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Exploring 'endangered living fossils' (ELFs) among monotypic genera of plants and animals of the world

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The recently proposed concept of 'endangered living fossils' (ELFs) integrates high-endangered status and evolutionary singularity for any species. In this review, I gathered monotypic genera (single-species genera) that satisfy the three ELF criteria: (i) scarcity and narrow distribution of populations, i.e., considering every species categorized 'critically endangered' or contemporary 'extinct' by IUCN criteria; (ii) evolutionary singularity, i.e., both morphological and phylogenetic singularities of a single-species lineage as a result of a null net diversification rate; and (iii) ancient divergence, i.e., split from the closest extant relatives predating a particular geological epoch. A total of 3,706 monotypic genera of vertebrates and angiosperms were analyzed. I found 109 critically endangered and contemporary extinct genera of which 57 were ELFs. The emergent patterns are: (1) taxonomy (generic level) is a reliable first approach to identifying ELFs; (2) 'morphological singularity' displayed by monotypic genera does not always help identify ELFs on islands; (3) species of monotypic genera tend to be more threatened than average species; (4) extinction appears to be biased against some animal and plant groups; (5) contemporary extinct genera are strongly associated with distribution on islands, particularly for flightless birds vulnerable to human prosecution; and (6) the ELF approach is a relatively quick method to identify the species of floras and faunas most urgently in need of protection in the world. This approach is complementary to any method searching for phylogenetic diversity (e. g. EDGE), which is also discussed. I argue that ELFs should be prioritized in conservation because they are the most threatened lineages representing an exceptional evolutionary heritage in the world.

KEYWORDS

angiosperms, EDGE, endangered genera, IUCN, phylogenies, Pleistocene, vertebrates

1. Introduction

Shortly after proposing the concept of 'endangered living fossils' (ELFs) (Vargas et al., 2020), we are observing its application by zoologists (Bond et al., 2020), botanists (Jiménez-Mejías et al., 2021; Miguez et al., 2022) and science journalists (Davenport, 2021). The reason for this may be related to the benefit of narrowing down the complex interpretations of the living fossil concept that biologists are still debating (Lidgard and Love, 2018; Turner, 2019; Lidgard and Love, 2021). Indeed, any researcher can test whether candidate species are considered ELFs based on three complementary criteria: (1) scarcity and narrow distribution of endangered species recognized by international red lists; (2) 'evolutionary singularity' in phylogenetic reconstructions; and (3) ancient divergence regarding early geological epochs.

While species abundance and distribution are based on thorough search for populations in the field and locations in museum collections, phylogenies rely on sufficiently representative sampling and sufficiently resolved topologies. In any case, the majority of well-resolved phylogenies are asymmetrical, i.e., some clades are rich in species whereas some others are rather poor, including early diverging clades that contain a low number of species (Ronquist, 2014). The result is a ladderized or asymmetrical topology in which basal-most clades can even show as few species as a single one. Causes for this pattern are typically two: decline of a former species-rich clade (evolutionary extinction) or low diversification over long periods of time (evolutionary stasis) (Eldredge et al., 2005). Phylogenies of living organisms do not help at this point, which make fossils come into play. However, paleontological evidence is missing for the majority of organism groups of the tree of life. In any case, the use of fossils at different calibration points makes time-calibrated phylogenies the most comprehensive tool to test ELF (Vargas et al., 2020).

The budding speciation pattern found in many phylogenies at low taxonomic levels (species) (see Otero et al., 2022) is congruent with an asymmetrical pattern at deeper levels (classes, phyla, orders) (Rabosky et al., 2012). Indeed, the tree of life is profoundly asymmetrical in such a way that clades currently rich in species show a derived position nested within a group with older clades (Vargas and Zardoya, 2014). In other words, a general phylogenetic pattern shows pervasive paraphyly that affects any taxonomic treatments. Lack of reciprocal monophyly for many group pairs compromises recognition of the same taxonomic rank, as accepted in the past for two groups taxonomically at the same level that turned out to be paraphyletic. In particular, we can observe multiple cases where one of the two groups is included in the other group: monocotyledons in former dicotyledons (angiosperms), bilaterians in former radiolarians (eumetazoans), insects in former crustaceans (panarthropods), birds in former reptiles (sauropsids), tetrapods in former fishes (sarcopterigians), among others.

Since the last century, some studies have acknowledged the importance of phylogenetic singularity in conservation. One of the first approaches evaluating evolutionary trees in conservation used cladistic classifications and a measure of taxonomic distinctness (taxic diversity) (Vane-Wright et al., 1991). Shortly after, molecular (mtDNA) phylogenies were used to prevent from pervasive homoplasy in cladograms based on a few morphological characters (Faith, 1992). The accurate measurement of branch lengths and divergences using DNA sequence-based phylogenies, together with lower impact of convergence and increasingly lower costs of DNA sequencing, made molecular phylogenetics a basic tool in conservation. Currently, the most followed method is Evolutionarily Distinct and Globally Endangered (EDGE), which relies on phylogenetic diversity and distinctiveness (Isaac et al., 2007; Isaac and Pearse, 2018). However, this approach considers taxonomy only for sampling, while evolutionary singularity needs to consider 'morphological singularity' as well to fit into the concept of 'living fossils' (see Vargas et al., 2020).

In this paper, the concept of ELF is explored across representative branches of the tree of life (flowering plants and vertebrates) to infer distinctive lineages formed by a single species that is on the brink of extinction. As a working hypothesis, early-divergent lineages of singular animals and plants are investigated, which may predate geological boundaries in the global chronostratigraphic scale (see Vargas et al., 2020). To this aim, single-species groups (monotypic

genera) considered IUCN 'critically endangered' and contemporary 'extinct' single-species groups are evaluated, followed by searches for reliable publications in academic databases to obtain time-calibrated phylogenies that include those monotypic genera. Emerging patterns related to ancient divergence and survival through geological epochs are further discussed. In more practical terms, any species tested for ELF criteria will be recommended to be further prioritized for conservation based on evolutionary singularity, i.e., including morphological singularity and early divergence from living species.

2. Materials and methods

2.1. Spatio-temporal approach

A spatio-temporal hypothesis is herein considered to identify ELFs that combine both narrow geographic distributions of the species and isolated evolutionary history of the lineage (Vargas et al., 2020). This approach will be performed in plants (flowering plants) and vertebrates (tetrapods) because they are two groups that gather a great deal of detailed information (taxonomy, geographic distributions, population abundance, robust time-calibrated phylogenies), which is essential to evaluate ELFs. In particular, I analyzed monotypic genera of five groups of organisms: eudicots, amphibians, non-avian reptiles, avian reptiles (hereafter birds) and mammals.

