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RESEARCH ARTICLE

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What factors influence the rediscovery of lost tetrapod species?

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Abstract

We created a database of lost and rediscovered tetrapod species, identified patterns in their distribution and factors influencing rediscovery. Tetrapod species are being lost at a faster rate than they are being rediscovered, due to slowing rates of rediscovery for amphibians, birds and mammals, and rapid rates of loss for reptiles. Finding lost species and preventing future losses should therefore be a conservation priority. By comparing the taxonomic and spatial distribution of lost and rediscovered tetrapod species, we have identified regions and taxa with many lost species in comparison to those that have been rediscovered—our results may help to prioritise search effort to find them. By identifying factors that influence rediscovery, we have improved our ability to broadly distinguish the types of species that are likely to be found from those that are not (because they are likely to be extinct). Some lost species, particularly those that are small and perceived to be uncharismatic, may have been neglected in terms of conservation effort, and other lost species may be hard to find due to their intrinsic characteristics and the characteristics of the environments they occupy (e.g. nocturnal species, fossorial species and species occupying habitats that are more difficult to survey such as wetlands). These lost species may genuinely await rediscovery. However, other lost species that possess characteristics associated with rediscovery (e.g. large species) and that are also associated with factors that negatively influence rediscovery (e.g. those occupying small islands) are more likely to be

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extinct. Our results may foster pragmatic search protocols that prioritise lost species likely to still exist.

KEYWORDS
conservation biology, extinct species, IUCN Red List, Lazarus species, lost species, missing species, Re:wild, rediscovered species

1 | INTRODUCTION

Lost species are those that cannot be confirmed to be alive in the wild by photographic, audio or genetic information, and that have no ex situ population under human care (Long & Rodríguez, 2022). Re:wild (https://www.rewild.org/), in consultation with the IUCN Species Survival Commission (SSC) (IUCN, 2023), has compiled a list of over 2000 species that have not been confirmed alive in the wild for over 10 years, including plants (e.g. ferns, grasses, orchids and cacti), invertebrates (e.g. corals, molluscs, worms, crustaceans and insects) and vertebrates (fish, amphibians, reptiles, birds and mammals) (Re:wild, 2023). Species can become lost because they are adversely affected by threats (e.g. habitat loss, water and air pollution, overexploitation of resources, climate change and invasive species) (IPBES, 2019), which cause the size of their populations to decline [49% of bird species worldwide have declining populations (Lees et al., 2022)] until they are so small that they cannot be found when searched for. The glaucous macaw (*Anodorhynchus glaucus*) is one such species—its population has declined to such an extent that it has not been seen in South America for several decades. Its disappearance is attributed to habitat loss and capture for the cagebird trade (BirdLife International, 2019).

However, species can become lost for other reasons. They may inhabit remote, inhospitable or inaccessible regions of the world (e.g. dense forests or politically unstable regions), which hampers efforts to search for them. The El Tambo harlequin toad (*Atelopus longibrachius*) has not been seen in Colombia since 2002, and it has not been recently searched for because it occupies a region affected by civil unrest (IUCN, 2017). The taxonomy and/or location of a lost species may have been poorly described on initial discovery, making it difficult to know what to search for and where. The location of the initial discovery of the Fito leaf chameleon (*Brookesia lambertoni*), not seen in Madagascar since 1921, was described as 'Fito', which may refer to a town, a forest or an administrative area (Jenkins et al., 2011). Lost species may be difficult to find because of their life-history traits (e.g. fossorial species which spend much of their life underground, such as the La Hotte blindsnake (*Typhlops agoralionis*), not seen in Haiti since 1991) (Inchaustegui et al., 2016) or because they are naturally rare with extremely small populations (as is believed to be the case for Rück's blue flycatcher (*Cyornis ruckii*), a lost bird species from Sumatra not seen since 1918) (BirdLife International, 2021). Lost species may not be searched for regularly or effectively because they occur in regions where capacity for research is limited (conservation effort is biased towards high-income regions) (Moussy et al., 2022), or because they are less valued by humans (e.g. reptiles tend to receive less conservation attention than mammals, possibly because they are considered less charismatic) (Clark & May, 2002). Therefore, while some lost species may be threatened with extinction, or may actually be extinct, others may not be threatened, and their status as a lost species remains independent of their threat category on the IUCN Red List of Threatened Species (Long & Rodríguez, 2022). For example, the largescale lizard (*Ptychoglossus eurylepis*), last seen in Colombia in 1984, is listed by the IUCN as Near Threatened (NT) due to its restricted distribution (approximately 10 km^2) (Velasco & Bolívar, 2015). By comparison, Osgood's Ethiopian toad (*Altiphrynoides osgoodi*), last seen in Ethiopia in 2003, is listed as Critically Endangered (CR). Its precipitous population decline has been attributed to habitat loss due to widespread conversion of its montane forest habitat for subsistence farming (IUCN, 2020).

Some lost species have been rediscovered, including many tetrapod species [at least 150 bird species and 100 species each of amphibians and mammals (Hume, 2017; Scheffers et al., 2011); there are no published lists for reptiles]. Sometimes referred to as 'Lazarus' species (Keith & Burgman, 2004; Meijaard & Nijman, 2014; Watson & Davis, 2017), these rediscovered species attract significant public interest, offering inspiration for future conservation action (Conservation Optimism, 2023). They include the Endangered (EN) Travancore bush frog (*Raorchestes travancoricus*), unrecorded for over 100 years until its rediscovery in India in 2004 (Biju & Bossuyt, 2009), the Jamaican rock iguana (*Cyclura collei*) (CR), unrecorded for several decades until its rediscovery in Jamaica in 1970 (Woodley, 1980), and the Talaud fruit bat (*Acerodon humilis*) (EN), unrecorded for over 100 years until its rediscovery in Indonesia in 1999 (Riley, 2002).

The frequency of rediscoveries of amphibian, bird and mammal species has been found to be increasing over time (Scheffers et al., 2011). For example, <20 lost amphibian species had been rediscovered by 1990; approximately 100 had been rediscovered by 2010 (Scheffers et al., 2011). This suggests it may be possible to find many more lost species. Rediscovered species also tend to be highly threatened. For example, >85% of all amphibian, bird and mammal species rediscovered before 2011 were considered to be threatened at the time of their rediscovery (Scheffers et al., 2011). A recent example is the blue-bearded helmetcrest (*Oxypogon cyanolaemus*), unrecorded for almost 70 years until its rediscovery in Colombia in 2015—this bird species is categorised as CR on the IUCN Red List and is most likely on the verge of extinction (Rojas & Vásquez, 2015). Therefore, it is important to find lost species as early as possible and develop measures to improve their chances of survival before they disappear forever. Indeed, at the Fifteenth meeting of the Conference of the Parties to the Convention on Biological Diversity (COP 15), nations adopted 23 global targets for 2030, including Target 4 which requires urgent management actions to halt human-induced extinction of known threatened species and for the recovery and conservation of species, in particular threatened species (CBD Secretariat, 2022). However, it will be easier to develop effective management actions for threatened species that are not lost, informed by information such as their population size and distribution. As an example, following the rediscovery of the blue-eyed ground-dove (*Columbina cyanopis*), SAVE Brasil and the Rainforest Trust purchased land to create a 1483-acre nature reserve specifically for this species, and the government of Minas Gerais subsequently created Botumirum State Park, protecting 89,000 acres of Cerrado which overlaps with the nature reserve, enlarging the protected area (Park, 2021). SAVE Brasil has been monitoring the blue-eyed ground-dove population, searching (successfully) for additional populations, raising awareness among local communities and developing ecotourism opportunities that benefit these communities (Park, 2021). These actions would not have been taken had the species not been rediscovered. Thus, rediscoveries provide an evidence base for targeted, informed management of threatened species. They also improve the accuracy of datasets such as the IUCN Red List that may be used to inform strategic conservation action, and they provide hope and inspiration for future efforts to save threatened species.

Several studies have examined the topic of lost and rediscovered species. A conceptual framework (Ladle et al., 2011) proposed loss and rediscovery to be influenced by interacting factors such as the presence of people with the motivation to find lost species, and the accessibility of the habitats they occupy. A global review of the number, distribution and conservation status of rediscovered amphibian, bird and mammal species (Scheffers et al., 2011) found most to have restricted ranges and small populations, and to be located within megadiverse countries of the tropics, albeit with variation between taxonomic classes across different ecoregions. Three studies have identified factors that influence the rediscovery of lost species. First, a global analysis of plant extinctions by Humphreys et al. (2019) found many species to have been incorrectly declared extinct and then rediscovered. Location, lifeform and range size were all found to influence rediscovery; reports of extinctions on islands and in the tropics, of shrubs and trees, and of species with narrow ranges were less likely to be refuted by rediscovery. Second, a comparison of 99 lost and 68 rediscovered mammal species by Fisher and Blomberg (2011) found reports of extinctions caused by habitat loss more likely to be refuted by rediscovery than reports of extinctions caused by predatory alien species and diseases, except for species with restricted ranges. The authors concluded that the highest rates of rediscovery in mammals would arise from searches for lost species threatened by habitat loss rather than for those that are charismatic. Search effort was found to be associated with rediscovery, whereby most species afforded 'low' search effort remained lost, while most afforded 'intermediate' search effort were rediscovered. However, no mammal species afforded 'high' search effort were rediscovered. Third, using an updated version of this dataset on mammals, Lee et al. (2017) found the probability of rediscovery for large-bodied mammals to increase with greater search effort, but not the probability of rediscovery for small-bodied species. The authors concluded that this may be because small-bodied species are less prone to extinction and are therefore rediscovered without the need for increased search effort.

