70 Ocean, for example, suffered significant declines starting in the 1970s due to habitat  
71 modification and the effects of introduced species (13). In response to the crisis, two endemic  
72 lizard species were rescued into *ex situ* care in 2009, providing refuge from outright  
73 extinction before the last individuals were recorded in the wild in 2012 (13). In other cases,  
74 species were collected for scientific or hobbyist interest and only acquired conservation  
75 relevance once the situation in the wild subsequently became dire. For example, in 1925, 17  
76 Socorro doves (*Zenaida graysoni*) were collected from Socorro Island in the Pacific Ocean  
77 and transported to an aviculturist in California, United States (14), forming the basis for an *ex*  
78 *situ* collection that is today distributed in small numbers in captive facilities across North  
79 America and Europe (15). On its native Socorro, however, the dove entered an abrupt decline  
80 sometime after 1958, and was last seen in the wild in 1972 (15, 16). In other instances,  
81 collection into *ex situ* maintenance is itself the principal driver of extinction in the wild. Wild  
82 populations of Southern African cycad species such as the escarpment cycad (*Encephalartos*  
83 *brevifoliolatus*) and Heenan’s cycad (*Encephalartos heenanii*) have disappeared due to  
84 collection for the trade in ornamental plants (17, 18), yielding *ex situ* collections that  
85 nonetheless represent potential sources for eventual recovery in the wild.  
86 Though the circumstances surrounding their procurement are diverse, these species share a  
87 dependence on human care, combined with a wild context that—historically at least—has  
88 presented threats sufficiently severe to lead to their extirpation.

89 EW species occupy a curiously overlooked space in the Red List, our framework for  
90 evaluating and comparing species' risk of extinction. The assessment process evaluates states  
91 and trends in the geographic ranges and populations of species, as well as their threats, and  
92 allocates categories of extinction risk accordingly. These categories range in increasing risk  
93 from "Least Concern" through "Near Threatened", "Vulnerable", "Endangered", "Critically  
94 Endangered", "Extinct in the Wild", and "Extinct". Species in the Vulnerable, Endangered,  
95 and Critically Endangered categories are classed as "threatened" with extinction. EW species  
96 are not, despite being categorised as facing higher extinction risk. In fact, because the Red  
97 List process concerns itself solely with wild populations, the populations of EW species—  
98 whether thriving or on the brink—are not subject to assessment. The broader conservation  
99 community has consequently largely ignored the extent of—and variation in—extinction risk  
100 among the very group of species for which humans are most responsible, and whose futures  
101 are amongst the least assured.

102 Here, harnessing global *ex situ* databases and the academic and grey literature, we reveal the  
103 dynamic and often perilous state occupied by EW species, assessing their current populations  
104 as well as summarising the journeys and fates of all species known to have been restricted to  
105 *ex situ* care since 1950. Extending our analysis beyond the introduction in 1994 of the EW  
106 category (19), we chose 1950 to approximate the beginning of the modern era of species  
107 conservation (20). This time window enabled us to build a comprehensive list of species in a  
108 comparable context, minimising the risk of biasing our selection towards well-known cases.

109 Our dataset therefore included the assessments of the 84 species (40 animals and 44 plants)  
110 categorized as EW on Red List version 2022-2 (4). Of these, two (both animals) have gone  
111 extinct since their most recent assessment (Table 1). The assessments of a further 10 appear  
112 erroneous: two are extinct having never been in *ex situ* care, three are likely extant in the wild  
113 having never been extirpated, three are synonyms of species that remain extant in the wild,  
114 and the statuses of two are unknown (Table S1). We added a further 21 species that were *ex*  
115 *situ*-restricted at some point since 1950, but now occupy a different state (i.e., they are either  
116 extinct or considered wild again). These species were identified through a review of the  
117 IUCN summary statistics for genuine status changes, the Red List narrative texts of extinct  
118 species, and the assessments of extant species with populations indicated as originating from  
119 reintroductions or assisted colonisations (21). Twelve of these additional species are now  
120 wild again (Table 2), and a further nine have gone extinct (Table 1). In total we identified and  
121 summarised the conservation history and statuses of 95 species (52 animals and 43 plants)  
122 known to have been EW or restricted to *ex situ* care since 1950, 72 of which (33 animals and  
123 39 plants) are considered to remain in this state as of 2022.

124 For each species, we collected information on the history of the collection, *ex situ*  
125 maintenance, and conservation of each, namely: the periods over which founders of the *ex*  
126 *situ* population were collected from the wild; the number of individuals collected to initiate  
127 the *ex situ* population; the number of founder lineages represented in the present population  
128 (where this is noted as a separate number); the year the species was last recorded in the wild;  
129 and the timing and status of any attempts to re-establish the species in the wild through  
130 conservation translocations. The status of the *ex situ* populations of currently EW species was  
131 assessed by quantifying the number of institutions holding them; the type of institution for  
132 plants (i.e., botanical garden or seed bank); the total *ex situ* population size for animals (this  
133 is not generally quantified or reported for plants); whether an animal species was subject to  
134 metapopulation management or had a studbook; and whether any Population Viability  
135 Analyses (PVAs) had been carried out for *ex situ* populations. Data was collated primarily  
136 from Red List assessments, supplemented where necessary using recovery project

137 documentation, academic literature, targeted Google and Google News searches, and contact  
138 with relevant taxon experts and conservation practitioners (21). Information on *ex situ*  
139 populations of currently EW species was derived from Species360's Zoological Information  
140 Management System (22), Association of Zoos and Aquariums' database of Species Survival  
141 Programs (SSPs) (23), the European Association of Zoos and Aquaria's list of EEPs (24),  
142 Australasia's Zoo Aquarium Association's list of Species Management Programs (SMPs)  
143 (25), and the World Association of Zoos and Aquariums' list of Global Species Management  
144 Plans (26) (for animal species) and Botanic Gardens Conservation International's PlantSearch  
145 (27) (for plant species).

## 146 **THE VARIED AND WORRYING STATE OF EW SPECIES**

147 We found considerable variation and alarming deficiencies amongst EW species in factors  
148 critical to their long-term recovery. A minimum of between 30 and 50 individuals is  
149 recommended to found an *ex situ* population to capture an adequate representation of the  
150 genetic diversity of the wild population (28, 29). Most currently EW animal populations for  
151 which such information is available (eight of 13) were founded by fewer than 30 individuals,  
152 and amongst the less well documented plants we report that at least seven of 40 EW  
153 populations were founded by just a single individual (Table 3). Most *ex situ* populations of  
154 EW species were thus imperilled to begin with, and require population growth to enhance  
155 demographic security and reach a size at which loss through drift of the genetic diversity that  
156 remains is at a tolerably low level (Fig. 3A).

157 Of the 30 EW animal species currently maintained in *ex situ* institutions for which we could  
158 find data, only 6 have populations exceeding 1500 individuals, and half are below 500 (Fig.  
159 1). Given that botanic gardens often hold just one or a few individuals of each species (30),  
160 we expect that the populations of EW plant species may be extremely small. What constitutes  
161 a viable population size is highly context specific, depending on the biology of the species,  
162 aspects of its management and environment, as well as varying definitions of "viable" (31).  
163 Viability can be expressed in demographic terms, for example the population size needed to  
164 have a specific probability of persistence over a specific period of time or number of  
165 generations. Meta-analyses of minimum viable population sizes calculated across hundreds of  
166 species have reported medians of 1377 (for a 90% probability of persistence over 100 years  
167 across 1198 animal and plant species) (32), 4169 (standardised to a 99% probability of  
168 persistence over 40 generations across 212 animal and plant species) (33), and 5816 (for a  
169 99% probability of persistence over 40 generations across 102 vertebrate species) (34), with  
170 wide and positively-skewed distributions. Most EW species for which data on population  
171 sizes are available are well below these estimates. Though population viability analyses were  
172 at some point carried out for at least eight currently EW species (all animals), we are only  
173 aware of three that currently use these tools to inform management (Table S2).

174 Managers of *ex situ* populations must also consider the impact population size has on  
175 retention of genetic diversity. In situations such as those faced by EW species, where  
176 supplementation of populations with individuals from elsewhere (i.e., the wild) is impossible,  
177 an effective population size ( $N_e$ ) of at least 500 is thought to be required for even well-  
178 founded populations to avert the loss of genetic diversity, and it has been argued that  $N_e =$   
179 1000 is a better approximation to maintain evolutionary potential (35).  $N_e$  corresponds to the  
180 number of individuals contributing to the next generation, and is generally considerably  
181 smaller than the total number of individuals in the population, the census population size ( $N$ ).  
182 In *ex situ* populations of threatened animals, the ratio of effective population size to census  
183 population size ( $N_e/N$ ) has been estimated to average 0.26 (36), implying that most  
184 populations should exceed 1900 individuals at the very least to maintain genetic diversity

185 (37). 80% of known populations of EW animals fall below this level, and half have census  
186 population sizes below even the minimum recommended  $N_e$ . These figures do not represent  
187 universal thresholds delineating viable populations from lost causes, but rather standards that  
188 enable us to highlight populations that may be at risk. In this light, the shortfall for EW  
189 species is stark.

190 Holding species across multiple collections provides a buffer against institutional-level risks  
191 such as disease outbreaks, catastrophes, and the financial insecurity and logistical challenges  
192 deepened by global crises such as the COVID-19 pandemic (38, 39). Worryingly, most EW  
193 animal species are reported at four or fewer institutions (Fig. 2, Table S2). The median  
194 number of holders for an EW plant species is eight, but we note that six EW plant species are  
195 reported at just a single institution (Fig. 2, Table S2). Reassuringly, it is not the same few  
196 institutions holding these species: The 43 species with fewer than 10 holders are spread  
197 across 93 institutions (53 zoological and 40 botanical). Overall, EW species are held by at  
198 least 501 institutions globally (239 zoological and 262 botanical).