For the spatial approach, the 'endangered' component of ELF includes limited geographic distributions once intensive searches in the field and specimen collections have been performed. In a first approach performed in this study, only single-species genera (hereafter monotypic genera) with few and scarce populations that hold a 'critically endangered' category using IUCN (2017) criteria will be considered. In addition, contemporary disappearance (IUCN 'extinct') is also analyzed to interpret causes of extinction.

For the temporal approach, the 'living fossil' component is considered when a unique morphology is associated with a lineage illustrating long-term isolation. The evolutionary origin (evolutionary distinctiveness) is also based on the concept of phylogenetic singularity (Isaac et al., 2007; Mishler et al., 2014; Rosauer and Jetz, 2015). Time-calibrated phylogenies using DNA sequences are preferred in the search for early divergence times considering geological boundaries in a global chronostratigraphic scale.¹ The Miocene–Pliocene boundary is chosen based on two main reasons: (1) dramatic climatic events have been described worldwide during and after the Miocene, which are responsible for global extinction of numerous plant and animal lineages (Steinhorsdottir et al., 2021); and (2) a considerable time window of over 5 million years has been demonstrated to provide enough time for divergence and speciation. Indeed, active speciation (evolutionary radiations) has even been described in the Pliocene–Pleistocene for angiosperms (Valente et al., 2010; Soltis et al., 2019), lizards (Reaney et al., 2018) and marsupials (Couzens and Prideaux, 2018), among others. The taxonomic rank of 'genus' is used because it often reflects considerably morphological differentiation and old divergence, and thus a higher probability of finding evolutionary singularity (Vargas et al., 2020). Besides, the

¹ stratigraphy.org/chart

genus rank has historically been used as the taxonomic entity that connects paleontology and neontology (Campbell, 1944). It has also been successfully used as a proxy for pre-Pliocene divergence using time-calibrated phylogenies to investigate the origin of species-rich and species-poor groups in the Mediterranean Floristic Region (Vargas et al., 2018). Lastly, an approach at the genus level fits into the taxonomic standards established by the IUCN Red List of Threatened Species (IUCN, 2022).

2.2. Endangered living fossil testing procedure

A three-step procedure is herein performed to search for ELF of plants (eudicots) and animals (amphibians, non-avian reptiles, birds and mammals) of the world:

(1) Assessing narrow distribution and population scarcity of endangered species taxonomically considered monotypic genera. For a first search, two web pages that comprehensively collect over 3,000 monotypic genera were used for plants (Plantdrew, JarrahTree, Notwith, 2018a) and vertebrates (Plantdrew, JarrahTree, Notwith, 2018b). Indeed, the use of Wikipedia pages has been successfully used in biodiversity and conservation studies (see Mittermeier et al., 2021). Searches in the IUCN database² were additionally performed for two purposes: (i) cross-validation on the taxonomy of monotypic genera; and (ii) withdrawing genera with the two highest conservation categories (CR and EX). In addition, specialized databases were used to make final taxonomic and distributional decisions: plants,³ amphibians,⁴ non-avian reptiles,⁵ birds⁶ and mammals (Wilson and Reeder, 2005).

(2) Searching for ‘evolutionary singularity’ (phylogenetic and morphological singularities), which includes null net diversification rate as a result of (i) speciation followed by pervasive extinction (high extinction rates); (ii) no speciation at all (evolutionary stasis); or (iii) anagenetic evolution. All available phylogenies found in publications withdrawn using Google Scholar were analyzed. The aim of this phylogenetic search is also to investigate the sister group of every CR and EX monotypic genus retrieved at step (1). Useful phylogenies were considered when including reliable sample size and robust DNA-based phylogenetic resolution.

(3) Identifying ancient divergence regarding a chronostratigraphic scale based on time-calibrated phylogenies. A phylogenetic search for scientific publications including singular lineages of every CR and EX monotypic genus was performed using Google Scholar. Divergence times for the node between the monotypic genus and its sister groups (stem node) were obtained straight from the publication. In a few cases of non-dated phylogenies, the computational tool of TimeTree (Kumar et al., 2017) was used to calculate divergence times. Only phylogenetic divergence that predates the Pliocene was considered for ELFs.

3. Results

A total of 3,706 monotypic genera were ELF tested (Tables 1, 2). Cross-validation of monotypic genera of plants and animals were checked with the IUCN database, which resulted in high taxonomic congruence. To control for reliable information before the analysis (species numbers, distributions, ‘critically endangered’ or ‘extinct’ status), I further used specialized websites that were also congruent to a great extent. Adjustments on taxonomy, distributions and updated IUCN categories were performed in a few cases.

3.1. Taxonomy

Searches for monotypic genera resulted in a great congruence among databases. However, I found some taxonomic disagreements. On the one hand, a considerable number resulted in non-monotypic genera, i.e., they showed a higher number (typically two) of living species in the IUCN database for angiosperms (6), non-avian reptiles (4), amphibians (6), birds (47) and mammals (11) (see Supplementary Tables S1, S2). These genera were accordingly not considered. On the other hand, some monotypic genera such as the angiosperms *Horstrissea* (Crete) and *Pleiomeris* (Canary Islands) were only found in the IUCN database, and consequently analyzed. The final lists of CR and EX genera analyzed for ELFs are shown in Tables 1, 2.

3.2. Conservation categories

The IUCN conservation categories herein considered need to be updated for some plants and animals (see Cazalis et al., 2022). Some CR monotypic genera have larger distributions and population abundance than previously considered (see Supplementary Table S2). For instance, the plant *Nardostachys jatamansi* showed a large distribution to have a CR status: “Bhutan; China; India (Uttaranchal, Sikkim, Himachal Pradesh, Arunachal Pradesh); Myanmar; Nepal” (IUCN, 2022). In addition, insufficient distribution data are observed in some birds (IUCN, 2022), which indicate the need of further field work in many countries as indicated in Supplementary Table S2 for *Heliopais personatus*, *Houbaropsis bengalensis*, *Necrosyrtes monachus*, *Rhinoplax vigil*. The same is true for the turtle *Eretmochelys imbricata*. Therefore, these genera were not included in the analysis because they do not meet the requirement of scarce populations in narrow distributions (CR category).