These studies have provided useful insights regarding the distribution and characteristics of lost and rediscovered species. However, they also indicate that comparisons of the temporal, spatial and taxonomic distribution of lost and rediscovered tetrapod species have yet to be undertaken. Indeed, there is no current and comprehensive database of lost and rediscovered tetrapod species from which to undertake such a study. There is, for instance, no published list of rediscovered reptile species, and a significant proportion of all lost amphibian and mammal species has been rediscovered since the most recent list of rediscovered amphibian and mammal species was published in 2011 (Scheffers et al., 2011) (from 2011 to 2020, at least 18 amphibian and 11 mammal species have been rediscovered; approximately 18% of all rediscovered amphibian species and 10% of all rediscovered mammal species, respectively) (see Appendix E in Supporting Information for a list of rediscovered tetrapod species). Furthermore, studies identifying factors that influence rediscovery have so far only been undertaken for plants (Humphreys et al., 2019) and mammals (Fisher & Blomberg, 2011; Lee et al., 2017). As such, we neither have a complete and current picture of the distribution of lost and rediscovered tetrapod species, nor a comprehensive understanding of the factors that may influence their rediscovery. Yet a good understanding of their temporal, spatial and taxonomic distribution may direct searches to find lost species, and identifying factors that influence their rediscovery may improve our ability to find lost species.

Here we present a dataset of lost and rediscovered tetrapod species (amphibians, birds, mammals and reptiles), which we use to examine patterns in their taxonomic, spatial and temporal distribution, and to identify factors that may influence their rediscovery. Based on the results of previous studies, we hypothesise that numbers of lost and rediscovered tetrapod species are not randomly distributed across (i) taxonomy, (ii) location or (iii) time (Hypothesis H1) (Table S1). With regard to taxonomy, research is biased towards large, charismatic species (particularly large, charismatic mammals and birds), with amphibians and reptiles neglected by comparison (Cox et al., 2022). Therefore, we expect to find fewer rediscovered amphibian and reptile species. However, even within classes of charismatic tetrapods (e.g. mammals), smaller species tend to be neglected in terms of conservation action (Kennerley et al., 2021), including the effort invested in searching for them (Fisher & Blomberg, 2011). Therefore, we also expect to find variation within taxonomic classes, with for example, fewer rediscoveries from orders and families of small mammal species in comparison to those of large mammal species. However, the largest vertebrate species have elevated extinction risk due to direct killing by humans (Ripple et al., 2017), so while larger species may be easier to find, we also expect to see fewer rediscoveries among particularly large-bodied taxa. Extinction risk varies across tetrapod classes but tends to be particularly high for amphibians (Cox et al., 2022), so we expect to see fewer rediscoveries of these species. We also expect to see fewer rediscoveries among families and orders of species with small geographic ranges, as they are less likely to have populations that remain undiscovered.

With regard to location, we expect to find species in regions that are difficult to access (e.g. politically unstable regions) to be less frequently rediscovered because they are seldom searched for. Species on islands tend to be more vulnerable to extinction than their mainland counterparts (Fromm & Meiri, 2021; Slavenko et al., 2016), particularly those inhabiting small islands (Valente et al., 2020), so we expect island species to be less frequently rediscovered. The number of rediscovered amphibian, bird and mammal species varies across different ecoregions (although these numbers have not been compared to those for lost species within these ecoregions), but rediscoveries tend to be associated with tropical regions (Scheffers et al., 2011). This is where we expect to find the greatest number of rediscovered tetrapod species. Tropical regions are characterised by high rates of species diversity and endemism (Pillay et al., 2022), but also multiple threats, which may result in declining populations of many species (Newbold et al., 2020). However, tropical regions are also associated with lower capacity for monitoring and research to understand which species are genuinely lost (Moussy et al., 2022), so while many species may be declared lost, they may also be rediscovered.

With regard to time, rates of rediscovery for lost amphibian, bird and mammal species are increasing over time (Scheffers et al., 2011) (although these rates have not been compared to those for lost species). Nevertheless, we expect to see a general trend for increasing rates in the rediscovery of tetrapod species over time. Larger New World snake species (superfamily Colubroidea) tend to be described earlier than those that are smaller (Vilela et al., 2014), as do larger frogs (Anurans) of the Brazilian Cerrado (Diniz-Filho et al., 2005), possibly because they are easier to detect. This suggests that early rediscoveries will tend to be of larger tetrapod species (broadly, mammals and birds when compared to amphibians and reptiles), with more recent rediscoveries tending to be of those that are smaller. Indeed, the mean body size of rediscovered mammal species has fallen sharply since the start of the 19th century (Fisher, 2011). Carnivore and primate species with larger geographical ranges also tend to be discovered earlier (Collen et al., 2004), perhaps because these species are more likely to be discovered, and therefore we expect to find early rediscoveries to be of more widely distributed species.

We further hypothesise that there are at least three broad reasons why some species are rediscovered while others remain lost: characteristics of lost species (Hypothesis H2) and of the environment (Hypothesis H3) and human activities (Hypothesis H4) will all influence rediscovery. We provide detailed reasoning for these hypotheses, including several sub-hypotheses in Table S1.

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Lost species

For a species to qualify as lost, we adopted the definition proposed by Long and Rodríguez (2022), whereby a species must not have been observed in the wild for over 10 years (and must not have an ex situ population under human care). This 10-year cut-off is arbitrary, but it was determined through consultation with the IUCN SSC. As lost species tend to be highly threatened (Scheffers et al., 2011), it was considered that a longer cut-off period would potentially prevent the identification of lost species for this study that are in urgent need of protection. We also stipulated that these species must have been searched for within the time period that they are lost. We used the published list of 1008 lost tetrapod species compiled by Re:wild and the IUCN SSC as the starting point for our list of lost species. However, this list is not exhaustive, so we undertook a literature review to identify additional lost taxa, including subspecies (see Appendix A in Supporting Information for methods). The resulting list of candidate lost species was then reviewed by a team of species experts, including members of various IUCN SSC taxon Specialist Groups (IUCN, 2023). During this review, we removed from our list all species that were not considered to be lost (based on expert knowledge of confirmed sightings in the wild—e.g. the Tsaratanana chameleon [*Calumma tsaratananense*]), and all species considered to be extinct (beyond reasonable doubt, based on expert opinion). Indeed, 66 species that we removed were listed as Extinct (EX) on the IUCN Red List of Threatened Species. Other species that we removed were not listed as EX, but we believe they should be (e.g. the white-chested white-eye [*Zosterops albogularis*] [CR]; the Nubian wild ass [*Equus africanus africanus*] [CR Possibly Extinct, PE]; Prakke's reed snake [*Calamaria prakkei*] [CR (PE)]; and the rough-footed mud turtle [Viesca mud turtle] [*Kinosternon hirtipes megacephalum*] [Least Concern, LC]). We did not remove a small number of species classified as EX where expert opinion suggested there was a slight chance they might still be extant (five EX species from the Re:wild-IUCN SSC list; one additional EX species identified through the literature review). We also removed all species for which available information was insufficient to confidently determine their taxonomic identity, and all species which had not been searched for either through target surveys or through general surveys (based on expert opinion). See Appendix F (Supporting Information) for the list of removed species.

Some lost species have been rediscovered but then not recorded in the wild again for many decades because they have not been searched for. We did not reclassify these species as being lost. However, rediscovered species that subsequently became lost for more than 10 years in the wild despite searches were reclassified as being lost. This process resulted in a list of 856 species considered to be lost as of 2020 (thus not seen after 2010 in the wild). This list mainly comprises reptiles (469 species) and amphibians (285 species), with smaller numbers of birds (53 species, including two subspecies) and mammals (49 species, including three subspecies). See Appendix E (Supporting Information) for a complete list of lost species; see Table S2 for a summary of the differences between the published Re:wild-IUCN SSC lost species list and the lost species list produced for this study.

2.1.2 | Rediscovered species

To qualify as being rediscovered, a lost species or subspecies must have been confirmed to have been rediscovered through scientific publication or direct consultation with species experts. To be consistent with our requirements for lost species, rediscovered species must have been lost for at least 10 years. We included species rediscovered up to and including 2020.

