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Review article

Rewilding in cold blood: Restoring functionality in degraded ecosystems using herbivorous reptiles

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ABSTRACT

Rewilding constitutes an ecological recovery approach that has been promoted to restore vanished ecological functions by replacing recently extinct or extirpated species through the reintroduction of the missing species or the introduction of their non-native functional analogues. In recent years we have witnessed many rewilding projects worldwide, with emphasis on (re) introducing large-bodied mammals (megafauna) in order to restore top-down trophic interactions and the associated trophic cascades and to promote self-regulating biodiverse ecosystems (i.e., trophic rewilding). However, this emphasis on large-sized mammals in conservation initiatives have ignored the importance of other taxa, such as reptiles, which can equally serve as potential candidates in rewilding projects. There appears to be a gap in the scientific literature in regard to the importance and effect of different taxa with the potential to play equal and important roles in ecosystem functionality and restoration. Consequently, there is a need for a comprehensive and systematic review of the subject. Here, we highlight the significance of rewilding using reptiles, focusing on herbivorous species, for the purpose of ecological restoration; and discuss how the taxonomic bias in rewilding initiatives has led to uneven conservation goals for certain vertebrate groups. Finally, we outline the consequences for reptilian rewilding under climate change and relate to how this group may fare in these conservation initiatives.

1. Introduction

The fast-paced extinction around the world of a multitude of animals and plants, caused by human actions (e.g., land-use change; Scanes, 2018), has led to the need for the establishment of large protected natural areas, along with the listing (i.e., classifying species' status) and protection of rare and threatened species (Noss et al., 1997; Cantú-Salazar and Gaston, 2010; Jepson, 2016). Several conservation plans have been proposed to mitigate or halt this biodiversity crisis, from creating large networks of nature reserves (e.g., Kavango Zambezi Transfrontier Conservation Area) to actively restoring ecosystems (e.g., revegetation) and even calling for the protection of 50% of the earth for non-human organisms (85% of remaining biodiversity, Fraser, 2009; Palmer et al., 2016; Wilson,

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2016; Büscher et al., 2017). Although these strategies are fundamentally critical in preventing species' extinction, the anthropogenic impact on natural systems is so pervasive that strategies that complement the impact of protected areas are urgently needed (Laurance et al., 2012; Buscher and Fletcher, 2020). The human impact is not only manifested in the decline of species locally, but also in the loss of the interactions of such species in their ecosystem (Valiente-Banuet et al., 2015; Genes and Dirzo, 2022). Thus, it is necessary to restore not only the species, but also the functional interactions between them (Sandom et al., 2013; Valiente-Banuet et al., 2015; Galetti et al., 2017; Carver et al., 2021; Pires, 2024).

The consequences of globally or locally extinct species, particularly large-bodied vertebrates, have created impoverished ecosystems where many ecological processes are missing or disrupted (Sodhi et al., 2009; Sandom et al., 2014; Ripple et al., 2017; Galetti et al., 2018; Ceballos et al., 2020). These large animals have experienced severe declines in population abundance over the last few decades, making them particularly threatened and vulnerable (Dirzo et al., 2014; Ceballos et al., 2015). Such declines are critical, due to the significant roles that these large vertebrates play in ecosystems, such as plant diversity maintenance (Galetti, 2004; Sandom et al., 2013; Svenning et al., 2016; Pringle et al., 2023). The main strategies used today by conservationists for mitigating population declines and reversing functionality loss in natural ecosystems are: 1) translocation of a certain number of specimens into an existing population of the same species within its natural range (i.e., reinforcement; IUCN/SSC, 2013); 2) intentionally moving and releasing individuals of the same species outside of their native range (i.e., assisted migration; IUCN/SSC, 2013); 3) reintroducing or introducing species that were previously extirpated or extinct, or their ecological proxies (taxonomic substitutions for extinct native species that once underpinned the delivery of key ecological functions; du Toit and Pettorelli, 2019) in order to restore top-down trophic interactions and associated trophic cascades (i.e., trophic rewilding; Svenning et al., 2016).