3.3. Time-calibrated phylogenies

Sister group relationships and divergence times were found in most CR and EX monotypic genera. However, I failed to find 17 of 38 eudicots, 2 of 8 amphibians, 2 of 10 non-avian reptiles, 12 of 41 birds and 3 of 13 mammals (Tables 1, 2). This result indicates that the plant and animal groups chosen for the analysis have complete information for ELF testing in the majority of the cases. We encourage researchers to investigate the remaining monotypic genera to obtain time-calibrated estimates in the near future. Most of the divergence times fall into the Miocene (9 plants, 29 animals), followed by Pleistocene

² iucnredlist.org/search

³ powo.science.kew.org/; robot.org

⁴ amphibiansoftheworld.amnh.org

⁵ reptile-database.org

⁶ avibase.bsc-eoc.org/; birdsoftheworld.org/; ebird.org/; worldbirdnames.org/

TABLE 1 List of 38 monotypic genera of plants (Eudicotyledoneae) considered CR or EX in the IUCN website, including species names, family names, distributions, divergence times of the stem group (mean value as provided by every publication), bibliographic references for the phylogenetic studies and consideration of endangered living fossils.

Plant species	Family	Distribution	Divergence time (mean)	Reference	Endangered Living Fossil?
<i>Apterosperma oblata</i>	Theaceae	China (Guangdong)	61.98 Ma	Su et al. (2011)	Yes
<i>Agasthiyamalaia pauciflora</i>	Clusiaceae	India (Tamil Nadu, Kerala)	?	–	Dated phylogeny needed
<i>Aubregria taiensis</i>	Sapotaceae	W Ghana, E Ivory Coast	39 Ma	Armstrong et al. (2014) and Kumar et al. (2017)	Yes
<i>Avellara fistulosa</i>	Asteraceae	W Portugal, W Spain	12.0 Ma	Vargas et al. (2020)	Yes
<i>Castrilanthemum debeauxii</i>	Asteraceae	SE Spain	17.0 Ma	Vargas et al. (2020)	Yes
<i>Duvaliandra dioscoridis</i>	Apocynaceae	Yemen (E Socotra)	?	-	Dated phylogeny needed
<i>Ecuadendron acostasolianum</i>	Fabaceae	Ecuador (Manta Real)	< 1 Ma	Schley et al. (2018)	No
<i>Eligmocarpus cynometroides</i>	Fabaceae	SE Madagascar	36 Ma	Bruneau et al. (2008)	Yes
<i>Emicocarpus fissifolius</i>	Apocynaceae	S Mozambique	?	-	Dated phylogeny needed
<i>Euchorium cubense*</i>	Sapindaceae	NW Cuba	?	Buerki et al. (2021)	Dated phylogeny needed
<i>Euryodendron excelsum</i>	Pentaphragaceae	China (Guangdong)	20.51 Ma	Su et al. (2011)	Yes
<i>Franklinia alatamaha**</i>	Theaceae	United States (Georgia)	22.05 Ma	Cheng et al. (2022)	Yes
<i>Gadodia falikei</i>	Plantaginaceae	SE Spain	12.0 Ma	Vargas et al. (2020)	Yes
<i>Gyrocaryum oppositifolium</i>	Boraginaceae	W Spain	28.6 Ma	Vargas et al. (2020)	Yes
<i>Haptanthus hazlettii</i>	Buxaceae	N Honduras	?	-	Dated phylogeny needed
<i>Hesperalea palmeri</i>	Oleaceae	Guadalupe Island (Mexico)	20 Ma	Zedane et al. (2016)	Yes
<i>Hondurodendron urceolatum</i>	Aptandraceae	NE Honduras	?	Su et al. (2015)	Dated phylogeny needed
<i>Horstrissea dolinicola</i>	Apiaceae	Crete	?	Kljuykov et al. (2020)	Dated phylogeny needed
<i>Kanaloa kahoolawensis</i>	Fabaceae	United States (Kaho'olawe island)	?	Hughes et al. (2022)	Dated phylogeny needed
<i>Lebbiea grandiflora</i>	Podostemaceae	Guinea, Sierra Leone	?	-	Dated phylogeny needed
<i>Medusagyne oppositifolia</i>	Ochnaceae	Seychelles (main islands)	50 Ma	Schneider et al. (2021) and Kumar et al. (2017)	Yes
<i>Muehlbergella oweriniana</i>	Campanulaceae	Russia (Caucasus)	?	Xu and Hong (2021)	Dated phylogeny needed
<i>Naufraga balearica</i>	Apiaceae	Spain (N Majorca)	6.2 Ma	Vargas et al. (2020)	Yes
<i>Nesiota elliptica*</i>	Rhamnaceae	United Kingdom (Saint Helena)	34 Ma	He and Lamont (2022)	Yes
<i>Pentastelma auritum</i>	Apocynaceae	China (Hainan)	?	Liede-Schumann and Meve (2018)	Dated phylogeny needed
<i>Pladaroxylon leucadendron</i>	Asteraceae	United Kingdom (Saint Helena)	3.85 Ma	Pelser et al. (2012) and Kumar et al. (2017)	No, accelerated island differentiation
<i>Pleimeris canariensis</i>	Primulaceae	Spain (Canary Islands)	2.79 Ma	Kondraskov et al. (2015)	No
<i>Podadenia thwaitesii</i>	Euphorbiaceae	W Sri Lanka	?	-	Dated phylogeny needed
<i>Pseudomisopates rivasmartinezii</i>	Plantaginaceae	Central Spain	4.6 Ma	Vargas et al. (2020)	No
<i>Psilanthella eggertii</i>	Acanthaceae	Ecuador (Chimborazo, Guayas, Manabi)	5 Ma	McDade et al. (2020)	No
<i>Rosselia bracteata</i>	Burseraceae	N Papua New Guinea	?	-	Dated phylogeny needed

(Continued)

TABLE 1 (Continued)

Plant species	Family	Distribution	Divergence time (mean)	Reference	Endangered Living Fossil?
<i>Stephanostema stenocarpum</i>	Apocynaceae	N Tanzania	?	Simões et al. (2007)	Dated phylogeny needed
<i>Streblorrhiza speciosa</i> *	Fabaceae	Australia (Norfolk Islands)	?	-	Dated phylogeny needed
<i>Synapsis ilicifolia</i>	Schlegeliaceae	Cuba (central area)	10.8 Ma	Kumar et al. (2017)	Yes
<i>Tetradoxa omeiensis</i>	Viburnaceae	China (Sichuan)	15.6 Ma	Fan et al. (2018)	Yes
<i>Tetrataxis salicifolia</i>	Lythraceae	Mauritius Island	?	Graham (2010)	Dated phylogeny needed
<i>Trilepidea adamsii</i> *	Loranthaceae	New Zealand (North Island)	?	-	Dated phylogeny needed
<i>Vateriopsis seychellarum</i>	Dipterocarpaceae	Seychelles (main islands)	34.9 Ma	Heckenhauer et al. (2017)	Yes

*Extinct.