For amphibians, birds and mammals, we used published rediscovered species lists (Scheffers et al., 2011) as a starting point for our list (104, 144 and 103 species, respectively). For birds, we cross-referenced these species with a more recently published list of >150 species (Hume, 2017) [many bird species featured on both lists (Hume, 2017; Scheffers et al., 2011)]. As far as we are aware, there is no comprehensive, published list of rediscovered reptile species. We therefore undertook a literature review (Appendix A in Supporting Information) to produce a list of rediscovered reptile species and to update the lists of rediscovered amphibians, birds and mammals with species that have been rediscovered since the publication of the existing published lists (Hume, 2017; Scheffers et al., 2011). This process produced a list of 424 rediscovered tetrapod species (including 25 subspecies); 100 amphibians, 152 birds (including 23 subspecies; 15% of all bird rediscoveries), 105 mammals (including one subspecies) and 67 reptiles (including one subspecies) (Appendix E in Supporting Information).

To test our four hypotheses (H1–H4) and associated subhypotheses, we collected data on a series of predictor variables (Table S1; Appendix G in Supporting Information).

2.2 | Analysis

2.2.1 | Identifying variation in the (i) taxonomic, (ii) temporal and (iii) spatial distribution of lost and rediscovered tetrapod species (Hypothesis H1)

To identify any taxonomic and spatial variation, we undertook contingency table tests [χ^2 tests: the FunChisq package (Zhong & Song, 2019)] incorporating the 1280 species in our dataset (856 lost species; 424 rediscovered species). Using variable V1 (taxonomic status), we first compared the number of lost and rediscovered species distributed across each taxonomic class (amphibians, birds, mammals and reptiles) and then distributed across orders within each class. We then compared the number of lost species distributed across taxonomic orders with the total number of extant species (i.e. all living species, including rediscovered species) within these orders. Using variable V2 (countries/islands of occupancy), we compared the number of lost and rediscovered species distributed across different continents, and then the number of lost and rediscovered species distributed across small islands (<20,000 km^2) and mainland locations (including islands >20,000 km^2). For some contingency table tests, due to low sample sizes, some categories of interest were excluded or merged with other categories (for details, see the individual contingency table tests in Tables S8–S22).

To identify any temporal variation, we used variable V3 (the cumulative number of lost and rediscovered species within different decades) to plot the number of species that were last seen or rediscovered across different decades. For lost species, this was from the decade of the first recorded lost species up to and including decade 2001–2010; for rediscovered species, this was from the decade of the first recorded rediscovered species up to and including decade 2011–2020. We used Spearman's rank correlation tests to identify temporal trends in loss and rediscovery.

2.2.2 | Identifying factors that influence the rediscovery of lost tetrapod species (Hypothesis H2–H4)

Our dataset incorporates variables that are likely to be influenced by phylogeny (e.g. body mass). We constructed 100 randomly selected phylogenetic trees for each class (amphibians, birds, mammals and reptiles) using VertLife.org (https://vertlife.org/). For reptiles, phylogenetic trees were available for Squamata (scaled reptiles), so we excluded the single Crocodilia (crocodile) species and 11 Testudine (turtle) species in our dataset when constructing this tree (2% of the 536 reptile species in our dataset). Across all four classes, our dataset included some species that were not included in the VertLife dataset (although these were mainly reptile species). Where feasible, we used a closely related species (from the same genus) as a substitute for these species in order to construct our phylogenetic trees (e.g. we used the painted parakeet [*Pyrrhura picta*] as a substitute for the Sinú parakeet [*Pyrrhura subandina*]). However, for some species that were not included in the VertLife dataset, we were unable to confidently identify a closely related species, so these species were excluded from our analyses. For example, the pink-headed duck (*Rhodonessa caryophyllacea*) was excluded as it is the sole member of its genus. Our dataset also included subspecies, whereas subspecies are not included in the VertLife dataset. In these cases, we used the parent species as a substitute for the subspecies to construct the phylogenetic trees (e.g. we used the white-mantled barbet [*Capito hypoleucus*] as a substitute for the northern white-mantled barbet [*Capito hypoleucus hypoleucus*]). For a summary of the number of species (including substitute species) used to construct the phylogenetic trees for each taxonomic class, see Table S3. For the names of the species used to construct the phylogenetic trees (including substitute species and excluded species), see Appendix E in Supporting Information.

We used *phylo.d* (Fritz & Purvis, 2010) in the *caper* package (Orme et al., 2018) to calculate the *D* statistic, which is a measure of phylogenetic signal (here in rediscovery). We identified phylogenetic signal (average *D*: amphibians = 0.67, birds = 0.96, mammals = 0.75, reptiles = 0.74), with low probability of *D* resulting from no phylogenetic structure (average *p*: amphibians = 0, birds = .36, mammals = .013, reptiles = 0) or Brownian phylogenetic structure (average $p=0$ for all four classes). To account for this, we undertook phylogenetic linear regression using the *phylolm* package (Tung Ho & Ané, 2014) and our 100 randomly selected trees. We used the status of each species as a binary response variable (0 = lost; 1 = rediscovered) to assess the relationship between rediscovery and each predictor variable (V4–V11). First, we examined the effect of each predictor variable on rediscovery separately for each taxonomic class. Second, we undertook multivariate analyses of all variables together for each taxonomic class. We checked for multi-collinearity among variables using the *car* package (Fox & Weisberg, 2019) and found some evidence for multi-collinearity in the amphibian dataset (between V6 habitat breadth and V7f artificial terrestrial habitats). We removed V7f artificial terrestrial habitats, which was not found to be significantly associated with the rediscovery of amphibians in univariate analyses. This reduced variance inflation factor values to <3 (Table S5). We used the *dredge* function in the *MuMIn* package (Bartoń, 2020) to undertake automated model simplification, ranking model combinations by Akaike Information Criterion (AIC). We used the *importance* function (also in the *MuMIn* package) to obtain the Relative Importance Value (RIV) for each variable (the sum of the Akaike weights over all models for each variable). We log transformed three variables (time lost, body mass and human development). Third, we compared the number of lost and rediscovered species within each region using Pearson's product–moment correlation (Best & Roberts, 1975). Regions were defined as being a country or an island. All analyses were carried out in R (version 4.1.2) (R Core Team, 2021).

3 | RESULTS

3.1 | Hypothesis H1: the (i) taxonomic, (ii) temporal and (iii) spatial distribution of lost and rediscovered tetrapod species is not randomly distributed

3.1.1 | Taxonomic distribution

Of the 1280 tetrapod species in our dataset, 856 (67%) were lost species (including 5 subspecies) and 424 (33%) were lost species that have been rediscovered (including 25 subspecies) (see Figure 1, decade 2011–2020) (hereafter referred to as 'species' when discussing the overall list). Approximately 42% of these 1280 species were reptiles, 30% were amphibians, 16% were birds and 12% were mammals. A far smaller proportion of lost reptile and amphibian species have been rediscovered (13% and 26%, respectively) than lost mammal and bird species (68% and 74%, respectively). In particular, more lost bird species and fewer lost reptile species have been rediscovered than would be expected by chance (Table S7, contingency table test #1). For the complete results of the contingency table tests, see Tables S8–S22.

For amphibians and birds, we did not identify any non-random patterns regarding the number of lost species compared with the number of rediscovered species within orders. For mammals, there were more lost and fewer rediscovered Rodentia (rodents) than would be expected by chance (Table S7, contingency table test #4). For reptiles, fewer Scinciformata (skinks and allies) have been rediscovered, while fewer species of Serpentes (snakes) and Testudines (turtles, tortoises and terrapins) remain lost, and more have been rediscovered than would be expected by chance (Table S7, contingency table test #5).

For amphibians and mammals, we did not identify any non-random patterns regarding the number of lost species compared with the number of extant species (i.e. all living species including rediscovered species) within different orders. For birds, there were more lost Caprimulgiformes than would be expected by chance (from three families: Caprimulgidae [nightjars], Aegothelidae [owlet-nightjars] and Trochilidae [hummingbirds]). There were also more lost Gruiformes (only Rallidae species [rails]) and fewer lost Passeriformes (perching birds) than would be expected by chance (Table S7, contingency table test #7). For reptiles, there were more lost Dibamia (dibamids) and Scinciformata (skinks and allies) and fewer lost Serpentes (snakes) than would be expected by chance (Table S7, contingency table test #9).