199 However, distributing an EW species across several holders brings with it the potential for  
200 fragmenting an already compromised population into a set of smaller isolated groups. For  
201 animal species, breeding and transfer between different institutions comprising *ex situ*  
202 metapopulations can be managed regionally under formalised breeding programs: EAZA *Ex*  
203 *situ* Programmes (EEPs) in Europe, Species Survival Plans (SSPs) predominantly in North  
204 America, and Species Management Programs (SMPs) in Australasia. Global Captive  
205 Management Programs (GCMPs) have been proposed in recognition of the need for  
206 overarching global management, but these have struggled to gain traction, and no EW species  
207 has a GCMP despite the fact that at least eight are held across multiple regions (26). Despite  
208 their benefits, we find that SSPs are absent for 50% (5/10) of those held at North American  
209 institutions, while EEPs are absent for 18% (5/22) of EW animal species held at European  
210 institutions (Table S2). Even for species covered by a cooperative breeding program,  
211 implementation of management decisions can be challenging. Based on logistical, husbandry,  
212 demographic, or genetic factors, SSPs issue recommendations to transfer individuals between  
213 institutions or for individuals to breed with a specific mate or mates. However, a recent  
214 analysis has found that SSP recommendations to transfer individuals between institutions  
215 were fulfilled just 57% of the time, while the fulfilment rate of recommendations for specific  
216 individuals to breed was even lower at 20% (40).

217 Genetic management is informed by a reliable understanding of the pedigree of individuals  
218 within a population, generally recorded in a studbook. We were unable to find any indication  
219 of studbooks for 31% (10/32) of EW animal species managed *ex situ* (Table S2). Species  
220 missing studbooks were fish, amphibians, and invertebrates, taxa typically housed and bred in  
221 groups, a situation in which individual pedigrees are generally unavailable. However, such  
222 species can still be subject to genetic management using population genetic models and  
223 group-level information (41), as is deployed for *ex situ* populations of Polynesian tree snails  
224 (36, 42). Management of *ex situ* plant collections is hampered by poor knowledge of the  
225 provenance of populations, a limited ability to track them at an individual level, and a lack of  
226 coordination across institutions (30). Efforts to address these problems and develop pedigree-  
227 based metapopulation management techniques for plants are currently underway (30, 43).

228 For some plant species, storage of propagules in seed banking facilities offers an opportunity  
229 to pause generational turnover, and thus circumvent many of the processes that compromise  
230 genetic viability of *ex situ* populations over time. Though not suitable for all species (44), this  
231 technique—which can retain seed viability for potentially hundreds of years (45)—will be  
232 crucial in ensuring that at least 75 per cent of threatened plant species are maintained *ex situ*,

233 Target 8 of the Global Strategy for Plant Conservation (46). Using a seed storage prediction  
234 model (21, 47), we found that approximately 89% (31 of 35 species modelled, see Table S5)  
235 of EW plant species are predicted to produce desiccation-tolerant seeds suitable for seed  
236 banking. While it is possible that some accessions from living collections may refer to seeds,  
237 it is striking that only 28% (11/39) of EW plant species are reported by dedicated seed banks  
238 (Fig. 2).

239 Beyond loss of diversity through genetic drift, maintaining species in *ex situ* care across  
240 multiple generations brings the risk of adaptation to the conditions in which the species is  
241 kept (48), a risk that increases with population size and genetic diversity (38). Further, even  
242 optimal *ex situ* care cannot prevent *in situ* change: plants and animals held separate from wild  
243 environments for extended periods may not be well adapted to the shifting ecosystems to  
244 which we would like to return them (49).

245 The state of EW species should thus be regarded with a sense of urgency. With small founder  
246 and population sizes and a modest number of holding institutions, most risk genetic  
247 deterioration, declines, and extinction under our care. *Ex situ* conservation has been  
248 instrumental in preventing extinction in these species, but it is not a tool that can forestall it  
249 indefinitely. Re-establishment in the wild is a crucial step towards their recovery.

#### 250 **CONTRASTING FATES: EXTINCTIONS VS RETURNS TO THE WILD.**

251 We find that conservation translocations back to wild settings have been undertaken much  
252 less commonly for plant than animal species: only 26% (11/43) of historically (1950-2022) *ex*  
253 *situ*-restricted and 23% (9/39) of currently EW plant species, compared to the majority of  
254 both historically *ex situ*-restricted (32/53, 60%) and currently EW (22/33, 67%) animal  
255 species (Fig. 3, Tables 2, S2, and S4). The rate of translocations of plants from *ex situ*  
256 collections has been previously observed to be low (11), perhaps partly attributable to a lower  
257 level of attention and resource accorded to the conservation of plants when compared to that  
258 of animals (50). While the rate amongst animals is encouraging, overall we are still left with  
259 41 extant EW species (30 plants and 11 animals) that have never been subject to an attempt at  
260 a return to the wild. The Socorro dove (*Zenaida graysoni*), for example, collected from the  
261 wild in 1925 (14), is approaching a century—approximately 37 generations—in *ex situ* care.

262 The EW state can nevertheless represent a crucial waypoint on the pathway to recovery.  
263 There are 12 species (10 animals and two plants) that were once extirpated from the wild but  
264 are now considered to have wild populations again (Fig. 3, Table 2). These include the  
265 Jaramago de Alborán (*Diplotaxis siettiana*), now categorized as Critically Endangered on the  
266 red list; the Yarkon bream (*Acanthobrama telavivensis*), which has been downlisted to  
267 Vulnerable; and the European Bison (*Bison bonasus*), which has recovered out of the  
268 threatened categories to Near Threatened. But less fortunate fates are also possible: 11  
269 species have gone extinct after existing only in *ex situ* care (Fig 3, Table 1). These include the  
270 St Helena olive (*Nesiota elliptica*) and the Pinta giant tortoise (*Chelonoidis abingdonii*), both  
271 lost in the last decade.

#### 272 **THE NEED FOR AN IMPROVED SYSTEM OF ASSESSING *EX SITU*-** 273 **RESTRICTED TAXA**

274 Though we expanded our investigation of historically *ex situ*-restricted species beyond those  
275 assessed on the Red List as EW, we have deferred to the Red List in confirming present day  
276 extinction from the wild (21). This likely underrepresents the true number of species that  
277 currently merit the status or are approaching it. For example, a further 58 species (46 plants  
278 and 12 animals) currently assessed as Critically Endangered have been tagged as “Possibly  
279 Extinct in the Wild” (4, 51). In addition, the often slow pace of changes in Red List status

280 (52) combines with a conservative approach to declaring extinction (53) to produce a  
281 considerable lag between a species last being seen in the wild and it first being listed as EW:  
282 we find 11 years to be the median interval. Bearing in mind the threat of an oncoming wave  
283 of extinctions over the coming decades (54), a considerable number of *ex situ*-restricted  
284 species may therefore be accumulating with no reliable way of identifying them. Species that  
285 have recently been claimed to probably qualify as EW but are not yet assessed as such  
286 include the ‘ālua (*Brighamia insignis*) (43), a shrub native to Hawaii, the Vietnam pheasant  
287 (*Lophura edwardsi*) (55), and the Javan pied starling (*Gracupica jalla*) (56), all of which are  
288 classified as Critically Endangered, but only the first bearing the “Possibly Extinct in the  
289 Wild” tag.

290 It is clear, however, that designation as EW would not facilitate the evaluation of extinction  
291 risk or recovery potential. As is demonstrated in this study, the single EW category contains  
292 such variability in the viability of its species (and efforts to quantify that viability) as to  
293 potentially conceal the plight of the least secure. Might the Catarina pupfish (*Megupsilon*  
294 *aporus*) be with us today had its precarious status in the years running up to its demise been  
295 better characterised and communicated (57)? It is certainly not credible to place such a  
296 species in the same category of extinction risk as, say, the milu (Père David’s deer, *Elaphurus*  
297  *davidianus*) which, after over 35 years of reintroductions and conservation management,  
298 numbers over 9000 individuals of varying degrees of “wildness” distributed across its native  
299 range in China (58) while still being assessed as EW. An improved system for assessing the  
300 health and progress of EW species would be both beneficial and—given that the global  
301 databases that could inform such surveillance are already established—feasible.

## 302 **RECOMMENDATIONS**

303 The cases we depict chart more than 70 years of attempts to use *ex situ* conservation to  
304 prevent extinction and facilitate the recovery of species on the very brink, highlighting both  
305 the fragility of this status and the potential for success despite that fragility. Ensuring that the  
306 fortunes of EW species continue to bend away from extinction requires a redoubling of effort  
307 and a collective realisation—in the minds of the conservation community, legislators, and the  
308 public—of their existence and plight. In response, the IUCN World Conservation Congress  
309 2020 called for the re-establishment of current EW species in the wild by 2030 (59). This  
310 should be coupled with the identification of further currently threatened species whose  
311 recovery could be achieved through *ex situ* care. We urge a forward-looking approach to  
312 rescue, revitalize, release, and reinforce populations: rescue suitable species close to  
313 extinction into *ex situ* care, revitalise and strengthen current *ex situ* populations to ensure  
314 continued viability, engage in ambitious and innovative release programs to return species to  
315 the wild, and drive recovery of released populations through continued reinforcement and  
316 management.