**Extinct in the wild.

TABLE 2 List of 71 monotypic genera of animals (amphibians, non-avian reptiles, avian reptiles (birds), mammals) considered CR or EX in the IUCN website.

Animal species	Order (Family)	Distribution	Divergence time (mean)	Reference	Endangered Living Fossil?
Amphibians					
<i>Anilany helenae</i>	Anura (Microhylidae)	Madagascar (Ambohitantely)	35 Ma	Feng et al. (2017)	Yes
<i>Balebreviceps hillmani</i>	Anura (Brevicipitidae)	Ethiopia (Bale Mountains)	50 Ma	Loader et al. (2014)	Yes
<i>Churamiti maridadi</i>	Anura (Bufonidae)	Tanzania (Ukaguru Mountains)	20 Ma	Liedtke et al. (2017)	Yes
<i>Ericabatrachus baleensis</i>	Anura (Pyxicephalidae)	Ethiopia (Bale Mountains)	70 Ma	Siu-Ting et al. (2014)	Yes
<i>Microbatrachella capensis</i>	Anura (Pyxicephalidae)	South Africa (W Cape)	28 Ma	Bittencourt-Silva et al. (2016)	Yes
<i>Nimbaphrynoides occidentalis</i>	Anura (Bufonidae)	Guinea, Ivory Coast, Liberia	12 Ma	Liedtke et al. (2017)	Yes
<i>Parhoplophryne usambarica</i>	Anura (Microhylidae)	Tanzania (Usambara Mountains)	?	-	Phylogeny needed (only type material known)
<i>Siamophryne troglodytes</i>	Anura (Microhylidae)	W Thailand	?	Suwannapoom et al. (2018)	Dated phylogeny needed
Non-avian reptiles					
<i>Bolyeria multocarinata</i> *	Bolyeridae	Mauritius Island	?	-	Dated phylogeny needed
<i>Dermatemys mawii</i>	Dermatemydidae	Belize, Guatemala, Mexico	90 Ma	Joyce et al. (2013)	Yes
<i>Erymnochelys madagascariensis</i>	Podocnemididae	Madagascar (Mouroundava)	96 Ma	Gumbs et al. (2018)	Yes
<i>Gavialis gangeticus</i>	Gavialidae	Bangladesh, India, Nepal	65 Ma	Rio and Mannion (2021)	Yes
<i>Leucocephalon yuwonoi</i>	Geoemydidae	Indonesia (N Sulawesi)	37 Ma	Ascarrunz et al. (2021)	Yes
<i>Malacochersus tornieri</i>	Testudinidae	Kenya, Tanzania, Zambia	30 Ma	Lourenço et al. (2012)	Yes
<i>Orlitia borneensis</i>	Geoemydidae	Indonesia (Kalimantan, Sumatra), Malaysia (Peninsular Malaysia)	20 Ma	Lourenço et al. (2013)	Yes
<i>Platysternon megacephalum</i>	Platysternidae	SE Asia	18 Ma	Luo et al. (2019)	Yes
<i>Pseudemydura umbrina</i>	Chelidae	W Australia (Perth)	66 Ma	Holley et al. (2020)	Yes

(Continued)

TABLE 2 (Continued)

Animal species	Order (Family)	Distribution	Divergence time (mean)	Reference	Endangered Living Fossil?
Avian reptiles (birds)					
<i>Aphanapteryx bonasia</i> *	Rallidae	Mauritius Island	?	-	Dated phylogeny needed
<i>Cabalus modestus</i> *	Rallidae	New Zealand	< 4.3 Ma	Brown et al. (2022)	No; see new taxonomic changes
<i>Calyptura cristata</i>	Tyrannidae	Brazil (Rio de Janeiro State)	56 Ma	Ohlson et al. (2012)	Yes
<i>Camptorhynchus labradorius</i> *	Anatidae	NE North America	?	Buckner et al. (2018)	Dated phylogeny needed
<i>Chaunoproctus ferreorostris</i> *	Fringillidae	Japan (Bonin Islands)	12.5 Ma	Tietze et al. (2013)	Yes
<i>Chaetoptila angustipluma</i> *	Mohoidae	United States (Hawai'i Islands, Big Island)	10 Ma	Fleischer et al. (2008) and Kumar et al. (2017)	Yes
<i>Cyanolimnas cerverai</i>	Rallidae	Cuba (Matanzas Province)	6 Ma	Brown et al. (2022)	Yes; further dated phylogeny needed
<i>Cyanopsitta spixii</i> **	Psittacidae	Brazil (Pernambuco)	15.9 Ma	Schirtzinger et al. (2012)	Yes
<i>Didunculus strigirostris</i>	Collumbidae	Polynesia (Samoa)	21.3 Ma	Bruaux et al. (2018)	Yes
<i>Dysmorodrepanis munroi</i> *	Fringillidae	United States (Hawai'i Islands, Lanai Island)	?	-	Dated phylogeny needed
<i>Ectopistes migratorius</i> *	Columbidae	United States, Canada	13 Ma	Soares et al. (2016)	Yes
<i>Eulidia yarrellii</i>	Trochilidae	N Chile	6.7	Licona-Vera and Ornelas (2017) and Kumar et al. (2017)	Yes; further dated phylogeny needed
<i>Eutrichomyias rowleyi</i>	Monarchidae	Malaysia (Sulawesi Island)	10 Ma	Buckner et al. (2018)	Yes
<i>Fregilupus varius</i> *	Sturnidae	France (Reunion Island)	4 Ma	Zuccon et al. (2008)	No
<i>Gymnogyps californianus</i>	Cathartidae	United States (California, Arizona)	8.5 Ma	Johnson et al. (2016)	Yes
<i>Heteralocha acutirostris</i> *	Callaeidae	New Zealand (N Island)	4.5 Ma	Gibb and Sheperd (2022)	No, accelerated island differentiation
<i>Lathamus discolor</i>	Psittacidae	SE Australia	13 Ma	Schweizer et al. (2013)	Yes
<i>Leucopezia semperi</i>	Parulidae	Saint Lucia Island	4 Ma	Lovette et al. (2010) and Kumar et al. (2017)	No
<i>Lophopsittacus mauritianus</i> *	Psittacidae	Mauritius Island	?	-	Dated phylogeny needed
<i>Loxioides bailleui</i>	Fringillidae	United States (Hawai'i, Big Island)	2.8 Ma	Lerner et al. (2011)	No, accelerated island differentiation
<i>Macrocephalon maleo</i>	Megapodiidae	Indonesia (Sulawesi Island)	14 Ma	Harris et al. (2014)	Yes
<i>Mascarinus mascarinus</i> *	Psittacidae	France (Reunion Island)	6 Ma	Kundu et al. (2012)	Yes; further dated phylogeny needed
<i>Melamprosops phaeosoma</i> *	Fringillidae	United States (Hawai'i Islands, Maui)	5.77 Ma	Lerner et al. (2011)	Yes; further dated phylogeny needed
<i>Microgoura meeki</i> *	Columbidae	Solomon Islands	?	-	Dated phylogeny needed
<i>Necropsar rodericanus</i> *	Sturnidae	Rodrigues Island	?	-	Dated phylogeny needed
<i>Ophrysia superciliosa</i>	Phasianidae	NW India	?	Chen et al. (2021)	Considered extinct by some authors