3.1.2 | Temporal distribution

The number of lost tetrapod species is increasing decade on decade at a faster rate than the number of species being rediscovered. Thus, the total number of lost tetrapod species is increasing with each passing decade, and this rate of increase shows no signs of slowing (Spearman's rho = 0.99; df = 15; $p<.001$) (Figure 1). This trend is driven primarily by rates of loss for reptiles, which are significantly faster than rates of rediscovery (Figure 1). That said, rates of rediscovery for reptiles are increasing decade on decade (Spearman's rho = 0.89; df = 15; $p<.001$); more than twice the number of reptiles rediscovered in decade 2001–2010 were rediscovered in decade 2011–2020 (Figure 1). Rates of loss for amphibian species have also been faster than rates of rediscovery (up to decade 2001–2010), but they may be slowing, as the number of lost species is similar for decades 1991–2000 and 2001–2010. However, since then (during decade 2011–2020) a relatively small number of amphibian species have been rediscovered. The total number of lost bird and mammal species peaked in the 1970s. After this time, rates of rediscovery were faster than rates of loss such that the

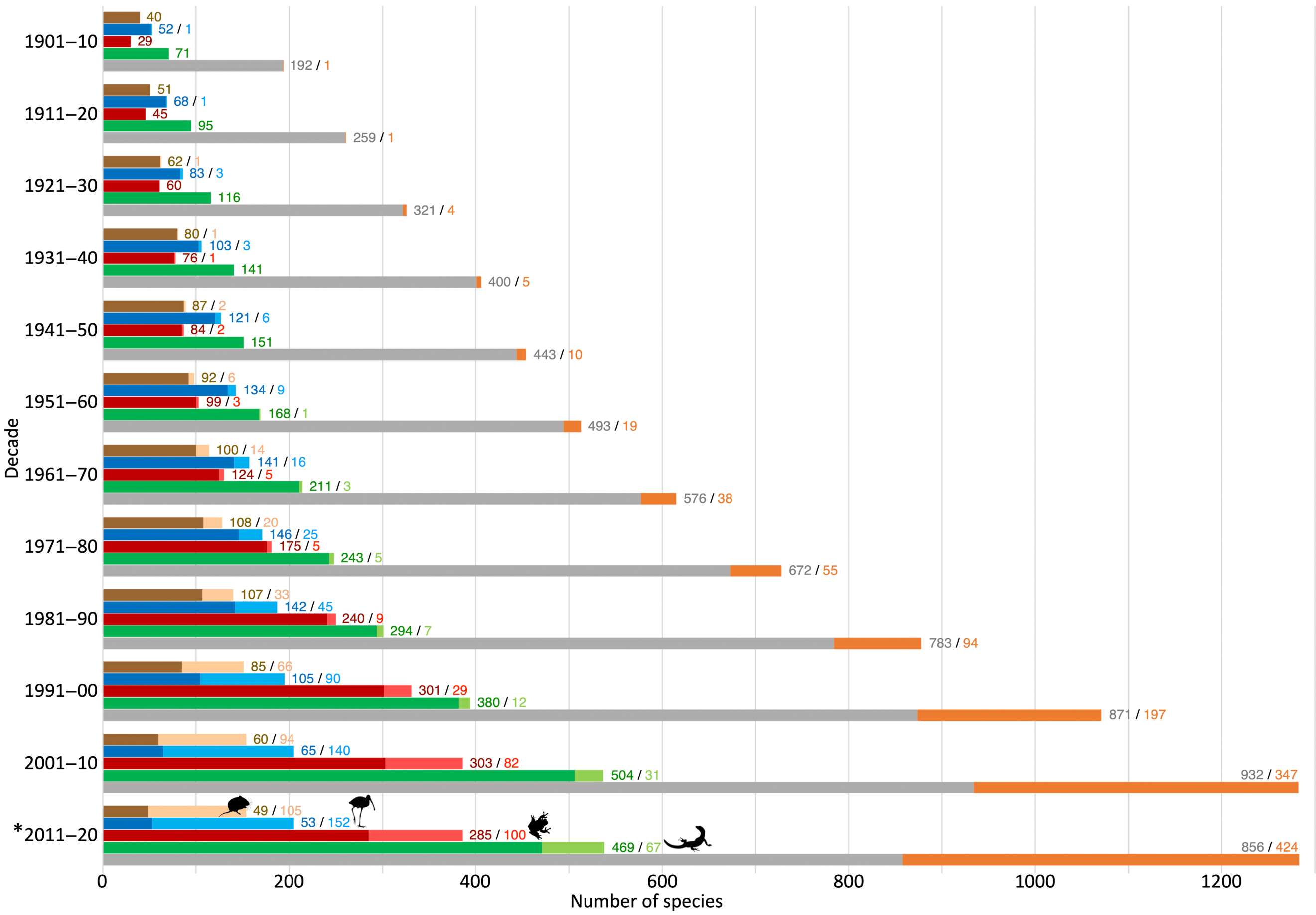

FIGURE 1 The cumulative number of lost and rediscovered tetrapod species across decades. Grey and orange = lost and rediscovered tetrapod species, respectively. Green, red, blue and brown = reptiles, amphibians, birds and mammals, respectively (dark shades = lost species; light shades = rediscovered species). Lost and rediscovered species occurring before 1901 were grouped within decade 1901–1910. *For decade 2011–20, the cumulative number of rediscovered species was calculated including species rediscovered within this decade, but the cumulative number of lost species was calculated using species lost up to and including 2010 (but not those lost within Decade 2011–2020). This is because to be considered lost, a species must not have been observed in the wild for at least 10 years, and this dataset was collated in 2020. All species silhouettes from www.phylopic.org (CC0 1.0).

number of lost species in both taxonomic classes has declined sharply. However, rates of rediscovery have slowed in recent years; less than one-third of the number of bird species and half the number of mammal species rediscovered in decade 2001–2010 were rediscovered in decade 2011–2020 (Figure 1).

Despite adopting the 10-year cut-off, the average time lost for all species in our dataset was 54 years (median = 41 years); for lost species it was 49 years (median = 35.5 years); for rediscovered species it was 65 years (median = 57 years) (for results by taxonomic class, see Table S23).

3.1.3 | Spatial distribution

Lost and rediscovered species are broadly distributed across the globe (Figure 2). Both lost and rediscovered species occur in greatest numbers in tropical regions, particularly mega-diverse countries such as Colombia and Indonesia. Indeed, the number of lost and rediscovered species occurring within regions is positively correlated ($r = .86$, df = 142, $p < .001$) (Figure S1). Nevertheless, there are regions with many lost species where no rediscoveries have been reported, particularly in Africa and the Middle East, and islands of the Pacific Ocean and Caribbean Sea (Figure 2). No lost species have been reported in some regions, including several countries in Africa and Central Asia and most countries in Europe (Figure 2).

Taking all tetrapod species together, fewer have been rediscovered in North and Central America than would be expected by chance, given the number of lost species there (Table S7, contingency table test #10). Regions with high proportions of lost tetrapod species in comparison to those that have been rediscovered include Hawaii (6 lost; 1 rediscovered), Haiti (22; 2) and Guadeloupe (4; 0) (Figure 2). Nevertheless, some regions outside North and Central America also have high proportions of lost tetrapod species, including New Caledonia (27; 3), Venezuela (37; 6) and the Democratic Republic of Congo (15; 4). Some regions with high numbers of lost species also have high rates of rediscovery, such as Australia (21; 26) and India (28; 28).