317 Deciding where, when, and whether to rescue species is not a trivial task and is confounded  
318 by risky (that is uncertain) outcomes and strong emotions. From a biological perspective, the  
319 removal of a species to *ex situ* care may be challenging such that the attempt accelerates  
320 extinction and, combined with downstream consideration of the likelihood of successful wild  
321 releases from *ex situ* care, should be weighed against *in situ* alternatives (60). Decisions about  
322 rescue will always go beyond biological perspectives to include a mix of financial, ethical,  
323 social and cultural considerations. For example, at least four Hawaiian forest bird species  
324 face extinction in the coming decade as a result of avian malaria (61). The immediate  
325 removal of individuals into *ex situ* care, and thus the likely creation of EW populations, is  
326 seen as the management action with the highest probability of extinction avoidance for at  
327 least one of these species, the ‘akikiki (*Oreomystis bairdi*), with an estimated wild population



328 in 2021 of just 45 individuals (61). The location of *ex situ* facilities must balance Native  
329 Hawaiians' preference not to remove birds from Hawai'i (61). Such multi-objective decisions  
330 are inevitable in conservation and influence what alternatives are available and how a best  
331 one is selected. We encourage adopting a transparent and deliberative approach to decision  
332 making on a case by case basis, such that values are clearly identified and decisions are  
333 rationally made in light of these (62). We must be bold and take urgent risky action, but this  
334 does not mean abandoning critically important recognition of values and drawing on  
335 available science to inform what this action is and how we best implement it. We wish to  
336 avoid cases such as the Christmas Island pipistrelle (*Pipistrellus murrayi*), for which *ex situ*  
337 care was proposed and eventually agreed upon, but, through delay and indecision, inaction  
338 and extinction became the action inadvertently chosen (63).

339 Similarly, *ex situ* institutions such as zoos and botanic gardens must balance multiple values,  
340 of which EW species conservation is just one. In most cases, revitalisation of *ex situ* EW  
341 populations will require significant additional resources: more individuals require more  
342 space, infrastructure, and staff time. This must be balanced with the contributions *ex situ*  
343 institutions also play in non-EW species conservation, education, visitor experience and the  
344 space and financial constraints required to deliver these. Whilst we are indebted to such  
345 institutions for being the only things standing between EW species and extinction, we  
346 encourage a much more strategic approach to EW species *ex situ* care whereby decision  
347 science is used to develop unified management plans informed, at the least, by population  
348 viability analysis and genetic management. In addition, we call on funders to support the  
349 delivery of *ex situ* care and consequent recovery in the wild via release and reinforcement.

350 As recovery in the wild ought to be an ultimate objective for all EW species, management  
351 plans for *ex situ* populations should be integrated with *in situ* planning, as is envisaged in the  
352 IUCN's "One Plan Approach" (64), which has not, as far as we can identify, been adopted for  
353 any EW species. There are many reasons why some EW species have never been released  
354 into the wild. For some plants, such as the seven EW *Brugmansia* species native to South  
355 America, historic wild localities are simply not known (65). For some species, such as the  
356 sihek (or Guam kingfisher, *Todiramphus cinnamominus*), their indigenous range remains  
357 inhospitable to their return. However, reasoned and bold actions may allow wild recovery  
358 either through proactive removal of *in situ* extinction drivers, or releases beyond indigenous  
359 range (66, 67). For example, Christmas Island blue-tailed skinks (*Cryptoblepharus egeriae*)  
360 have been released to the wild on the Cocos (Keeling) islands (68) and proposals for sihek  
361 releases on Palmyra Atoll are under consideration (69). Whilst release is a landmark  
362 moment—and is rightly celebrated—this should typically mark the beginning of a long-term  
363 commitment to recover the species *in situ*. Pioneering work has returned 10 formerly-  
364 extirpated Polynesian tree snail species to the Society Islands, but considerable obstacles to  
365 the recovery of many of these species remain in part due to the ongoing threats posed by the  
366 non-native predatory New Guinea flatworm (*Platydemus manokwari*) (70). Rather than give  
367 up, those involved in Polynesian tree snail recovery are learning and modifying how to best  
368 attempt new releases and reinforce all wild populations. With sustained support and adaptive  
369 management, the Polynesian tree snails and others can emulate the successful paths back to  
370 recovery in the wild forged by species such as the Yarkon bream and European bison.

371 Real opportunities to prevent extinction and return previously lost species to the wild abound.  
372 We must take them.

373

374 **References**

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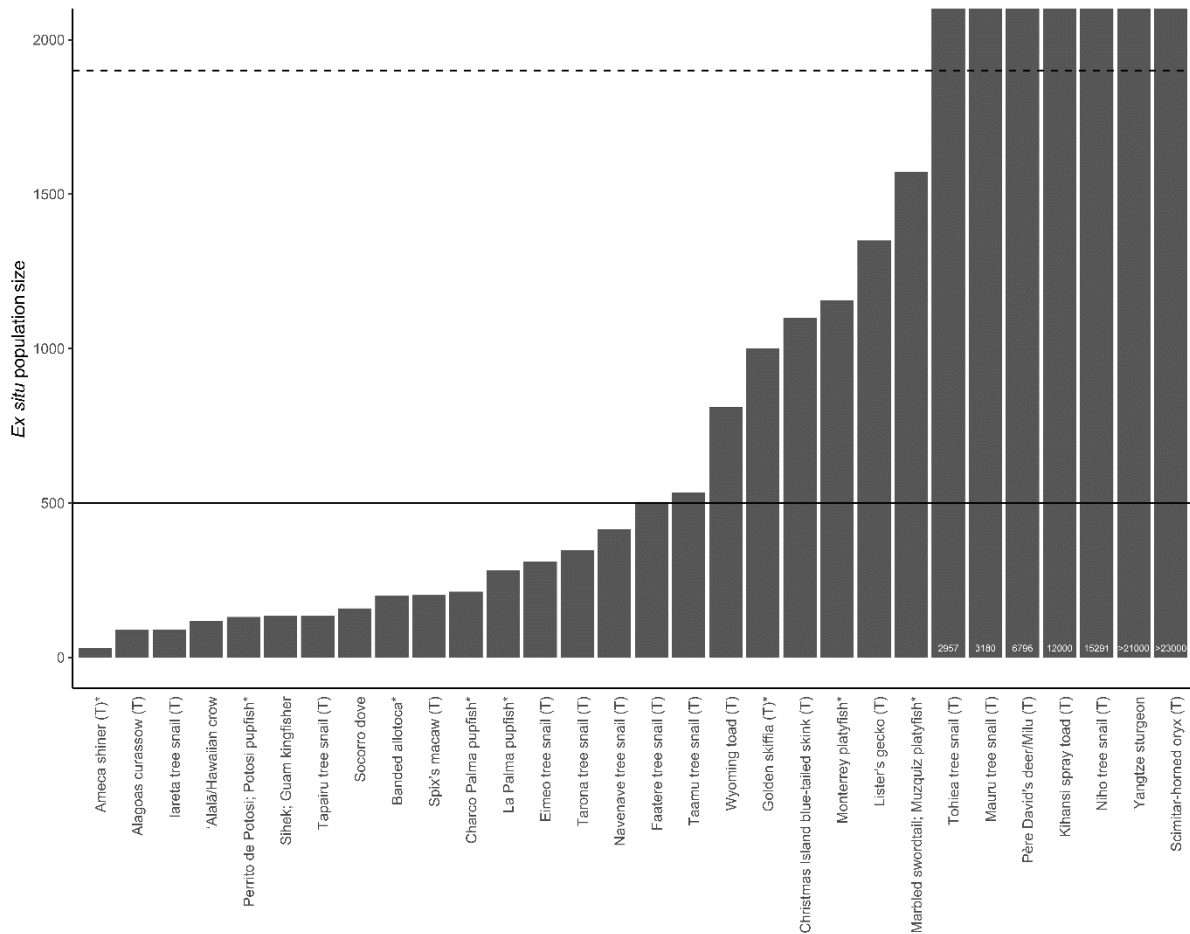
748 **Supplementary Materials**