(Continued)

TABLE 2 (Continued)

Animal species	Order (Family)	Distribution	Divergence time (mean)	Reference	Endangered Living Fossil?
<i>Oreomystis bairdi</i>	Fringillidae	United States (Hawai'i Islands, Kauai)	3.94 Ma	Lerner et al. (2011)	No, accelerated island differentiation
<i>Palmeria dolei</i>	Fringillidae	United States (Hawai'i Islands, Maui)	1.36 Ma	Lerner et al. (2011)	No, accelerated island differentiation
<i>Pezophaps solitaria</i> *	Columbidae	Rodrigues Island	13 Ma	Soares et al. (2016)	Yes
<i>Pithecophaga jefferyi</i>	Accipitridae	Philippines	12 Ma	Mindell et al. (2018)	Yes
<i>Pseudonestor xanthophrys</i>	Fringillidae	United States (Hawai'i Islands, Maui)	2.76 Ma	Lerner et al. (2011)	No, accelerated island differentiation
<i>Psittirostra psittacea</i>	Fringillidae	United States (Hawai'i Islands)	?	-	Dated phylogeny needed; probably extinct
<i>Raphus cucullatus</i> *	Columbidae	Reunion Island	13 Ma	Soares et al. (2016)	Yes
<i>Rhodonessa caryophyllacea</i>	Anatidae	Bangladesh, India, Myanmar	2.8 Ma	Ericson et al. (2017)	No
<i>Rowettia goughensis</i>	Thraupidae	Saint Helena, Ascension and Tristan da Cunha (Tristan da Cunha Island)	14.1 Ma	Burns et al. (2016)	Yes
<i>Sarcogyps calvus</i>	Accipitridae	SE Asia	7 Ma	Mindell et al. (2018)	Yes. A detailed dated phylogeny needed
<i>Sceloglaux albifacies</i> *	Strigidae	New Zealand	0.54 Ma	Wood et al. (2017) and Valente et al. (2019)	Dated phylogeny needed (included now in <i>Ninox</i>)
<i>Strigops habroptila</i>	Strigopidae	New Zealand	27.48 Ma	Valente et al. (2019)	Yes
<i>Sypheotides indicus</i>	Otididae	India	?	Collar and Morales (2022)	Dated phylogeny needed
<i>Thaumatibis gigantea</i> (= <i>Pseudibis gigantea</i>)	Threskiornithidae	Cambodia, Laos, Vietnam	?	Jetz et al. (2014)	Absolute dated phylogeny needed
<i>Viridonia sagittirostris</i> *	Fringillidae	United States (Hawai'i, Big Island)	?	Lerner et al. (2011)	Dated phylogeny needed
Mammals					
<i>Aproteles bulmerae</i>	Pteropodidae	C Papua New Guinea	14 Ma	Almeida et al. (2020)	Yes
<i>Beatragus hunteri</i>	Bovidae	Kenya-Somalia	4 Ma	Calamari et al. (2021)	No
<i>Dicerorhinus sumatrensis</i>	Rhinocerotidae	India-SW China	14.8 Ma	Liu et al. (2021)	Yes
<i>Diceros bicornis</i>	Rhinocerotidae	SW Africa	6.8	Liu et al. (2021)	Yes; further dated phylogeny needed
<i>Eudiscoderma thongareeae</i>	Megadermatidae	S Thailand	?	-	Dated phylogeny needed
<i>Hypogeomys antimena</i>	Nesomyidae	Madagascar (Menabe region)	14.1 Ma	Wright et al. (2010) and Kumar et al. (2017)	Yes
<i>Indri indri</i>	Indriidae	NE Madagascar	14 Ma	Chatterjee et al. (2009)	Yes
<i>Megaoryzomys curioi</i> *	Cricetidae	Ecuador (Galapagos Islands)	5 Ma?	Ali and Fritz (2021)	Dated phylogeny needed
<i>Mirimiri acrodonta</i>	Pteropodidae	Fiji Islands	14 Ma	Almeida et al. (2020)	Yes
<i>Nilopegamys plumbeus</i>	Muridae	N Ethiopia	2.35 Ma	Giarla et al. (2021)	No
<i>Pharotis imogene</i>	Vespertilionidae	S Papua New Guinea	?	-	Dated phylogeny needed
<i>Prolemur simus</i>	Lemuridae	E Madagascar	7.5 Ma	Hawkins et al. (2018)	Yes
<i>Simias concolor</i>	Cercopithecidae	Indonesia (Sumatra, Mentawai Islands)	2.22 Ma	Kumar et al. (2017) and Fleagle and Seiffert (2020)	No

The table includes species names for each entry, order and family names, distributions, divergence times of the stem group (mean value as provided by each publication), bibliographic references for the phylogenetic studies and consideration of endangered living fossils.

*Extinct.

**Extinct in the wild.

TABLE 3 Summary figures of total number of genera (data taken from Vargas and Zardoya, 2014), monotypic genera (see the text for databases used), CR genera [data taken from IUCN, 2022], EX genera [data taken from IUCN (2022)] and ELFs genera supported, rejected and uncertain.

Genera organism group	No. genera (% of CR+EX)*	no. monotypic genera (% of CR+EX)*	CR genera	EX genera	ELFs genera supported/rejected/uncertain
Angiosperms (Eudicotyledoneae)	10,400 (0.36%)	2,086 (1.8%)	34	4	16/5/17
Amphibians	500 (1.6%)	122 (6.56%)	8	0	6/0/2
Non-avian reptiles	770 (1.17%)	270 (3.33%)	8	1	8/0/1
Avian reptiles (birds)	2,100 (1.95%)	904 (4.54%)	22	17	20/9/12
Mammals	1,500 (0.87%)	323 (4.02%)	12	1	7/3/3
Total	15,270	3,705	84	25	57/17/35

*% of CR + EX with respect to this number of genera.

(1 plant, 25 animals), Pliocene (4 plants, 9 animals), Eocene (5 plants, 2 animals), Oligocene (1 plant, 4 animals), Cretaceous (0 plants, 5 animals) and Paleocene (1 plant, 1 animal).