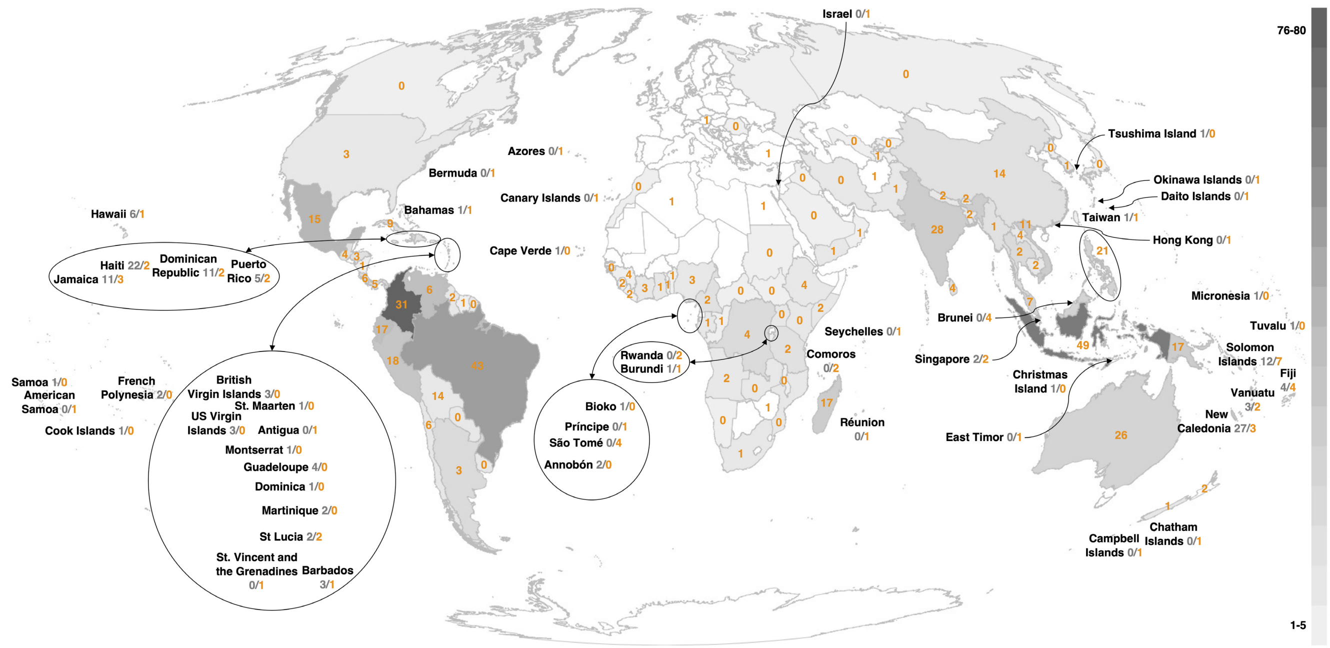

FIGURE 2 The global distribution of lost and rediscovered tetrapod species. Grey shading and text = the number of species within a region (a country or an island) that are currently lost (globally); orange text = the number of rediscovered species with a range incorporating this region; white regions (without orange numbers) = no data on lost or rediscovered species; white regions (with orange numbers) = regions where lost species have been rediscovered and no (known) lost species remain. A lost species with a range that, for example, incorporates three regions is counted as being lost within each of those three regions. Should that species be rediscovered (in just one (or more) of those regions), it is counted as being rediscovered within all three of those regions. Multiple islands within an island group are treated as one region. Oceanic islands are treated as separate regions; off-shore islands are treated as being part of their associated mainland region. For ease of visual reference, numbers of both lost and rediscovered species are provided for small regions including islands (in grey/orange, respectively). The authors have created this map for illustrative purposes and do not make any political claims regarding the status of the regions shown on the map.

More lost amphibian species have been rediscovered in Asia than would be expected by chance (Table S7, contingency table test #11), particularly across Indonesia (2; 8) (Figure S2). Some regions have high proportions of lost amphibian species, including Colombia (65; 5), Honduras (11, 1) and Malaysia (5, 1).

More lost bird species are located in North and Central America and Oceania than would be expected by chance (Table S7, contingency table test #12). In North America, these regions include the United States (3; 0) and Mexico (4; 1); in Oceania, they include Hawaii (6; 1) and New Caledonia (5; 0) (Figure S3). Some regions have high rates of rediscovery, including Madagascar (0; 7), Papua New Guinea (0; 5) and São Tomé (0; 4). Most lost bird species on islands of the Atlantic and Indian Oceans have been rediscovered. Almost half (48%) of remaining lost bird species are located on islands, mainly in the Caribbean and the Pacific, and in particular Hawaii and New Caledonia (Figure S3).

No non-random patterns were identified regarding the spatial distribution of lost and rediscovered mammals across continents (Table S7, contingency table test #13). Regions with high proportions of lost mammal species include South Africa (4; 1) and Mexico (7; 4). Regions with high rates of rediscovery include Brazil (2; 8), China (1; 4) and Vietnam (2; 5) (Figure S4).

More reptile species have been rediscovered in North and Central America, and fewer have been rediscovered in Africa than would be expected by chance (Table S7, contingency table test #14). In North and Central America, regions with relatively high rates of rediscovery include Cuba (5; 5), Guatemala (2; 2) and Mexico (8; 5). There are many countries In Africa with lost reptile species where none have been rediscovered. Regions in Africa with high proportions of lost reptile species include Madagascar (24; 3), the Democratic Republic of Congo (10; 0) and Tanzania (8; 1). Other regions with high proportions of lost reptile species include Indonesia (59; 3), Vietnam (23; 0), Haiti (17; 0) and Sri Lanka (8; 0) (Figure S5).

No non-random patterns were identified regarding the distribution of lost and rediscovered tetrapod species on small islands (<20,000 km^2) in comparison to mainland locations (Table S7, contingency table test #15).

3.2 | Hypotheses H2–H4: characteristics of tetrapod species (H2), characteristics of the environment (H3), and human activities (H4) all influence rediscovery

3.2.1 | Univariate analysis

Variables associated with all three hypotheses (H2–H4) were found to be significantly correlated with rediscovery (Table 1). Regarding

TABLE 1 Relationships between rediscovery and predictor variables.

Hypotheses	Predictor variable	Amphibians			Birds			Mammals			Reptiles (Squamata)			Figure reference
		Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*	Est.	SE	*p*	
H2: Species characteristics influence rediscovery	V4 Time lost	−0.05	0.08	.59	−0.12	0.11	.28	−0.06	0.11	.6	0.09	0.05	.05	Figure 3
	V5 Body mass	**0.37**	**0.07**	***	−0.02	0.13	.89	0.01	0.1	.9	**−0.18**	**0.06**	**.001******	Figure S6
	V6 Habitat breadth	**0.22**	**0.05**	***	**0.23**	**0.1**	**.02***	0.09	0.14	.5	0.009	0.07	.89	Figure S7
H3: Characteristics of the environment influence rediscovery	V7a Forest	0.002	0.06	.97	**−0.66**	**0.07**	***	**0.37**	**0.08**	***	0.008	0.05	.87	Figure S8
	V7b Savanna	x	x	x	0.23	0.22	.29	−0.01	0.19	.95	−0.005	0.07	.94	Figure S9
	V7c Shrubland	**0.26**	**0.06**	***	**0.36**	**0.06**	***	−0.12	0.13	.37	**−0.3**	**0.05**	***	Figure S10
	V7d Grassland	**0.19**	**0.05**	***	**0.28**	**0.13**	**.04***	0.16	0.11	.17	−0.15	0.08	.08	Figure S11
	V7e Wetlands (inland)	0.05	0.09	.57	0.25	0.17	.13	−0.17	0.17	.32	**0.27**	**0.12**	**.03***	Figure S12
	V7f Artificial terrestrial	0.05	0.09	.6	**0.36**	**0.07**	***	0.07	0.11	.53	−0.02	0.07	.73	Figure S13
	V8 Small island/mainland	−0.08	0.17	.63	−0.14	0.11	.2	**−0.15**	**0.07**	**.03***	0.04	0.05	.49	Figure S14
H4: Human activities influence rediscovery	V9a Alien species threat	**−0.15**	**0.07**	**.02***	**0.34**	**0.07**	***	0.19	0.11	.09	0.06	0.06	.33	Figure S15
	V9b Habitat loss threat	0.07	0.04	.1	−0.14	0.08	.1	0.09	0.07	.21	**0.1**	**0.03**	**.006******	Figure S16
	V9c Overexploitation threat	**0.2**	**0.03**	***	0.07	0.07	.37	**0.16**	**0.08**	**.04***	0.03	0.04	.47	Figure S17
	V9d Climate change threat	0.05	0.05	.28	**0.55**	**0.08**	***	0.1	0.12	.36	0.14	0.08	.1	Figure S18
	V10 Human development	0.53	0.39	.17	**−1.15**	**0.37**	**.002******	−0.52	0.35	.14	0.18	0.19	.36	Figure S19
	V11 Survey effort	**−0.09**	**0.02**	***	−0.01	0.03	.69	**−0.16**	**0.03**	***	0.02	0.02	.37	Figure S20

Note: All parameters in this table have been derived from phylogenetic linear regression using the *phylolm* package (Tung Ho & Ané, 2014) to account for potential autocorrelation among species due to their phylogenetic relatedness. Significant relationships ($p < .05$) are highlighted in bold. Amphibians = 377 species (lost = 279; rediscovered = 98); birds = 200 species (lost = 48; rediscovered = 152); mammals = 151 species (lost = 47; rediscovered = 104); reptiles = 480 species (lost = 428; rediscovered = 52). References to associated figures are provided in the final column of this table. x = not tested due to low sample size. Significance codes: ***$p < .001$, **$p < .01$, *$p < .05$.

Abbreviations: Est., estimated coefficient; SE, standard error.

the characteristics of species (Hypothesis H2), time lost was not found to be significantly associated with rediscovery, while body mass was positively associated with the rediscovery of amphibians and negatively associated with the rediscovery of reptiles (Squamata), and habitat breadth was positively associated with the rediscovery of amphibians and birds. Plots showing the distribution of lost and rediscovered species for time lost are shown in Figure 3. Plots for all other variables are provided in Figures S6–S20. These plots do not account for the potential phylogenetic relatedness of the species in our dataset.

Regarding characteristics of the environment (Hypothesis H3), forests were negatively associated with the rediscovery of birds but positively associated with the rediscovery of mammals; shrublands were positively associated with the rediscovery of amphibians and birds but negatively associated with the rediscovery of reptiles; and grasslands were positively associated with the rediscovery of amphibians and birds. Inland wetlands were positively associated with the rediscovery of reptiles, and artificial terrestrial habitats were positively associated with the rediscovery of birds. Small islands were negatively associated with the rediscovery of mammals (Table 1).