749 Materials and Methods

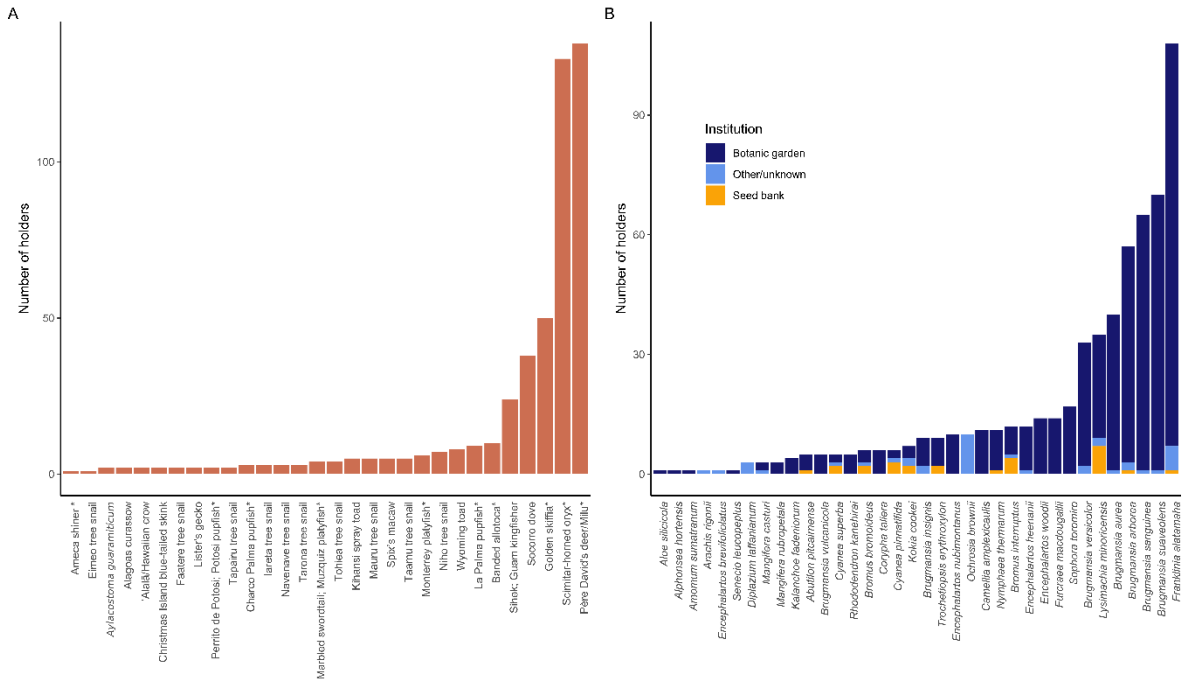
750 Tables S1 to S5

751 References (93 – 137)





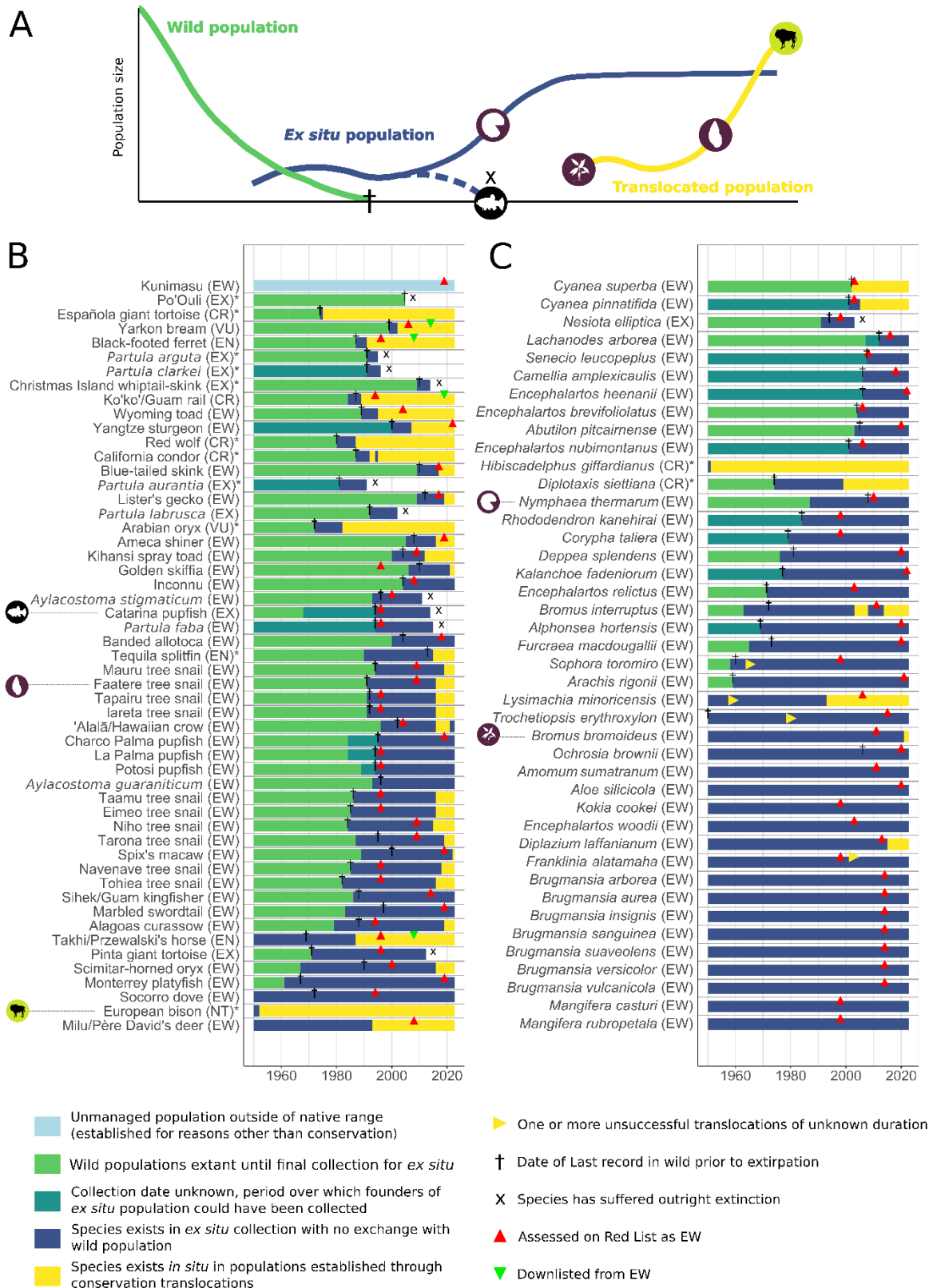
756 **Fig. 1. Estimated *ex situ* population sizes of EW animal species.** Solid horizontal line:  
 757 Minimum  $N_e$  recommended to minimise loss of genetic diversity (500). Dashed horizontal  
 758 line: minimum census population size expected to ensure effective population size of 500  
 759 (1900 individuals, see (37)). Where population sizes are above 2000, the total size is denoted  
 760 at the base of the bar. Population estimates are for 30 of the 32 EW animal species held *ex*  
 761 *situ*. They were compiled using Zoological Information Management System (ZIMS) (22), a  
 762 database representing the real-time holdings of more than 1100 zoological and aquarium  
 763 collections globally, combined with academic and grey literature, and advice from relevant  
 764 taxon experts and conservation practitioners. Species marked with an asterisk (\*) may have  
 765 additional individuals kept by hobbyists. Species marked with (T) have additional *in situ*  
 766 populations as a result of conservation translocations, but these are not yet considered wild  
 767 under the Red List.



768

769 **Fig. 2. Holders of *ex situ* EW species.** Panel A: Estimates number of holders for 30 of the 32  
 770 EW animal species held *ex situ*. Estimates produced as for Fig. 1. Species marked with an  
 771 asterisk (\*) may have additional individuals kept by hobbyists. Panel B: Estimates for number  
 772 and type (botanical garden, seed bank, or unknown) of *ex situ* holders of 36 of the 39 EW  
 773 plant species. Compiled using PlantSearch, a database reporting the living plant, seed, and  
 774 tissue holdings of more than 1100 botanical collections globally (27), combined with  
 775 academic and grey literature, and advice from relevant taxon experts and conservation  
 776 practitioners.

777



778

779 **Fig. 3. The conservation history of all species known to have met the definition of EW**  
 780 **since 1950. (A)** Schematic showing stages in the process of recovery of highly threatened  
 781 species through collection for *ex situ* care, *ex situ* population growth and maintenance,  
 782 and return to the wild through translocations. Pathways through these stages or towards extinction  
 783 are illustrated with icons representing example species in panels B and C. **(B & C)** Timelines

784 representing the history of this process for all animal (**B**) and plant (**C**) species that would  
785 have met the definition of EW since 1950. Colours represent the population status and  
786 activity over the time period depicted. Species are listed in ascending order of time spent in  
787 *ex situ* care experiencing no exchange with wild populations (using the minimum possible  
788 duration where this is not known with certainty). The present Red List status is listed in  
789 parentheses after the common name (animals) or scientific name (plants). Species marked  
790 with an asterisk (“\*”) have never been listed as EW on the Red List.



**Table 1. Species that have gone extinct after having been *ex situ*-restricted since 1950.**

Scientific name	Common name	Kingdom	Class	Year last recorded in wild	Extinction year	Published Red List assessments	Notes	Additional references
<i>Aylacostoma stigmaticum</i>		Animals	Gastropoda	1996	2011	EW (2000).	Collected from the wild into <i>ex situ</i> care in 1993 prior to the filling of a reservoir in its native habitat. The last known wild population disappeared by 1996. This species became extinct outright in 2011 due to a disease outbreak in <i>ex situ</i> facilities whose causal agent was unidentified but was suspected to be viral.	
<i>Chelonoidis abingdonii</i>	Pinta giant tortoise	Animals	Reptilia	1972	2012	EX (2016); EW (1996, as <i>Geochelone nigra abingdoni</i> )	The last known individual of the species, known as Lonesome George, survived in <i>ex situ</i> care from his collection in 1972 until his death in 2012 marked the extinction of the species.	
<i>Emoia nativitatis</i>	Christmas Island whiptail-skink	Animals	Reptilia	2010	2014	EX (2017); CR (2010).	Declines in wild first reported 1998, likely driven by introduced species. Three females caught in 2009 in an attempt to start captive breeding. Last known individual of species died <i>ex situ</i> in 2014.	(13)
<i>Melamprosops phaeosoma</i>	Po'Ouli	Animals	Aves	2004	2004	EX (2019); CR (1994, 1996, 2000, 2004, 2007, 2008, 2009, 2012, 2013, 2016, 2018); T (1988).	By 1997, only three individuals were known. The last sightings for two of these were in December 2003 and January 2004. The last known individual was captured in September 2004, but died in captivity 78 days later in November 2004.	(72)
<i>Megupsilon aporus</i>	Catarina pupfish	Animals	Actinopterygii	1994	2014	EX (2019); EW (1996); E (1994, 1990, 1988, 1986).	Was endemic to Potosi Spring, which dried out due to groundwater extraction. The species was difficult to maintain in captivity, being sensitive to environmental conditions and vulnerable to infections. Serious declines occurred in 2013, and its scattered distribution across multiple holders likely inhibited full appreciation of the significance of these. The last remaining individual died in 2014.	(57)
<i>Nesiota elliptica</i>	St Helena olive	Plants	Magnoliopsida	1994	2003	EX (2016, 2004); EW (2003, 1998).	This species, native to Saint Helena, was rediscovered in the remnants of its native habitat in 1977. This last known wild individual died in 1994, but seeds and cuttings taken from the tree led to attempts to cultivate	(73)