3.4. Endangered living fossils in plants

Eudicotyledoneae (eudicots) genera were chosen because they contain the majority (71.1%) of angiosperm diversity in terms of species numbers. In particular, a total of 2,087 monotypic genera of about 10,400 eudicot genera were analyzed, of which 38 are categorized either CR (34) or EX (4). The proportion of CR plus EX genera over the number of total monotypic genera of eudicots is 1.8%, a figure lower than in any animal groups (Table 3). Among the 21 time-calibrated phylogenies, 16 genera meet the three criteria to be considered ELFs. Two families showed the highest number of ELFs (four each), in agreement with high numbers of total genera: Apocynaceae (366) and Fabaceae (765) (Table 1). In contrast, two other small families displayed a higher proportion of ELF genera/total family genera: Theaceae (2/9) and Plantaginaceae (2/90) (Figure 1).

3.5. Endangered living fossils in animals

The four groups of vertebrates (tetrapods) rendered relatively similar proportions of CR (plus EX) genera related to monotypic genera: amphibians (6.56%), non-avian reptiles (3.33%), birds (4.54%) and mammals (4.02%). Likewise, the number of CR (plus EX) genera and the total number of genera of each animal group have comparable proportions (Table 3).

Amphibians. A total of 122 monotypic genera of 500 amphibian genera were investigated, of which eight have an IUCN conservation status of CR (Table 2). There are dated phylogenies only for six of the eight genera, all of which can be considered ELFs. Divergence times from their six living sister groups range between 70 and 12 Ma, which fall into the Cretaceous-Miocene. The family with a higher proportion of ELFs/total family genera is the Brevicipitidae (1/5), followed by the Pyxicephalidae (2/12) and Microhylidae (2/57) (Figure 1).

Non-avian reptiles. A total of 270 monotypic genera of the 770 non-avian reptile genera were analyzed, of which 9 are categorized

either CR (8) or EX (1) (Table 2). Time-calibrated phylogenies reveal that at least eight of these 9 genera meet the three criteria to be considered ELFs. The families with a higher proportion of ELFs/total family genera are the Platysternidae (1/1) and Dermatemydidae (1/1), followed by Gavialidae (1/2), Podocnemididae (1/3) and Geoemydidae (2/19) (Figure 1).

Birds. A total of 904 monotypic genera of 2,100 bird genera were investigated, of which 41 have an IUCN conservation status of either CR (22) or EX (19) (Table 2). The majority of them (20 of 29 reliably tested) fit into definition of ELF (Table 3). Numerous monotypic genera of birds from islands are extinct (17), while a considerable number (nine) show divergent times postdating the Miocene, which prevented from being considered ELFs. The bird family with the highest proportion of ELFs/total family genera is the Strigopidae (1/2) and Mohoidae (1/2), followed by Fringillidae (8/49), Megapodiidae (1/7), Psittacidae (4/37), Columbidae (5/51), Otididae (1/9) and Rallidae (3/38). The families with a higher number of extinct genera are: Fringillidae (4), Columbidae (4), Psittacidae (2), Sturnidae (2) and Rallidae (2) (Figure 1).

Mammals. A total of 323 monotypic genera of the 1,500 mammal genera were analyzed, of which 13 are categorized either CR (12) or EX (1) (Table 2). Time-calibrated phylogenies revealed that 7 of these 13 genera meet the criteria for ELF, while three do not. Two of the four genera of Rhinocerotidae are ELFs, while Pteropodidae has also two ELFs of 49 family genera (Figure 1).

4. Discussion

The 'endangered living fossil' (ELF) concept integrates results from three biological sciences: taxonomy, conservation and phylogenetics. The use of monotypic genera of flowering plants and vertebrates benefits from numerous scientific publications and specialized websites of biodiversity that use taxonomic results (Giles, 2005; Mittermeier et al., 2021; IUCN, 2022). The approach presented herein using 3,706 monotypic genera detected a considerable number of ELFs that require the highest priority in urgent conservation programs (Lean, 2017).