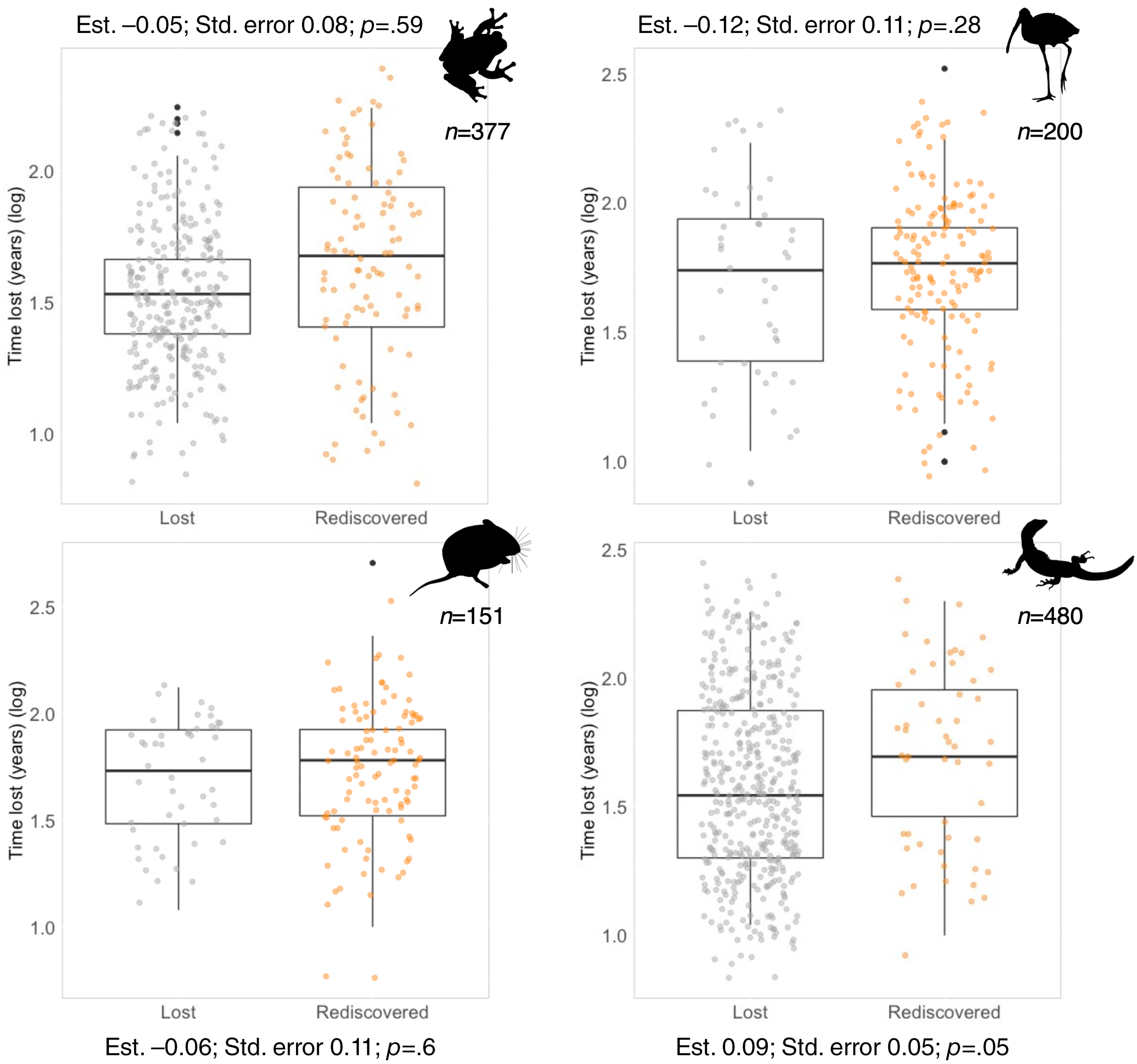

FIGURE 3 Lost and rediscovered species distributed by the length of time they have been lost for (lost species), or the length of time they were lost for before being rediscovered (rediscovered species). Boxplots show the median and the first and third quartiles (the 25th and 75th percentiles) with outliers plotted individually in black. The results of the univariate analysis (as presented in Table 1) are displayed next to each plot for ease of reference. Est., estimated coefficient; Std. error, standard error. All four species silhouettes were downloaded from www.phylopic.org (CC0 1.0).

Regarding the characteristics of human activities (Hypothesis H4), the threat of alien species was negatively associated with the rediscovery of amphibians but positively associated with the rediscovery of birds, and the threat of habitat loss was positively associated with the rediscovery of reptiles. The threat of overexploitation was positively associated with the rediscovery of amphibians and mammals, and the threat of climate change was positively associated with the rediscovery of birds. Human development was negatively associated with the rediscovery of birds, and survey effort was negatively associated with the rediscovery of amphibians and mammals (Table 1).

3.2.2 | Multivariate analysis

Regarding the characteristics of species (Hypothesis H2), the best model, as ranked by AIC, indicated that time lost was positively associated with the rediscovery of reptiles (Squamata), and body mass was positively associated with the rediscovery of amphibians but negatively associated with the rediscovery of reptiles. The RIVs for all variables were high (0.83 or higher) (Table 2). For model combinations ranked by AIC, see Table S6.

Regarding characteristics of the environment (Hypothesis H3), forests were positively associated with the rediscovery of amphibians and mammals but negatively associated with the rediscovery of birds; shrublands were positively associated with the rediscovery of amphibians and birds but negatively associated with the rediscovery of reptiles; and grasslands were positively associated with the rediscovery of amphibians and mammals. The RIVs for these variables were relatively high (0.78 or higher). Inland wetlands and small islands were negatively associated with the rediscovery of mammals, but the RIVs for these variables were relatively low (0.58 and 0.63, respectively) (Table 2).

Regarding the characteristics of human activities (Hypothesis H4), the threat of alien species was negatively associated with the rediscovery of amphibians but positively associated with the rediscovery of mammals; and the threat of habitat loss was positively associated with the rediscovery of amphibians and mammals but negatively associated with the rediscovery of birds. The threat of overexploitation was positively associated with the rediscovery of amphibians and birds; and the threat of climate change was positively associated with the rediscovery of birds, mammals and reptiles. Human development was positively associated with the rediscovery of amphibians but negatively associated with the rediscovery of birds; and survey effort was negatively associated with the rediscovery of amphibians, birds and mammals. The RIVs for all variables tended to be high (all 0.89 or higher, except for the threat of habitat loss for mammals [0.6]) (Table 2).

4 | DISCUSSION

Much progress has been made to find lost species, which continue to be rediscovered despite severe global declines in the abundance of wildlife (Westveer et al., 2022). However, spatial and taxonomic patterns in rediscovery are not uniform. There are regions and taxonomic groups with unusually high numbers of lost species—our results can help to prioritise searches for them. These searches should be a global conservation priority as we are losing tetrapod species more quickly than they are being rediscovered.

The complete absence of lost and rediscovered species within some regions may reflect lack of knowledge (including baseline data on the presence of species) (Amano & Sutherland, 2013), perhaps due to taxonomic and geographic biases in monitoring schemes (Moussy et al., 2022), linked to a lack of research capacity (Moreno et al., 2023). For example, there are very few lost and rediscovered amphibian species across tropical Africa even though this is a hotspot of amphibian diversity (Kanga et al., 2021). More broadly, for example, knowledge of extinction risk for two mammal orders (Rodentia [rodents] and Eulipotyphla [shrews, moles and hedgehogs]) is not uniform, with DD species on the IUCN Red List tending to aggregate in regions with limited research capacity (Kennerley et al., 2021). Conversely, the complete absence of lost and rediscovered species in some regions with high research capacity and economic stability, particularly Europe, may reflect greater knowledge of the distribution and persistence of species in this region, higher levels of conservation funding (Moussy et al., 2022) and low numbers of endemic species (Jenkins et al., 2013).

Habitat breadth is the species characteristic (Hypothesis H2) with a consistent positive association with rediscovery across taxonomic groups. This may be because species occupying a broad range of habitats are likely to be more abundant and widespread and therefore easier to find. They are also less likely to be extinct, as they may not be affected by adverse impacts throughout the different habitats they occupy, and because they may be able to shift their distribution when faced with unfavourable conditions. Indeed, generalist birds tend to be less vulnerable to extinction (Sekercioglu, 2011) and to be less severely affected by landscape fragmentation and disturbance (Devictor et al., 2008). We did not test the effect of range size on rediscovery, due to a lack of range size data for many lost species. However, the size of a species range has been used as a proxy for habitat breadth (Evans et al., 2018), as species with larger ranges are likely to occupy a broader range of habitats. We therefore expect the effect of range size on rediscovery to be captured (at least in part) by habitat breadth. Indeed, mammals (Fisher & Blomberg, 2011) and plants (Humphreys et al., 2019) with larger ranges are more likely to be rediscovered.