							the species <i>ex situ</i> . It proved difficult to maintain, and fungal infections killed the final seedlings and cuttings in 2003.	
<i>Partula arguta</i>		Animals	Gastropoda	1991	1995	EX (1996, 2009); EN (1994).	Endemic to Huahine, Society Islands. As is the case for the other <i>Partula</i> species covered by this study, this species was collected into <i>ex situ</i> care prior to extirpation from the wild due to the introduction of the carnivorous snail <i>Euglandina rosea</i> . Last known individual died <i>ex situ</i> in 1995.	(42, 74, 75)
<i>Partula aurantia</i>	Moorean viviparous tree snail	Animals	Gastropoda	1981	1991	EX (2019, 2009, 2006); EN (1994).	Endemic to Moorea, Society Islands. As is the case for the other <i>Partula</i> species covered by this study, this species was collected into <i>ex situ</i> care prior to extirpation from the wild due to the introduction of the carnivorous snail <i>Euglandina rosea</i> . The last individual died in <i>ex situ</i> care in 1991	(76–78)
<i>Partula clarkei</i> (Reclassified from <i>P. turgida</i> )		Animals	Gastropoda	1991	1996	EX (1994, 1996, 2009).	Endemic to Raiatea, Society Islands. As is the case for the other <i>Partula</i> species covered by this study, this species was collected into <i>ex situ</i> care prior to extirpation from the wild due to the introduction of the carnivorous snail <i>Euglandina rosea</i> . Last known individual died <i>ex situ</i> in 1996 after abrupt population declines attributed to microsporidian parasites (70), but the causal agent has since been questioned (14).	(42, 79)
<i>Partula faba</i>		Animals	Gastropoda	1994	2015	EW (2009, 1996); E (1994).	Endemic to Raiatea and Tahaa, Society Islands. As is the case for the other <i>Partula</i> species covered by this study, this species was collected into <i>ex situ</i> care prior to extirpation from the wild due to the introduction of the carnivorous snail <i>Euglandina rosea</i> . The last individual died in <i>ex situ</i> care in 2015.	(42)
<i>Partula labrusca</i>		Animals	Gastropoda	1992	2002	EX (2009); EW (1996); E (1994).	Endemic to Raiatea, Society Islands. As is the case for the other <i>Partula</i> species covered by this study, this species was collected into <i>ex situ</i> care prior to extirpation from the wild due to the introduction of the carnivorous snail <i>Euglandina rosea</i> . The last individual died in <i>ex situ</i> care in 2002.	(42)

Not all species were listed on the Red List as EW, see “published Red List assessments” column for details. Key to Red List

categories: CR: Critically Endangered; E: Endangered (pre-1994 category); EN: Endangered; EX: Extinct; EW: Extinct in the Wild;

NT: Near Threatened; T: Threatened (pre-1994 category); VU: Vulnerable

**Table 2. Species that have regained IUCN wild status after having been *ex situ*-restricted since 1950.**

Scientific name	Common name	Kingdom	Class	Last reported in wild	Number of individuals collected (of which, number of founders)	Year conservation translocations started (R: Reintroduction, AC: Assisted Colonization)	Published Red List assessments	Notes	Additional references
<i>Acanthobrama telavivensis</i>	Yarkon bream	Animals	Actinopterygii	1999	150	R: 2002	VU (2014); EW (2006).	Native to coastal streams of Israel, this species declined across the second half of the twentieth century until a severe drought in 1999 dried out the last remnants of its habitat. To secure the future of the species, 150 fish were brought into <i>ex situ</i> care in the days prior to extirpation. Reintroduction attempts followed just three years later which were further refined in subsequent years alongside habitat restoration. The species now has a growing population in the wild again.	(80)
<i>Bison bonasus</i>	European bison	Animals	Mammalia	1927	54 (12)	R: 1952	NT (2020); VU (2008); EN (2000, 1996); V (1994, 1990, 1988); "Very rare but believed to be stable or increasing" as <i>B. b. bonasus</i> (1965)	Once distributed across western, central, and south-eastern Europe. Declined alongside human expansion with its associated hunting pressure and ecosystem alteration. Finally extirpated from the wild in 1927, but survived in European zoos. A breeding project commenced in Białowieża, Poland, in 1929, leading to the first reintroductions back into the wild in 1952. Wild populations have grown to the point of the current categorisation of Near Threatened, though the species still depends on conservation management.	(81, 82)
<i>Canis rufus</i>	Red wolf	Animals	Mammalia	1980	14 (12)	R:1987	CR (2018, 2004, 1996); E (1994, 1990, 1988, 1986, 1982)	Once common in the eastern United States, the red wolf declined due to human persecution and hybridisation with coyotes ( <i>Canis latrans</i> ). 400 canids were collected from the wild between 1973 and 1980, from which what were believed to be the last fourteen pure red wolves were selected to initiate an <i>ex situ</i> population.	(83)
<i>Chelonoidis hoodensis</i>	Española giant tortoise	Animals	Reptilia	1974	15 (15)	R: 1975 AC: 2015	CR (2017, 2016, 1994 as <i>Geochelone</i>	Endemic to Española, the Galápagos Islands, exploitation for human consumption and habitat degradation drove the wild population to a low	(84, 85)

							<i>nigra hoodensis</i> )	point of 14 in 1974, at which point all remaining individuals were removed to establish an <i>ex situ</i> population (joined by an additional male already present in San Diego Zoo). Reintroductions commenced the following year. Used as an ecological replacement for a now-extinct tortoise species on Santa Fe island from 2015.	
<i>Diploptaxis siettiana</i>	Jaramago de Alborán	Plants	Magnoliopsida	1974	Not reported	R: 1999	CR (2011, 2006); EX (1998)	Endemic to the island of Alborán, Spain. Extensive human modification of habitat, particularly the introduction of cattle, likely led to declines. Species was not seen after 1974. Reintroductions commencing in 1999 established a self-sustaining population.	(11)
<i>Equus ferus</i>	Takhi; Przewalski's Horse	Animals	Mammalia	1969	53 (12)	R: 1997	EN (2015, 2011); CR (2008); EW (1996).	Ranged across the Eurasian steppe from Russia east to northern China and Mongolia until the 1800s, around which point it began to decline. Remnant populations persisted until the last wild individual was recorded in the Dzungarian Gobi Desert in 1969. 11 of 12 founders contributing to present population had been captured into <i>ex situ</i> care between 1899 and 1902, with 1 additional mare caught in 1947. Reintroductions commenced in Mongolia in the 1990s.	(86)
<i>Gymnogyps californianus</i>	California condor	Animals	Aves	1987	22 (14)	R: 1992 & 1994	CR (2020, 2018, 2017, 2016, 2015, 2013, 2012, 2010, 2009, 2008, 2006, 2004, 2000, 1996, 1994); T (1988).	Precipitous population declines in the twentieth century driven largely by persecution and poisoning due to consumption of carcasses containing lead shot. The last known individuals of the species were collected from the wild by 1987 to initiate an <i>ex situ</i> population. Reintroductions started 1992. All reintroduced individuals were collected back into captivity in 1994 due to behavioural problems. Reintroductions recommenced 1995.	(87)
<i>Hibiscadelphus giffardianus</i>		Plants	Magnoliopsida	1930	1	R: 1951	CR (1998); E (1978)	Only one individual of this small tree native to Hawai'i was ever known. This tree died in 1930, but seeds were collected and the species was propagated <i>ex situ</i> . Replanted in original habitat between 1951 and 1964.	(88)
<i>Hypotaenidia owstoni</i>	Ko'ko'; Guam Rail	Animals	Aves	1987	22	AC: 1989 R: 1998	CR (2019); EW (2016); EW (2012, 2010, 2008, 2004, 2000, 1996, 1994, as	Extirpation from Guam in 1987 driven largely by brown tree snakes. Conservation translocations started on the island of Rota (outside of native range) in 1989, but, despite evidence of breeding here, this population is not considered to be self-sustaining due to the continued release efforts	(89, 90)

							<i>Gallirallus owstoni</i> ); T (1988, as <i>Rallus owstoni</i> ).	required to ensure its persistence. A 1998 release into a snake-controlled area in Guam failed due to destruction of the snake barrier by a typhoon in 2002. Releases on the island of Cocos starting in 2010 have seen breeding (by 2014), and this population is now considered self-sustaining and was the basis for downlisting to CR in 2019.	
<i>Oryx leucoryx</i>	Arabian oryx	Animals	Mammalia	1972	≥17 (17)	R: 1982	VU (2017, 2011); EN (2008,2003, 1996); E (1994, 1990, 1988, 1986); "Very rare and believed to be decreasing in numbers" (1965).	Once distributed across the Arabian Peninsula, experienced steep population declines in the twentieth century. Last reported in the wild in 1972. A captive program was commenced in 1962-63 in the USA with nine individuals, at least three of which were wild caught for conservation purposes. In parallel to this, a collection was established in Riyadh containing additional animals from Saudi Arabia and Qatar, as well as individuals from the USA herd. In 1993, the global population was reported to be derived from 17 wild-caught founders.	(91)
<i>Mustela nigripes</i>	Black-footed Ferret	Animals	Mammalia	1987	18 (7)	R: 1991	EN (2015, 2008); EW (1996); E (1994, 1990, 1988, 1986, 1982); "Very rare and believed to be decreasing in numbers" (1965)	The black-footed ferret was once distributed across west central North America, from southern Canada to northern Mexico, tightly linked to the habitat of its principal prey, prairie dogs ( <i>Cynomys</i> spp.). Habitat conversion, persecution of prairie dogs as an agricultural pest, and sylvatic plague led to precipitous ferret declines across the twentieth century. The species was thought lost in the 1970s until discovery of a declining small population in 1981. The last known individuals were captured into <i>ex situ</i> care in 1987. Multiple reintroductions starting in 1991 have resulted in at least three self-sustaining wild populations.	(92)
<i>Zoogoneticus tequila</i>	Tequila splitfin	Animals	Actinopterygii	2013	6	R: 2015	EN (2019); CR (2009)	Endemic to the upper Río Ameca in Jalisco, Mexico. Extirpated in 2013, probably due to the impacts of introduced species and habitat degradation. Reintroductions started in 2015, establishing a population that is currently growing.	