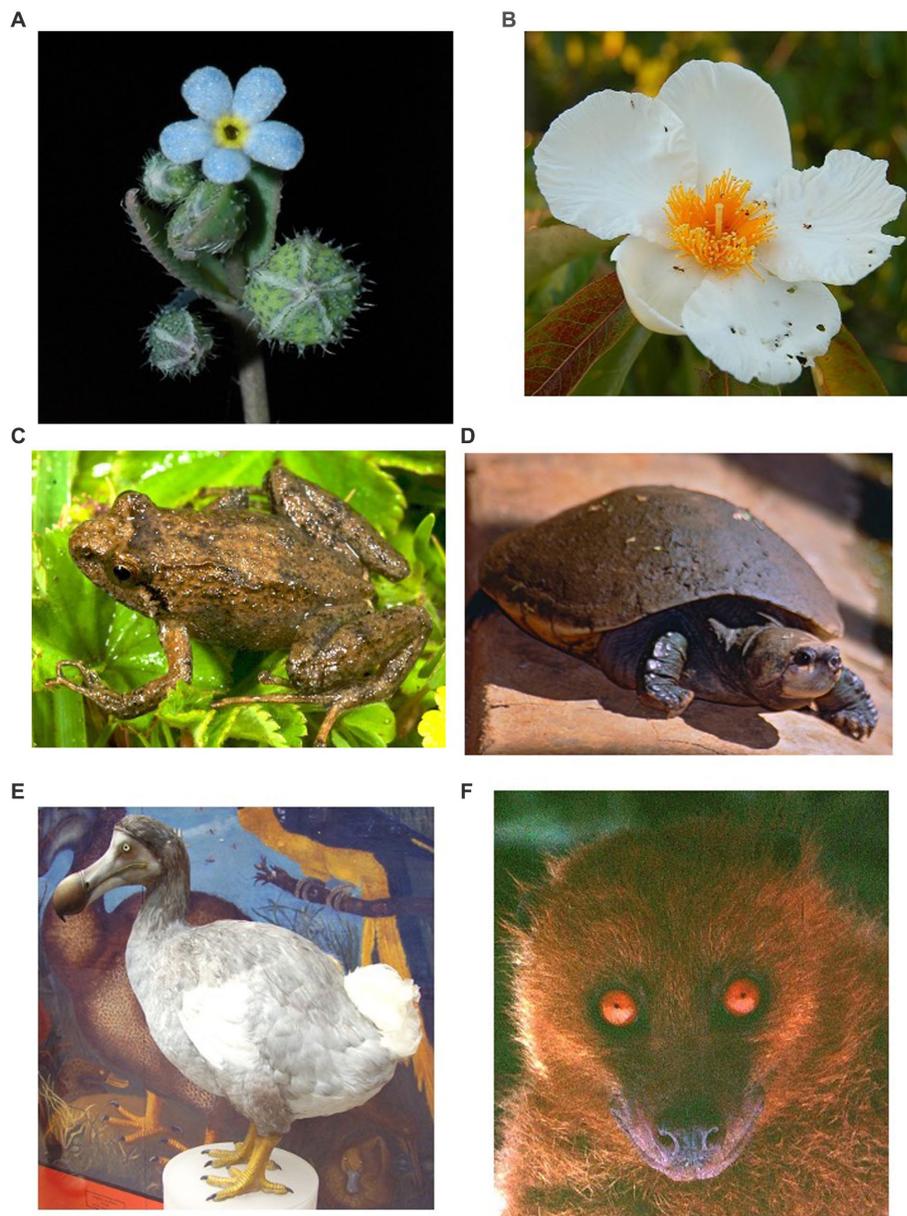


FIGURE 1

Representatives of ‘endangered living fossils’ (ELFs) of angiosperms (A,B), amphibians (C), non-avian reptiles (D), avian-reptiles (birds) (E) and mammals (F) that meet the three criteria to be considered ELFs. (A) *Gyrocarum oppositifolium* (CR eudicot, Boraginaceae) from Spain (Madrid and León mountains); (B) *Franklinia alatamaha* (eudicot extinct in the wild, Theaceae) from United States (Georgia); (C) *Ericabatrachus baleensis* (CR frog, Pyxicephalidae) from Ethiopia (Bale Mountains); (D) *Erymnochelys madagascariensis* (CR turtle, Podocnemididae) from Madagascar (Mouroundava); (E) *Raphus cucullatus* (extinct bird, Columbidae) from France (Reunion Island); and (F) *Mirimiri acrodonta* (CR mammal, Pteropodidae) from Fiji Islands. All photos were taken from Wikipedia (Wikimedia Commons), except for “A” (author: Pablo Vargas).

4.1. Monotypic genera as a first approach to identify ELFs

Taxonomy successfully helped the finding of 57 ELFs among the total number of monotypic genera (109) with a conservation status of CR (84) or EX (25), while only 17 of them were ELF rejected. I failed to find reliable information for the rest of them (35). This overall result is congruent with that found for plants of a small area such as the Iberian Peninsula (Vargas et al., 2020). Though the ELF concept has a strong spatial component, it turns out to be useful at both local areas

(Iberian Peninsula) and large ones (the world). Similarly, the IUCN conservation categories are closely related to narrow distributions and low number of populations, even though distributions of some plants and animals need to be revised (Supplementary Table S1; see Cazalis et al., 2022). I found also broad utility of this approach across unrelated branches of the tree of life. Indeed, taxonomy at the genus level was a reliable proxy irrespective of the organisms studied (angiosperms, amphibians, non-avian reptiles, birds, mammals).

As expected, a clear pattern of ladderized topologies within each branch of the tree of life was found (Vargas and Zardoya, 2014). The

most common phylogenetic relationship found in the phylogenies (109) with CR and EX genera was the monotypic genus sister to a group of multiple species (polytypic genus), followed by a pattern of a monotypic genus sister to a poorly differentiated genus. Furthermore, lineage singularity is observed in both cases because of the lineage in question underwent ancient divergence (ancient relicts; Vargas, 2007) plus no divergence into multiple living species (no changes in diversification rate; Ricklefs, 2007). In absence of a fossil record, it is difficult to distinguish between the two main causes of extant, endangered monotypic genera: decline of a former species-rich clade (evolutionary extinction) or no morphological differentiation over long periods of time (evolutionary stasis) (Eldredge et al., 2005). Indeed, the fossil record is needed to determine causes that account for a 'living fossil'. A textbook example of evolutionary extinction is the ginkgo (*Ginkgo biloba*) that has a characteristic leaf shape that helps identification of numerous ginkgo species from Cenozoic and late Cretaceous sediments of Eurasia and North America (Royer et al., 2003). When there is lack of macrofossils of an endangered species, the concept of 'endangered living fossils' gives an alternative perspective.

4.2. Evolutionary singularity: endangered living fossil vs. phylogenetic distinctiveness methods

Phylogenetic methods have been used to perform spatio-temporal analyzes for conservation purposes since the last century (Vane-Wright et al., 1991). On the one hand, geographic areas can be prioritized where accumulated lineages of animals (Rosauer and Jetz, 2015) and plants (Mishler et al., 2014) are located. On the other hand, the temporal component basically relies on early divergent lineages by using relative branching patterns (Isaac et al., 2007). Lineage length based on DNA sequence variation has been largely used to propose multiple metrics for phylogenetic diversity (PD) (see review in Isaac and Pearse, 2018). However, those metrics search for phylogenetic distinctiveness rather than evolutionary distinctiveness because phenotype variation is not considered. Indeed, molecular variation is not always closely related to morphological variation (see Isaac et al., 2007). Needless to say that phenotype variation directly links species and populations with the environment, which is an important component in any studies of the evolutionary change by natural selection.

The ELF approach makes a step further not only by integrating conservation criteria (by choosing critically endangered) and PD (using branch length in time-calibrated phylogenies) but also by integrating the morphological change (by considering genus-level or higher taxonomic ranks). In brief, the integration of three biological sciences in the ELF approach provides a complementary method to PD metrics such as EDGE (and related approaches) because: (1) ELF relies on morphology-based taxonomy, whereas EDGE is not affected by morphology, i.e., taxonomic treatments (Vargas et al., 2020). The lack of the use of taxonomy by EDGE decouples elementary PD with taxonomic ranks, which is the main tenet in IUCN conservation and international legislation. (2) ELF identifies divergence of a particular endangered lineage with respect to its sister group, while EDGE measures accurate scores within large organism groups (e.g., mammals, birds, etc.) (Isaac and Pearse, 2018). (3) Time-calibrated

phylogenies against the chronostratigraphic scale (absolute time) help determine association of ELF with particular geological events (e.g., dramatic climate changes, connection of land masses, emergence of new islands, etc.), while EDGE measures recent-to-early phylogenetic divergence and consequently a branching pattern order (relative time). In other words, ELF is designed to analyze ancient divergence by choosing any time limits of interest, which allow application of thresholds in hypothesis testing (see Vargas et al., 2014; Martín-Hernanz et al., 2023). (4) The use of absolute divergence times together with taxonomy by ELF directly connects neontology and paleontology in the exploration of causes of extinction (Wright et al., 2022). In any case, the two approaches use phylogenetic singularity, which make them partially sharing the same phylogenetic method and thus offering complementary perspectives.