The influence of other species characteristics (time lost and body mass) is less consistent and suggests that some lost species are extinct—particularly birds and mammals. Despite many successful rediscoveries of bird and mammal species in the past (Fisher & Blomberg, 2011; Tobias et al., 2006), this may explain why rates of rediscovery are slowing. Regarding time lost, we hypothesised that on average, lost species would be missing for shorter time periods than those that have been rediscovered, because there is less concern for recently lost species, so less effort is invested in searching for them (Figure S21). Indeed, we identified a positive association

TABLE 2 Relationships between rediscovery and predictor variables in multivariate analysis.

Hypotheses	Predictor variable	Amphibians Est.	Amphibians SE	Amphibians *p*	Amphibians RIV	Birds Est.	Birds SE	Birds *p*	Birds RIV	Mammals Est.	Mammals SE	Mammals *p*	Mammals RIV	Reptiles (Squamata) Est.	Reptiles (Squamata) SE	Reptiles (Squamata) *p*	Reptiles (Squamata) RIV
H2: Species characteristics influence rediscovery	V4 Time lost	-	-	-	-	0.15	0.09	.09	0.62	-	-	-	-	**0.1**	**0.04**	**.02****	0.83
	V5 Body mass	**0.23**	**0.06**	***	0.98	-	-	-	-	-	-	-	-	**−0.14**	**0.05**	**.008****	0.92
	V6 Habitat breadth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
H3: Characteristics of the environment influence rediscovery	V7a Forest	**0.19**	**0.07**	**.007****	0.93	**−0.46**	**0.08**	***	1	**0.21**	**0.09**	**.02***	0.78	-	-	-	-
	V7b Savanna	x	x	x	x	-	-	-	-	-	-	-	-	-	-	-	-
	V7c Shrubland	**0.19**	**0.05**	***	0.98	**0.17**	**0.06**	**.004****	0.84	-	-	-	-	**−0.28**	**0.05**	***	1
	V7d Grassland	**0.26**	**0.06**	***	1	-	-	-	-	**0.34**	**0.1**	**.001****	0.98	-	-	-	-
	V7e Wetlands (inland)	-	-	-	-	-	-	-	-	**−0.32**	**0.15**	**.03***	0.58	0.21	0.12	.07	0.66
	V7f Artificial terrestrial	-	-	-	-	-	-	-	-	0.18	0.09	.06	0.66	-	-	-	-
	V8 Small island/ mainland	−0.22	0.15	.13	0.43	-	-	-	-	**−0.13**	**0.06**	**.04***	0.63	-	-	-	-
H4: Human activities influence rediscovery	V9a Alien species threat	**−0.16**	**0.06**	**.005****	0.95	-	-	-	-	**0.23**	**0.1**	**.02***	0.73	-	-	-	-
	V9b Habitat loss threat	**0.15**	**0.04**	***	1	**−0.28**	**0.07**	***	0.99	**0.17**	**0.06**	**.008****	0.6	**0.1**	**0.03**	**.003****	0.93
	V9c Overexploitation threat	**0.2**	**0.03**	***	1	**0.18**	**0.06**	**.005****	0.91	-	-	-	-	-	-	-	-
	V9d Climate change threat	0.08	0.05	.07	0.61	**0.43**	**0.08**	***	1	**0.26**	**0.09**	**.007****	0.94	**0.24**	**0.08**	**.003****	0.91
	V10 Human development	**2.59**	**0.57**	***	1	**−1.08**	**0.44**	**.02***	0.89	-	-	-	-	-	-	-	-
	V11 Survey effort	**−0.1**	**0.02**	***	1	**−0.12**	**0.02**	***	1	**−0.19**	**0.04**	***	1	-	-	-	-
	Intercept	0.37	0.66	.57		1.05	0.44	.02*		0.46	0.92	.62		0.13	0.37	.72	

Note: This table shows the best reduced model identified using the *dredge* function in the *MuMIn* package (Bartoń, 2020). All parameters in this table have been derived from phylogenetic linear regression using the *phylolm* package (Tung Ho & Ané, 2014) to account for potential autocorrelation among species due to their phylogenetic relatedness. Significant relationships ($p<.05$) are highlighted in bold. Relative importance values (RIVs) (the sum of the Akaike weights over all models for each variable) were obtained using the *importance* function (*MuMIn* package) (Bartoń, 2020). - = variable did not feature in model. x = not tested due to low sample size. Amphibians: AIC = 583.5, log-likelihood = −278.7. $R^2=.35$, Adjusted $R^2=.33$. Birds: AIC = 293.5, log-likelihood = 136.7. $R^2=.52$, Adjusted $R^2=.5$. Mammals: AIC = 265.5, log-likelihood = −121.7. $R^2=.36$, Adjusted $R^2=.32$. Reptiles: AIC = 679.8, log-likelihood = −331.9. $R^2=.12$, Adjusted $R^2=.11$. Amphibians = 377 species (lost = 279; rediscovered = 98); birds = 200 species (lost = 48; rediscovered = 152); mammals = 151 species (lost = 47; rediscovered = 104); reptiles = 480 species (lost = 428; rediscovered = 52). Significance codes: ***$p<.001$, **$p<.01$, *$p<.05$.

Abbreviations: Est., estimated coefficient; SE, standard error.

between time lost and the rediscovery of reptiles (Table 2). Yet lost bird and mammal species have, on average, been missing for a similar length of time as those that have been rediscovered (Figure 3). In fact, analyses incorporating all species in our dataset (including those excluded from the phylogenetic analyses) indicates that lost bird species have, on average, been missing for longer than rediscovered bird species (Table S23). Approximately 28% of remaining lost bird species have been missing for over 100 years; the average time lost for bird species that have been rediscovered is 66 years.

With regard to body mass, we hypothesised that larger tetrapod species are more likely to be rediscovered because they are more charismatic and thus more frequently searched for, and because they are easier to find. This may be why Lee et al. (2017) found large-bodied mammal species more likely to be rediscovered than small-bodied mammal species. However, we found body mass to be negatively associated with the rediscovery of reptiles (Tables 1 and 2), even though rediscovered reptiles are on average larger than those that are lost (Figure S6; Table S23). This counterintuitive result is influenced by phylogeny. Among different subgroups of reptiles, lost Serpentes (snakes) and Anguimorpha (monitor lizards and glass lizards) are on average heavier than those that have been rediscovered, and species from these two subgroups are among the largest squamates (scaled reptiles) in our dataset (Figure S6). If, as we hypothesise, larger lost species are more likely to be rediscovered, it is possible that some of these larger reptile species are not lost, but extinct—greater success may come from searching for smaller lost reptile species. Indeed, newly described reptile species have increased steadily over the last decade (Uetz et al., 2022). However, these species are mainly lizards, especially geckos, which tend to be smaller than species from other groups of reptiles. In fact, these newly described lizard species also tend to be small compared to other lizards (Meiri, 2016). This trend in discovery also suggests that rediscovered reptile species will be small. It is likely that the larger species have either already been discovered or have gone extinct. Lost bird and mammal species are, on average, heavier than those that have been rediscovered (Table S23). It is also possible that some of these large bird and mammal species are not lost, but extinct.

Results for variables associated with Hypothesis H3 (characteristics of the environment) and Hypothesis H4 (human activities) also suggest some lost species are extinct. Human development is negatively associated with the rediscovery of lost bird species (Tables 1 and 2; Figure S19) and yet regions with high human development are those with greater capacity for conservation. In contrast, human development is positively associated with the rediscovery of amphibians (Table 1; Figure S19). As lost amphibians also tend to be smaller than those that have been rediscovered (Tables 1 and 2; Figure S6), it could be concluded that a greater proportion of lost amphibian species may be rediscovered (particularly those that are small-bodied and located in low-income regions) than lost bird and mammal species, and species from certain squamate subgroups (e.g. snakes and monitor lizards). That said, the adverse impact of the chytrid pathogen *Batrachochytrium dendrobatidis* may explain the low rates of rediscovery for amphibians. *B. dendrobatidis* is an invasive alien species that has caused the decline and extinction of many amphibian species across the globe (Scheele et al., 2019). Nevertheless, some amphibian species that have exhibited severe population declines due to *B. dendrobatidis* now show signs of recovery (Puschendorf et al., 2011; Scheele et al., 2014), and the low rates of rediscovery we identified (Figure S15) may reflect the very small population size of recovering species, which makes them difficult to detect. Further time and additional survey effort may be required to confidently assess the effect of *B. dendrobatidis* on the rediscovery of lost amphibian species.

Most bird, reptile and mammal species extinctions have occurred on islands (Fromm & Meiri, 2021; Slavenko et al., 2016; Szabo et al., 2012; Turvey & Fritz, 2011), where tetrapod species are disproportionately vulnerable to multiple threats (Fernández-Palacios et al., 2021). We found small islands to be negatively associated with the rediscovery of lost mammal species (Tables 1 and 2) and suggest that island extinctions may be underreported, as 35% of remaining lost mammal species are endemic to islands. Furthermore, some of these islands are parts of well-resourced countries where capacity to search for lost species is high (e.g. the Bramble Cay melomys [*Melomys rubicola*], on Bramble Cay, Australia). Searches for lost species may also be easier on some of the smallest islands in comparison to mainland locations as the search area is likely to be smaller—indeed, Bramble Cay is just 340 m long and 150 m wide. If extant, lost species on small islands like Bramble Cay should perhaps have been rediscovered by now.