Not all species were listed on the Red List as EW, see “published Red List assessments” column for details. Key to Red List categories: CR: Critically Endangered; E: Endangered (pre-1994 category); EN: Endangered; EX: Extinct; EW: Extinct in the Wild; NT: Near Threatened; T: Threatened (pre-1994 category); VU: Vulnerable

**Table 3. Number of individuals initiating *ex situ* populations, and—where reported—number of founder lineages currently represented, of animal (left) and plant (right) EW species.**

<b>Animal species</b>	<b>Number of individuals collected (of which, number of founders)</b>	<b>Plant species</b>	<b>Number of individuals collected</b>
Alagoas curassow	5 (3)	<i>Abutilon pitcairnense</i>	1
Ameca shiner	6	<i>Cyanea pinnatifida</i>	1
Wyoming toad	10	<i>Encephalartos relictus</i>	1
‘Alalā (or Hawaiian crow)	10 (9)	<i>Encephalartos woodii</i>	1
Spix’s macaw	17 (7)	<i>Kokia cookei</i>	1
Socorro dove	17	<i>Sophora toromiro</i>	1
Milu (or Père David's deer)	18 (11)	<i>Cyanea superba</i>	3

Sihek (or Guam kingfisher)	29 (16)	<i>Diplazium laffanianum</i>	5
Lister's gecko	43		
Golden skiffia	<50		
Scimitar-horned oryx	48-60		
Blue-tailed skink	66		
Kihansi spray toad	499		

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## Supplementary materials

### Materials and Methods

We compiled a list of all species historically qualifying for the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Red List) category of Extinct in the Wild (EW) (4). The EW category is applied to any species “known only to survive in cultivation, in captivity or as a naturalized population (or populations) well outside the past range” (12). We will hereafter refer to species that we regard as having met one of the first two conditions as having been *ex situ*-restricted and reserve the term EW for those species that have been officially assessed on the Red List as such. We are aware of only one species, the kunimasu (*Oncorhynchus kawamurae*), that has been assessed as EW on the basis of being restricted to naturalized populations outside of its native range established through intentional release for commercial fishing purposes (93). This essentially wild state is not the primary focus of this study.

Though the EW category was first introduced by the IUCN in 1994 (19), we extended our analysis back to 1950, approximating the start of modern species conservation (20). This time window enabled us to build a comprehensive list of species in a comparable context, minimising the risk of biasing our selection towards well-known cases. Some species that were historically *ex situ*-restricted, such as the thylacine (*Thylacinus cynocephalus*) or passenger pigeon (*Ectopistes migratorius*), therefore fell outside of our scope.

The assessments of the 84 species (40 animals and 44 plants) currently categorised as EW were extracted from the Red List version 2022-2 (4). Species that were formerly EW but have since been assessed as extinct (three animal species, and one plant species Table 1) or have been downlisted to another category (i.e., an improvement in conservation status: four animal species, Table 2) were compiled from IUCN summary statistics for “genuine” status changes (4). Genuine Red List changes are reassignments in category as a result of true improvements or deteriorations in the species’ status, as opposed to revisions based on previously-unavailable information, taxonomic revision, correction of error, or an update in the criteria version used. We then identified additional species that would have been *ex situ*-restricted at any point between 1950 and the introduction of the EW category in 1994. Such a historical state is not currently recorded in any systematic way in the Red List, but the information is often contained within the narrative text of assessments. Therefore, to find cases of such species that have since gone extinct, we reviewed the narrative texts of the Red List assessments of all 180 extinct species with a “year last seen” reported as 1950 or later for descriptions of an *ex situ*-restricted state. It was not feasible to similarly manually review every assessment of an extant species, given that their number exceeds 140000. However, if any such species had once been *ex situ*-restricted, its populations that are now considered wild must have been established via a conservation translocation. We therefore reviewed the Red List assessments of all species that have distributions whose origins are coded as “reintroduced” or “assisted colonisation”. In case of incomplete or incorrect origin coding, we also searched the narrative text of all Red List assessments for the phrase “extinct in the wild” for mention of species that are acknowledged as having previously occupied the state without having been assessed as such.

Through these approaches, we identified 13 additional species (11 animals and two plants) that were at some point *ex situ*-restricted but never recorded on the Red List as EW (see Table 1



for the five species that have since gone extinct, and Table 2 for the eight species that have since returned to the wild). We also identified an additional plant species that is now extinct having previously been assessed as EW but was not included in IUCN summary statistics on genuine status changes (see Table 1).

Confirmation of outright extinction in the wild is an exhaustive process (53) beyond the scope of this study. We therefore refrained from searching for species whose purported recent extinction in the wild has not yet been confirmed in their Red List assessments. Similarly, while we have collated information on attempts to re-establish EW species into the wild, we have refrained from engaging in any consideration as to whether these *in situ* populations should be considered to have reached wild status, thus prompting a downlist of the species. We again defer to the Red List process to make such determinations. We considered any reported extinction in *ex situ* care of a species already assessed as EW to be unambiguous, however, and incorporated these where relevant (two species, see Table 1). We identified a further ten species (five animals and five plants) currently assessed as EW whose assessments appear erroneous: two are extinct having never been in *ex situ* care, three are likely extant in the wild having never been extirpated, three are synonyms of species that remain extant in the wild, and the statuses of two are unknown (Table S1).

We therefore report on 95 species (52 animals and 43 plants) that are known to have been extirpated to *ex situ* care since 1950, 72 of which (33 animals and 39 plants) are considered to remain in this state as of 2022. For each species, we collected information on the history of the collection, *ex situ* maintenance, and conservation of each, namely: the periods over which founders of the *ex situ* population were collected from the wild; the number of individuals collected to initiate the *ex situ* population; the number of founders represented in the present population (where this is noted as a separate number); the year the species was last recorded in the wild; and the timing and status of any attempts to re-establish the species in the wild through conservation translocations. Following IUCN guidelines for reintroductions and other conservation translocations (66), we considered conservation translocations as involving the intentional release of individuals into the wild for the purpose of the conservation of the species. Releases into indigenous range were counted as reintroduction attempts, and those outside of indigenous range were counted as assisted colonisations (66). Where this information was not contained in a Red List assessment, we sought it from recovery project documentation and academic literature. Where information appeared incomplete or unclear, we contacted taxon experts and conservation practitioners identified through the literature, studbook listings on ZIMS, and through the relevant IUCN taxonomic specialist group. We additionally ran targeted Google and Google News searches using the common and scientific names of each species and reviewed the first 30 results, as information on actions such as recent conservation translocations is often captured on project websites and news reports but not in the scientific or grey literature. Where information was obtained from sources outside the Red List, it is indicated in the “additional references” column in Tables 1, 2, and S1-S4.

The status of the *ex situ* populations of currently EW species was assessed by quantifying the number of institutions holding them; the type of institution for plants (i.e., botanical garden or seed bank); the total *ex situ* population size for animals (this is not generally quantified or reported for plants); whether an animal species was subject to metapopulation management or had a studbook; and whether any Population Viability Analyses (PVAs) had been carried out for *ex situ* populations. Information on studbooks, the number of holders, and population sizes for animal species was obtained on January 3<sup>rd</sup> 2023 from the Zoological Information Management

System (ZIMS), a database representing the real-time holdings of more than 1100 zoological and aquarium collections globally, maintained by the conservation and wildlife care NGO Species360 (22). We recorded whether a species was part of a cooperative breeding program by consulting the Association of Zoos and Aquariums' database of Species Survival Programs (SSPs) (23), the European Association of Zoos and Aquaria's list of EEPs (24), Australasia's Zoo Aquarium Association's list of Species Management Programs (SMPs) (25), and the World Association of Zoos and Aquariums' list of Global Species Management Plans (26). Information for plant species was obtained from PlantSearch, a database reporting the living plant, seed, and tissue holdings of more than 1100 botanical collections globally, maintained by Botanic Gardens Conservation International (27). PlantSearch receives disaggregated collections data from individual gardens and also differentiates between seed bank and living plant collections. From this disaggregated data it is possible to calculate the number of different institutions that hold collections of any given taxon. However, it is not possible to assess whether these collections are of different provenances, meaning that PlantSearch data gives only a rough indication of the breadth of genetic diversity held *ex situ*. PlantSearch does not record population sizes; these are maintained on individual gardens' collection management databases, most of which were not available to this study. This situation is about to change with the development of a plant exchange pedigree tool, based on the zoo model, and due to be launched in 2023 (30, 43). To assess the usage of PVAs in the *ex situ* management of EW species, we ran Google searches for the species and common name combined with the terms "population viability analysis" and "PVA" and reviewed the first 30 results where present.

Through our review of the literature and other material described above, and by contacting individual institutions and taxon experts, we were able to incorporate additional information on EW species. *Ex situ* EW populations external to the ZIMS and PlantSearch databases were collated for seventeen species (thirteen animals and four plants) eight of which (four animals and four plants) were not otherwise represented. We were unable to obtain detailed information on the *ex situ* populations of three EW species (one animal and two plants, see Table S3 for details). Through this approach we have collated the most comprehensive and relevant overview of the *ex situ* populations of EW species feasible (Figs 1-2, Tables S2-S4). However, we acknowledge that there will be some material outside of the reach of our survey, such as that maintained by hobbyists and private collectors. We note, for example, that this is likely the case for eight Mexican freshwater fish species (see Fig. 1). Additionally, many institutions do not update their PlantSearch records regularly, so shifts in holdings may have occurred since species were last accessioned. However, we do not expect that any such alterations would significantly alter our population summaries.