Extension of the ELF approach to some other species-rich organisms such as ferns, gymnosperms, ray-finned fishes (Actinopterygii), butterflies or some other arthropods will be rapidly applied once detailed species distributions, IUCN categories and time-calibrated phylogenies are available. In particular, some gymnosperms have historically been considered living fossils. For instance, the genus *Wollemia* (*W. nobilis*) has a high EDGE score (Forest et al., 2018), which agrees with consideration of ELF for *Wollemia* because of evolutionary distinctiveness in terms of morphological (monotypic genus) and phylogenetic singularity (Lu et al., 2014). However, *Araucaria angustifolia* and *A. araucana* also rendered high EDGE scores but do not show significant morphological singularity (same genus), and thus no ELF consideration. In any case, the EDGE method is also based on phylogenetic distinctiveness and extinction risk, which helps propose strong ELF candidates in most of the cases.

In a historical context, it is interesting to note that the use of monotypic genera (and higher taxonomic ranks) in ELF evaluation *per se* entails considerable morphological differentiation provided by taxonomy (Lean, 2017). This is of paramount importance giving that ELF takes into account 'morphological singularity', which is expected in any living fossil evaluation ("anomalous forms" in Darwin, 1859).

4.3. Emerging patterns

In our study, absolute divergence times were successfully estimated using time-calibrated phylogenies. The time threshold of 5.33 million years (pre-Pliocene) used in this study helped determine whether diversification times of a CR monotypic genus and its sister group fall into the Miocene epoch or earlier. Our data support a common pattern of pre-Pliocene divergence in the majority of the cases because most of ELF divergence times were found between the Miocene and Cretaceous (see Tables 1, 2).

Though identification of a higher number of ELFs is expected in the near future, the considerable number of plants and animals (3,706 monotypic genera) surveyed in this review helps propose some emergent patterns.

- (1) Successful implementation of taxonomy (generic level) as a first approach to obtain a list of potential ELF candidates. However, taxonomic ranks vary quite significantly across organism groups of the tree of life. Contrary to Hennig (1966) expectations, dated phylogenies are currently not used to consider taxonomic ranks by temporal banding across the tree

of life (Ronquist, 2014). On the contrary, differences in taxonomic treatments render temporal inconsistencies at the genus level among angiosperms, amphibians, non-avian reptiles, birds and mammals.

- (2) Considerable ‘morphological singularity’ claimed for living fossils can be misleading in some cases. An extreme example of rapid morphological differentiation is found in monotypic genera endemic to oceanic islands, where divergent times at the genus level are similar to those at the species level in the continents (see references in Tables 1, 2; see Vargas, 2014). In other words, there is a clear potential for acceleration in rates of morphological change in animals and plants evolving on oceanic islands (Patiño et al., 2017).
- (3) Species of monotypic genera tend to be more threatened than average species of mammals and birds (Purvis et al., 2000). Indeed, our results additionally suggests that amphibians offer even a higher figure (6.56%) (see Bielby et al., 2006), while plants a lower percentage (1.8%) (Table 3).
- (4) Mass extinctions have dramatically affected some branches of the tree of life along their evolutionary history. In particular, disappearance of vertebrates appears to be taxonomically selective, rather than random (Purvis, 2008). Similarly, monotypic genera including CR and EX species do not seem to be equally distributed across animal families. The same is true for plants. An extreme case is the family Orchidaceae (c. 28,000 species, 736 genera, 144 monotypic genera; Chase et al., 2015) with no CR or EX monotypic genera, while the small family Aptandraceae (ca. 40 species, 8 genera) has three monotypic genera of which one is CR (Table 1).
- (5) Extinction of monotypic genera is particularly associated with recent population decrease and species extirpation of insular species. Among the 25 extinct monotypic genera studied in the present study, 22 occurred on islands, which indicate massive extinctions as similarly estimated at the species level (at least 800 insular species of animals and plants in the past 500 years, Fernández-Palacios et al., 2021). In particular, humans have dramatically exterminated flightless animals on remote islands (Fromm and Meiri, 2021; Maderspacher, 2022). These ‘extinct’ species can be seen as bellwethers indicators of patterns or trends that can help us shape the most urgent conservation actions (Matthews et al., 2022).
- (6) The ELF approach is a relatively quick method to identify the species of floras and faunas most urgently in need of protection in the world. Integrating biodiversity and evolutionary results help prioritize resources and conservation efforts in already long lists of endangered species (Forest et al., 2018), particularly in developing countries where vulnerable tropical habitats and remote islands harbor a high number of threatened species with extinction.

Admittedly, we are far from a comprehensive analysis of organisms across the tree of life to identify a significant number of ELF's because of three main reasons: (i) the available lists of monotypic genera overlook some genera; (ii) deficient data, particularly IUCN status and time-calibrated phylogenies of small organisms, prevent from having enough information to test the three ELF criteria for many monotypic genera; and (iii) large genera of hundreds of species will have more likelihood of including ancient lineages, although they may fail in

including significant morphological differentiation given that they are not considered different genera. In any case, the sample of five well-known organism groups of two main branches of the tree of life (eudicots and vertebrates) made possible testing the concept of ELF worldwide, which is equally applicable to any other organism groups. Indeed, the monotypic genus choice has already encouraged the search for more study cases in arthropods (Bond et al., 2020) and other angiosperms (Braz et al., 2021).

5. Concluding remarks

In this review, a considerable number of ELF's (57) from 3,706 monotypic genera of angiosperms, amphibians, non-avian reptiles, birds and mammals have been identified. The monotypic genera choice provides ideal candidate species in any region of the world, even though only a few genera meet the three ELF criteria (see Vargas et al., 2020; this paper). All these results highlight the necessity of using taxonomic, conservation and evolutionary approaches to provide a quick, albeit comprehensive method to integrate evolutionary information in conservation science (Lean, 2017). It is expected that the relatively small number of 57 ELF's identified so far will increase in the near future thanks to larger sample sizes, new conservation projects and more accurate methods in time-calibrated phylogenies. The test of ELF's can be considered a basic prioritization tool not only to stimulate research on morphologically isolated groups but also to quickly propose the list of urgent species in conservation programs worldwide. Once any species meets all the requirements to be considered an ELF, prioritization among ELF's should be performed by using evolutionary singularity, which has to consider both ancient lineage divergence (lineage singularity) and unique morphological differentiation (morphological singularity) into “anomalous forms” (Darwin, 1859). In sum, the ELF approach will help preserve the most exceptional evolutionary heritage before it is too late.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

The author confirms being the sole contributor of this work and has approved it for publication.

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Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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