The positive association between the rediscovery of mammals and the threat of alien species is counterintuitive. This result is likely to be influenced by human development, as all previously lost species of Diprotodontia (kangaroos, possums, wombats and allies) and Dasyuromorphia (Australian carnivorous marsupials) known to be threatened by alien species in Australia have been rediscovered (Figure S15). Over one-third of the mammal species in our dataset are Rodentia (rodents)—almost 70% that are known to be threatened by alien species have been rediscovered, and mainly in low-income regions. This result may suggest rodents are resilient to the impacts of alien species, but it more likely reflects a lack of knowledge regarding the true distribution of rodent species, which tend to be neglected by conservation scientists (Kennerley et al., 2021). The positive effect of three other threats on rediscovery (habitat loss, overexploitation and climate change) is also counterintuitive. However, our result for habitat loss supports those of Fisher and Blomberg (2011) who found mammal species affected by habitat loss that had been declared extinct were more likely to be rediscovered that those affected by threats such as overexploitation, diseases and alien species. A relatively small proportion (17%) of lost and rediscovered species affected by overexploitation are located on small islands, where threats to tetrapod species tend to be severe. Climate change impacts may have yet to become severe enough to manifest in IUCN Red List data, but we expect this threat to have a rapidly increasing adverse influence on the rediscovery of lost species.

The negative effect of survey effort on rediscovery for amphibians, birds and mammals may arise because searches are being conducted for species that are extinct. Indeed, some searches appear to be motivated by the challenge of finding long-lost species, including some that are considered extinct and hence not on our lost species list, such as the thylacine (*Thylacinus cynocephalus*) (Carlson et al., 2018). This may be why an analysis of survey effort for mammal species found none afforded 'high' effort to have been rediscovered, while most afforded 'intermediate' effort had been rediscovered (Fisher & Blomberg, 2011). However, we did not identify a negative effect of survey effort for reptiles. This suggests that rather than being extinct, at least some lost reptile species are particularly hard to find, probably because they tend to be small (on average, much smaller than those that have been rediscovered). Many lost reptile species may require greater survey effort than they have been afforded to date if they are to be rediscovered.

Our results suggest that tetrapod extinctions are likely to be underreported. Indeed, 202 (24%) of the 856 lost species in our dataset have been afforded survey effort graded as 'high' or 'very high', and many are allocated a threat status other than CR (PE) or EX on the IUCN Red List. They include, for example, the New Caledonian rail (*Gallirallus lafresnayanu*) (CR), which has not been seen since 1890. We suggest that IUCN Red List assessments for these species should be reviewed and amended (where appropriate) to more accurately reflect their threat status. Furthermore, a greater proportion of lost species are highly threatened [CR or CR (PE) = 81%] in comparison with rediscovered species (CR = 35%) (Figure S22). While this may be because the rediscovery of some lost species leads to their conservation and the subsequent downgrading of their threat category, it is also likely to be because the species we are rediscovering are those less threatened with extinction. Some of the lost species we are not finding may no longer exist. Underreporting of extinctions may reflect the difficulty, both scientifically and politically, of classifying a lost species as extinct (Martin et al., 2022). Nevertheless, this underreporting may be influencing the investment of resources (time, expertise and funding) to plan and undertake searches for species that no longer exist. As resources for conservation are limited (Joseph et al., 2009), it may be necessary to adopt a pragmatic approach that prioritises searches for species most likely to be extant. However, as our dataset includes rediscoveries of lost species that were long considered to be extinct, we are reluctant to suggest which species should or should not be searched for. An example is the Cebu flowerpecker (*Dicaeum quadricolor*) (Dutson et al., 1993) which was unrecorded for 86 years, has specific habitat requirements and is present on an island <20,000 km^2—the results of our study suggest this species was an unlikely rediscovery.

Indeed, rather than being extinct, some lost species may be neglected by conservation scientists, including for example, small mammals (Kennerley et al., 2021) which are less frequently searched for than large mammals (Fisher, 2011). This may be why 49% of lost mammal species are rodents (Rodentia). Across classes of tetrapod, research tends to be biased towards birds and mammals (Clark & May, 2002; Cox et al., 2022; Hecnar, 2009), possibly because they are considered more charismatic than reptiles (Albert et al., 2018). This may be why rates of loss are increasing rapidly for reptiles, but not for birds or mammals. This bias needs to be addressed to prevent the loss of more reptile species. Indeed, post hoc analysis indicates that more reptile species are afforded 'low' survey effort, and fewer are afforded 'high' survey effort than would be expected (Table S24). Comparing survey effort across different taxonomic groups within each class of tetrapod (Tables S25–S28) indicates that more Serpentes (snakes) have been afforded 'high' survey effort, more Anguimorpha (monitor lizards and glass lizards) have been afforded 'very high' survey effort (species from these groups are relatively large) (Feldman et al., 2016) and fewer Scinciformata (skinks) have been afforded 'very high' survey effort (these species tend to be small and less charismatic) (Table S28). For birds, more Psittaciformes (parrots) have been afforded 'very high' survey effort (Table S26)—parrots tend to be charismatic (Garnett et al., 2018). Across tetrapod species more generally, less survey effort is invested in smaller lost species (Figure S21).

Furthermore, rather than being extinct, some lost species may be particularly difficult to find, due to their specific characteristics (Stephenson et al., 2022) (Hypothesis H2) and characteristics of the environment they inhabit (Hypothesis H3). For example, approximately 9% of remaining lost bird species are nightjars (Caprimulgidae) or owlet-nightjars (Aegothelidae). These species are crepuscular/nocturnal and camouflaged, which makes them harder to find. The rediscovery of Heinrich's nightjar (*Eurostopodus diabolicus*) required the use of sound recordings to confirm its identity (Bishop & Diamond, 1970). Approximately 45% of lost reptile species are dibamids (Dibamidae) or skinks (Scincidae), many of which spend time underground in burrows. Approximately 10% of lost mammal species are golden moles or tenrecs (Afrosoricida), which are nocturnal species that often live underground. The effect of different habitats on rediscovery may reflect the varying difficulty in searching for the lost species that occupy them. Searches for birds may be easier in grasslands, shrublands and artificial terrestrial habitats than in forests, and searches for mammals may be easier in grasslands and forests than in wetlands. While searches for lost species in accessible habitats may therefore be more successful, some lost species may await rediscovery in more challenging environments. For example, Miss Waldron's red colobus (*Piliocolobus waldronae*) (CR) occupies mud forests and swamps of south-eastern Côte d'Ivoire where, due to the presence of snakes and crocodiles, residents and research scientists are reluctant to venture (Re:wild, 2021). The negative effect of shrublands on the rediscovery of reptiles is counterintuitive, as shrublands are not particularly inaccessible. However, this result is likely to be influenced by body mass, as the average weight of reptile species that do not occupy shrubland habitats is 158 g; for those that do, it is 26 g.

Broad measures such as the protection of known habitats of lost species may be a more efficient and effective conservation policy than conducting searches for species that have low chances of success (such as small, nocturnal or fossorial species). However, technological advances are leading to increased capability to detect species, including those that are rare, cryptic or hard to find. For example, eDNA has been used to detect burrowing seabirds on Macquarie Island (a remote sub-Antarctic island) (McInnes et al., 2021). Molecular analysis has detected the presence of Archey's frog (*Leiopelma archeyi*) (CR) in the diet of ship rats (*Rattus rattus*) (Egeter et al., 2019). Audio recordings have been used to develop a survey protocol for a nocturnal bird species (the night parrot, *Pezoporus occidentalis* [CR]) (Leseberg et al., 2022). Indigenous ecological knowledge has been used to improve the understanding of mammal population declines in Australia (Ziembicki et al., 2013). Camera trap arrays have improved the detection of mammal species of varying body sizes (O'Connor et al., 2017). Specific camera trap designs have been effective in detecting cryptic small mammal species (Thomas et al., 2020), and camera trap bycatch data could be exploited to monitor non-target species (Stephenson et al., 2022). These techniques could improve rates of rediscovery, particularly if incorporated into biodiversity monitoring in low-income countries (Stephenson et al., 2022). The integration of neglected species or those that are hard to detect into existing monitoring schemes may also improve rates of rediscovery. For example, smaller mammal species could be incorporated within established schemes for larger mammal species (e.g. tenrec species [Tenrecidae] within monitoring schemes for lemurs [Lemuroidea] in Madagascar) (Stephenson et al., 2021).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article and in Dryad (Appendix E, https://doi.org/10.5061/dryad.v6wwpzh31; Appendix F, https://doi.org/10.5061/dryad.1c59zw432; and Appendix G, https://doi.org/10.5061/dryad.c866t1gdf).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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