To predict the seed storage behaviour of EW plant species, we applied the model developed by Wyse and Dickie and available through the web interface presented at [https://seedcollections.shinyapps.io/seed\\_storage\\_predictor/](https://seedcollections.shinyapps.io/seed_storage_predictor/) (47). This model harnesses an extensive dataset to predict the probability that a given species will produce desiccation-sensitive (recalcitrant) seeds. This prediction is based on: published seed storage information, taxonomic relationships between the species in question and species with known seed storage behaviour, climate and elevation data for the species, woodiness, seed mass, and dispersal mode. The model is run at three different taxonomic levels—order, family, or genus—depending on the degree of information available, with predictions based on higher taxonomic levels giving less reliable results. Results based on species level are not model predictions, being instead directly based on existing information in the database for that species. The model returns a probability of a species

being recalcitrant between 0 (desiccation-tolerant (orthodox)) and 1 (recalcitrant). Results closer to 0.5 are less reliable. We were unable to obtain a prediction for four species: *Diplazium laffanianum*, *Encephalartos heenanii*, *Encephalartos relictus*, *Kalanchoe fadeniorum*. 31 of the remaining 35 species were predicted (27 species) or known (four species) to have orthodox seed storage behaviour, the remaining four species were predicted to have recalcitrant seeds. Predictions were mostly based on family (18 species) or genus (10 species). See Table S5 for detailed model output. These predictions give an indication of the extent of seed desiccation tolerance in our dataset, but we emphasise that experimentation and improved reporting of seed storage behaviour in EW plant species is a critical need.

**Table S1.**

<b>Scientific name</b>	<b>Kingdom</b>	<b>Class</b>	<b>Proposed true status</b>	<b>Justification</b>	<b>Additional references</b>
<i>Agave lurida</i>	Plants	Liliopsida	Synonym	Synonym of <i>Agave vera-cruz</i> , which is not yet assessed on the Red List but is extant in the wild in its native Mexico as well as introduced populations in South America and Asia.	(94, 95)
<i>Aylacostoma chloroticum</i>	Animals	Gastropoda	Extant in wild	Believed to be extirpated from the wild by 1996, but additional populations were discovered in 1997 and 2003. One population remains, though it is threatened by high parasitic worm burden.	
<i>Cyrtandra waiolani</i>	Plants	Magnoliopsida	Unknown	No indication of <i>ex situ</i> material in 2003 Red List EW assessment. 2019 US Fish and Wildlife review confirms the absence of <i>ex situ</i> material and suggests the possibility of rediscovery in the wild.	(96)
<i>Dombeya rodriguesiana</i>	Plants	Magnoliopsida	Extant in wild	Following IUCN Red List Categories and Criteria version 3.1 (11), we consider a species to be EW only when exhaustive surveys have failed to find an individual in the wild. As the last wild individual of this species remains <i>in situ</i> , we don't yet consider this species EW.	(12, 97)
<i>Euphorbia mayurnathanii</i>	Plants	Magnoliopsida	Synonym	Synonym of <i>Euphorbia antiquorum</i> , which is assessed as Least Concern.	(94)
<i>Erythroxylum echinodendron</i>	Plants	Magnoliopsida	Synonym	Synonym of <i>Erythroxylum minutifolium</i> , which is extant in the wild in Cuba	(94, 98)
<i>Leptogryllus deceptor</i>	Animals	Insecta	Unknown	No record of having been kept <i>ex situ</i> , or indeed having been seen or collected beyond its original description in 1910.	
<i>Partula dentifera</i>	Animals	Gastropoda	Extinct	This species was driven to extinction as a result of the introduction of the predatory snail <i>Euglandia rosea</i> to the Society Islands in the late 1980s. Individuals of <i>Partula navigatoria</i> in the <i>ex situ</i> program were initially misidentified as this species, and the taxon was consequently erroneously assessed as EW.	(42)
<i>Partula tristis</i>	Animals	Gastropoda	Extinct	This species was driven to extinction as a result of the introduction of the predatory snail <i>Euglandia rosea</i> to the Society Islands in the late 1980s. Individuals of <i>Partula garrettii</i> in the <i>ex situ</i> program were initially misidentified as this species, and the taxon was consequently erroneously assessed as EW.	(42)
<i>Thermosphaeroma thermophilum</i>	Animals	Malacostraca	Extant in wild	This species was almost extirpated when its native spring dried out in 1988. Flow was restored the following month, flushing out some individuals that had persisted in the plumbing adjoining the spring. The wild population was therefore never fully extirpated, and the species never truly EW.	(99)

**Species currently assessed (Red List 2022-2) as EW regarded in this study as erroneous.**

**Table S2.**

Scientific name	Common name(s)	Class	Last record from wild	Collection period	Number of individuals collected (of which, number of founders represented)	<i>Ex situ</i> population size	Number of <i>ex situ</i> holders	Population management	Year conservation translocations started (R: Reintroduction, AC: Assisted Colonization)	Additional references
<i>Acipenser dabryanus</i>	Yangtze sturgeon	Actinopterygii	2000	After 1980	Not reported	Over 21000 first- and second-generation mature fish. Breeding capacity over one million.	Not reported		R: 2007	(100)
<i>Allotoca goslinae</i> *	Banded allotoca	Actinopterygii	2004	2000	Not reported	200	<10	EEP, studbook		
<i>Anaxyrus baxteri</i>	Wyoming toad	Amphibia	1989	1989	10	811	8	SSP, studbook	R: 1995	(101)
<i>Aylacostoma stigmaticum</i>		Gastropoda	1996	1993	Not reported	Unknown	2			
<i>Corvus hawaiiensis</i>	‘Alalā; Hawaiian crow	Aves	2002	1970-1996	(9)	118	2	Studbook	R: 2016 (recaptured 2020)	(102, 103)
<i>Cryptoblepharus egeriae</i>	Blue-tailed skink	Reptilia	2010	2009	66	1100	2	PVAs used to guide harvesting for translocations	R: 2017 AC: 2019	(13, 68, 104)
<i>Cyanopsitta spixii</i>	Spix’s macaw	Aves	2000	1976	17 (7)	202	5	Studbook	R: 2022	(105)
<i>Cyprinodon alvarezi</i> *	Perrito de Potosi; Potosi pupfish	Actinopterygii	1994	1989	Not reported	131	2	EEP		(106)
<i>Cyprinodon longidorsalis</i> *	La Palma pupfish	Actinopterygii	1994	After 1984 (discovery) and before 1994 (extirpation)	Not reported	282	9	EEP		
<i>Cyprinodon veronicae</i> *	Charco Palma pupfish	Actinopterygii	1995	After 1984 (discovery) and before 1995 (extirpation)	Not reported	213	3	EEP		
<i>Elaphurus davidianus</i>	Milu; Père David’s deer	Mammalia	1868	Unknown	18 (11)	6796	138	SSP, studbook	R: 1993	(58, 107)
<i>Lepidodactylus listeri</i>	Lister’s gecko	Reptilia	2012	2009	43	1350	2	Studbook. PVAs used to guide harvesting for translocations	R: 2019	(13, 104)

<i>Mitu mitu</i>	Alagoas curassow	Aves	1988	1979	5 (3)	90	2	Studbook	R: 2019	(108, 109)
<i>Nectophrynoides asperginis</i>	Kihansi spray toad	Amphibia	2004	2000	499	12000	5		R: 2012	(110, 111)
<i>Notropis amecae*</i>	Ameca shiner	Actinopterygii	2008	2005	6	30	1		R: 2016	(112)
<i>Oryx dammah</i>	Scimitar-horned Oryx	Mammalia	Late 1980s, early 1990s	1937 - 1967	48-60	Approximately 23000	>133	SSP, EEP, SMP, studbook. PVAs previously conducted, but not used to manage global population.	R: 2016 (Considered here as first attempt to establish a wild population. However, releases into semi-wild contexts have taken place since 1985.)	(113-118)
<i>Partula garretti</i>	Iareta tree snail	Gastropoda	1992	1991	Not reported	91	3	EEP, studbook.	R: 2016	(42, 70)
<i>Partula hebe</i>	Tapairu tree snail	Gastropoda	1992	1991	Not reported	135	2	EEP, studbook.	R: 2016	(42, 70)
<i>Partula mirabilis</i>	Navenave tree snail	Gastropoda	1985	1984 - 1985	Not reported	414	3	EEP, studbook.	R: 2018	(42, 70)
<i>Partula mooreana</i>	Eimeo tree snail	Gastropoda	1985	1985	Not reported	310	1	EEP, studbook.	R: 2016	(42, 70, 76)
<i>Partula navigatoria</i>	Faatere tree snail	Gastropoda	1991	1991	Not reported	504	2	EEP, studbook.	R: 2016	(42, 70)
<i>Partula nodosa</i>	Niho tree snail	Gastropoda	1984	1984	Not reported	15291	7	EEP, studbook.	R: 2015	(42, 76)
<i>Partula rosea</i>	Tarona tree snail	Gastropoda	1987	1987	Not reported	348	3	EEP, studbook.	R: 2019	(42, 119)
<i>Partula suturalis</i>	Taamu tree snail	Gastropoda	1986	1980 - 1986	Not reported	533	5	EEP, studbook.	R: 2016	(42, 70)
<i>Partula tohiveana</i>	Tohiea tree snail	Gastropoda	1982	1982	Not reported	2957	4	EEP, studbook.	R: 2016	(42, 70, 76)
<i>Partula varia</i>	Mauru tree snail	Gastropoda	1994	1991 - 1994	Not reported	3180	5	EEP, studbook.	R: 2019	(42, 119)
<i>Skiffia francesae*</i>	Golden skiffia	Actinopterygii	2010	1976 - 2006	<50	>1000	>50	EEP	R: 2021	
<i>Todiramphus cinnamominus</i>	Sihek; Guam kingfisher	Aves	1988	1984 - 1986	29 (16)	135	24	SSP, studbook. PVAs used to inform management.		(120, 121)
<i>Xiphophorus couchianus*</i>	Monterrey platyfish	Actinopterygii	1967	1961	Not reported	1157	6	Studbook		(122)
<i>Xiphophorus meyeri*</i>	Marbled swordtail; Muzquiz platyfish	Actinopterygii	1997	1983	Not reported	1573	4	Studbook		(122, 123)
<i>Zenaida graysoni</i>	Socorro dove	Aves	1972	1925	17	159	38	EEP, studbook		(14, 124)

The collection history and present status of EW animal species held *ex situ*. Scientific names marked with an asterisk (“\*”) denote species for which we expect hobbyists and private collectors to hold additional individuals.

**Table S3.**

Scientific name	Common name	Kingdom	Class	Notes	Additional references
<i>Deppea splendens</i>		Plants	Magnoliopsida	Known from at least three <i>ex situ</i> collections, but suspected to be more widely distributed. Red List assessment indicates need for greater understanding of <i>ex situ</i> populations.	
<i>Encephalartos relictus</i>		Plants	Cycadopsida	The only known wild individual, a male, was collected in 1971 and relocated to the discoverer's farm. Two stems from this plant and material grown from these remain in private collections.	(125)
<i>Lachanodes arborea</i>		Plants	Magnoliopsida	Collected just prior to extirpation in the wild in 2012. Survives in cultivation in several plantations on its native Saint Helena, South Atlantic.	
<i>Stenodus leucichthys</i>	Inconnu	Animals	Actinopterygii	Construction of dams led to the loss of spawning grounds in the Volga, Ural, and Terek rivers. Species survives through artificial propagation, with any individuals in native range derived from releases from hatcheries, which we don't consider here to be reintroductions. No wild individuals or progeny of released individuals or are thought to exist.	(126)

**EW Species whose *ex situ* population information is not reported in this study.**

**Table S4.**

Scientific name	Class	Last record from wild	Collection period	Number of individuals collected	Number of <i>ex situ</i> holders	Year reintroductions started (no known attempted assisted colonizations for plants)	Additional references
<i>Abutilon pitcairnense</i>	Magnoliopsida	2005	2003	1	5		(127)
<i>Aloe silicicola</i>	Liliopsida	1920	1920	Not reported	1		
<i>Alphonsea hortensis</i>	Magnoliopsida	1969	Not reported	Not reported	1		

<i>Amomum sumatranum</i>	Liliopsida	1921	Not reported	Not reported	1		
<i>Arachis rigonii</i>	Magnoliopsida	1959	1959	Not reported	1		
<i>Bromus bromoideus</i>	Liliopsida	1935	Not reported	Not reported	6	2022	(128, 129)
<i>Bromus interruptus</i>	Liliopsida	1972	Not reported	Not reported	12	2003, 2013	
<i>Brugmansia arborea</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	57		
<i>Brugmansia aurea</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	40		
<i>Brugmansia insignis</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	9		
<i>Brugmansia sanguinea</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	65		
<i>Brugmansia suaveolens</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	70		
<i>Brugmansia versicolor</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	33		
<i>Brugmansia vulcanicola</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	5		
<i>Camellia amplexicaulis</i>	Magnoliopsida	Unknown	Not reported	Not reported	11		
<i>Corypha taliera</i>	Liliopsida	1979	Not reported	Not reported	6		
<i>Cyanea pinnatifida</i>	Magnoliopsida	2001	Not reported	1	6	2005	(130)
<i>Cyanea superba</i>	Magnoliopsida	Around 2000	Not reported	3	5	1998	(131)
<i>Deppea splendens</i>	Magnoliopsida	1981	1976	Not reported	Unknown		(132)



<i>Diplazium laffanianum</i>	Polypodiopsida	1905	Not reported	5	3	2014	(133)
<i>Encephalartos brevifoliolatus</i>	Cycadopsida	2004	Not reported	Not reported	1		
<i>Encephalartos heenanii</i>	Cycadopsida	2006	Not reported		12		
<i>Encephalartos nubimontanus</i>	Cycadopsida	2001	Not reported	Not reported	10		
<i>Encephalartos relictus</i>	Cycadopsida	1971	1971	1	Unknown		(125)
<i>Encephalartos woodii</i>	Cycadopsida	1916	Not reported	1	14		
<i>Franklinia alatamaha</i>	Magnoliopsida	1803	Not reported	Not reported	108	2002	(134)
<i>Furcraea macdougallii</i>	Liliopsida	1973	1953-1965	Not reported	14		
<i>Kalanchoe fadeniorum</i>	Magnoliopsida	1977	Not reported		4		
<i>Kokia cookei</i>	Magnoliopsida	1918	1915	1	7		
<i>Lachanodes arborea</i>	Magnoliopsida	2012	Not reported	Not reported	Unknown		
<i>Lysimachia minoricensis</i>	Magnoliopsida	1926	1926	Not reported	35	1959, 1993	
<i>Mangifera casturi</i>	Magnoliopsida	Pre-1986	Not reported	Not reported	3		
<i>Mangifera rubropetala</i>	Magnoliopsida	Never recorded in the wild	Not reported	Not reported	3		
<i>Nymphaea thermarum</i>	Magnoliopsida	2008	1987	Not reported	11		(135)
<i>Ochrosia brownii</i>	Magnoliopsida	2006	Not reported	Not reported	10		
<i>Rhododendron kanehirai</i>	Magnoliopsida	1984	Not reported	Not reported	5		
<i>Senecio leucocephalus</i>	Magnoliopsida	2007	Not reported	Not reported	1		

<i>Sophora toromiro</i>	Magnoliopsida	1960	1950-1956	1	17	Multiple failed reintroductions from 1965	(136, 137)
<i>Trochetiopsis erythroxylon</i>	Magnoliopsida	1950s	Not reported	Not reported	9	1980s	

**The collection history and present status of EW plant species held *ex situ*.**

**Table S5.**

<b>Species</b>	<b>Family</b>	<b>Order</b>	<b>Seed type predicted based on</b>	<b>Probability of recalcitrance</b>	<b>Predicted storage behaviour</b>
<i>Abutilon pitcairnense</i>	Malvaceae	Malvales	Genus	0.002883	Orthodox
<i>Aloe silicicola</i>	Xanthorrhoeaceae	Asparagales	Genus	0.001743	Orthodox
<i>Alphonsea hortensis</i>	Annonaceae	Magnoliales	Family	0.513798	Recalcitrant
<i>Amomum sumatranum</i>	Zingiberaceae	Zingiberales	Family	0.012481	Orthodox
<i>Arachis rigonii</i>	Leguminosae	Fabales	Family	0.010307	Orthodox
<i>Bromus bromoideus</i>	Poaceae	Poales	Species	0	Orthodox
<i>Bromus interruptus</i>	Poaceae	Poales	Species	0	Orthodox
<i>Brugmansia arborea</i>	Solanaceae	Solanales	Family	0.00953	Orthodox
<i>Brugmansia aurea</i>	Solanaceae	Solanales	Family	0.032387	Orthodox
<i>Brugmansia insignis</i>	Solanaceae	Solanales	Family	0.157526	Orthodox
<i>Brugmansia sanguinea</i>	Solanaceae	Solanales	Family	0.019821	Orthodox
<i>Brugmansia suaveolens</i>	Solanaceae	Solanales	Family	0.128313	Orthodox
<i>Brugmansia versicolor</i>	Solanaceae	Solanales	Family	0.049257	Orthodox
<i>Brugmansia vulcanicola</i>	Solanaceae	Solanales	Family	0.032461	Orthodox
<i>Camellia amplexicaulis</i>	Theaceae	Ericales	Family	0.165695	Orthodox
<i>Corypha taliera</i>	Arecaceae	Arecales	Family	0.726928	Recalcitrant
<i>Cyanea pinnatifida</i>	Campanulaceae	Asterales	Genus	0.001267	Orthodox
<i>Cyanea superba</i>	Campanulaceae	Asterales	Genus	0.003024	Orthodox
<i>Deppea splendens</i>	Rubiaceae	Gentianales	Family	0.007442	Orthodox
<i>Encephalartos brevifoliolatus</i>	Zamiaceae	Cycadales	Order	0.009372	Orthodox
<i>Encephalartos nubimontanus</i>	Zamiaceae	Cycadales	Order	0.01957	Orthodox
<i>Encephalartos woodii</i>	Zamiaceae	Cycadales	Order	0.013487	Orthodox
<i>Franklinia alatamaha</i>	Theaceae	Ericales	Family	0.013332	Orthodox

<i>Furcraea macdougallii</i>	Asparagaceae	Asparagales	Family	0.012481	Orthodox
<i>Kokia cookei</i>	Malvaceae	Malvales	Family	0.040725	Orthodox
<i>Lachanodes arborea</i>	Compositae	Asterales	Family	0.012481	Orthodox
<i>Lysimachia minoricensis</i>	Primulaceae	Ericales	Species	0	Orthodox
<i>Mangifera casturi</i>	Anacardiaceae	Sapindales	Genus	0.877644	Recalcitrant
<i>Mangifera rubropetala</i>	Anacardiaceae	Sapindales	Genus	0.92769	Recalcitrant
<i>Nymphaea thermarum</i>	Nymphaeaceae	Nymphaeales	Genus	0.022476	Orthodox
<i>Ochrosia brownii</i>	Apocynaceae	Gentianales	Family	0.004237	Orthodox
<i>Rhododendron kanehirai</i>	Ericaceae	Ericales	Genus	0.059085	Orthodox
<i>Senecio leucopelus</i>	Compositae	Asterales	Genus	0.001912	Orthodox
<i>Sophora toromiro</i>	Leguminosae	Fabales	Genus	0.006741	Orthodox
<i>Trochetiopsis erythroxyton</i>	Malvaceae	Malvales	Species	0	Orthodox

**Modelled predictions of seed storage behaviour for 35 EW plant species.**