Rewilding, as opposed to simply reintroducing a species into its former habitat, is mostly concerned with species with a high potential to exert an influence across several trophic levels (mostly top-down), and one that will have disproportionally large and beneficial effects on natural communities and ecosystem processes such as decomposition or nutrient cycling (Nogués-Bravo et al., 2016; Jepson and Blythe, 2022). Rewilding has expanded and changed its focus to beyond that of the 3 C (cores, corridors, and carnivores; Soulé and Noss, 1998; Foreman, 2004) or restoring ecosystems to their condition during the Pleistocene (2016; Galetti et al., 2017; Bakker and Svenning, 2018; Guyton et al., 2020). This strategy even took a more unusual shape, with the proposal to restore the vanished ecosystem functions of extinct species of large herbivores, by introducing ecological proxies (Galetti, 2004, Donlan, 2005; Hansen et al., 2010). The main objections to the use of ecological replacements in island systems for example, included the invasion by the introduced species itself, societal objections of unfamiliar species and ongoing ecosystem disruptions that could cause certain functions to become irrevocably lost (Rubenstein et al., 2006; Griffiths and Harris, 2010; Root-Bernstein et al., 2017). Nonetheless, ecological replacements may offer an effective solution for the mitigation of more recent mega-herbivore extinction events (Hunter et al., 2014; Hansen, 2015; Garrido et al., 2019; Garrido et al., 2021; Corson et al., 2022; Jones et al., 2022).

Rewilding can potentially serve as a complementary strategy to most conservation initiatives worldwide, by focusing less on individual species protection per se, and more on (re)introducing species that can restore the complexity and functionality of whole ecosystems (Navarro & Pereira, 2015; Root-Bernstein et al., 2018, Pires, 2024). As a strategy, rewilding had received mixed support (primarily due to the early focus on carnivore reintroduction or the goal of recovering Pleistocene ecosystems; Caro, 2007; Oliveira-Santos and Fernandez, 2010; Jørgensen, 2015; Hayward et al., 2019). Nowadays, the rewilding concept has evolved into a process-oriented, dynamic approach that emphasises the autonomy of natural processes ('wildness'), and the understanding of trophic networks of interaction dynamics between (re)introduced species and their physical environment, in order to restore lost ecological processes (Corlett, 2016; Svenning et al., 2016; Fernández et al., 2017b; Svenning & Faurby, 2017; Perino et al., 2019; Jepson & Blythe, 2022). Thus, rewilding conforms more closely to the current global conservation emphasis on restoring natural ecosystem functions or processes rather than addressing only extinction risk (Seddon et al., 2014; Svenning et al., 2016; Perino et al., 2019).

In many ecosystems, trophic regulation (top-down or vice versa) as well as non-trophic impacts (e.g., disturbance or seed dispersal), have become lost or reduced due to historical (<5000 years B.P., Late Holocene and Anthropocene) and prehistorical (<50,000 years before the present) defaunation (Dirzo et al., 2014), emphasizing the importance of (re)introducing functional species, i.e., species that produce significant cascade effects through modifying habitats (ecosystem engineers; Jepson and Blythe, 2022) that may reverse this trend (Sobral-Souza et al., 2017; Svenning et al., 2019; Dombrovski et al., 2022; Garrido et al., 2022; Mittelman et al., 2022; Ruble et al., 2022). Most rewilding projects (especially in Europe) emphasize the (re)introduction of mega-herbivores (Svenning et al., 2016; Garrido et al., 2022; Vasile, 2023), because of the new understanding of ecological processes and the emerging interplay between herbivore consumption (grazing and browsing), production (urine, dung and their carcases) and vegetation structure, primary production, nutrient cycling, disturbance regimes, habitat heterogeneity and seed dispersal (de Mazancourt et al., 1999; Couvreur et al., 2004; Massé and Côté, 2012; Olofsson and Post, 2018; Jepson and Blythe, 2022; Pringle et al., 2023). In South America and Africa, rewilding has been called "refaunation" and has a similar connotation; i.e. bring back species recently extinct to perform ecological roles that are missing (Fernandez et al., 2017a, Correia et al., 2017). The advances in ecological science have firmly positioned herbivore reintroduction at the core of trophic rewilding, with the emphasis on restoring natural processes that produce fully functioning ecosystems across all scales form the local to the planetary (Broughton et al., 2022; Cornelissen et al., 2014; Dvorský et al., 2022; Smit et al., 2015; van Klink et al., 2016, 2020).

Over the last 20 years the extent of the scientific literature concerning the importance of rewilding through the (re)introduction of species has primarily focused on mammalian herbivores or carnivores (Bubac et al., 2019). The emerged taxonomic bias in the scientific literature in regard to rewilding (Tanentzap and Smith, 2018), may direct the focus from the importance and effect of other taxa that may play equal and important roles (to mammalian megafauna) in ecosystem functionality and restoration. In this review, we seek to close this gap by discussing the importance of other groups (e.g., herbivorous reptiles) that may equally drive changes in their environments and act as potential rewilding agents for the restoration of ecosystem functioning and processes. We address the current

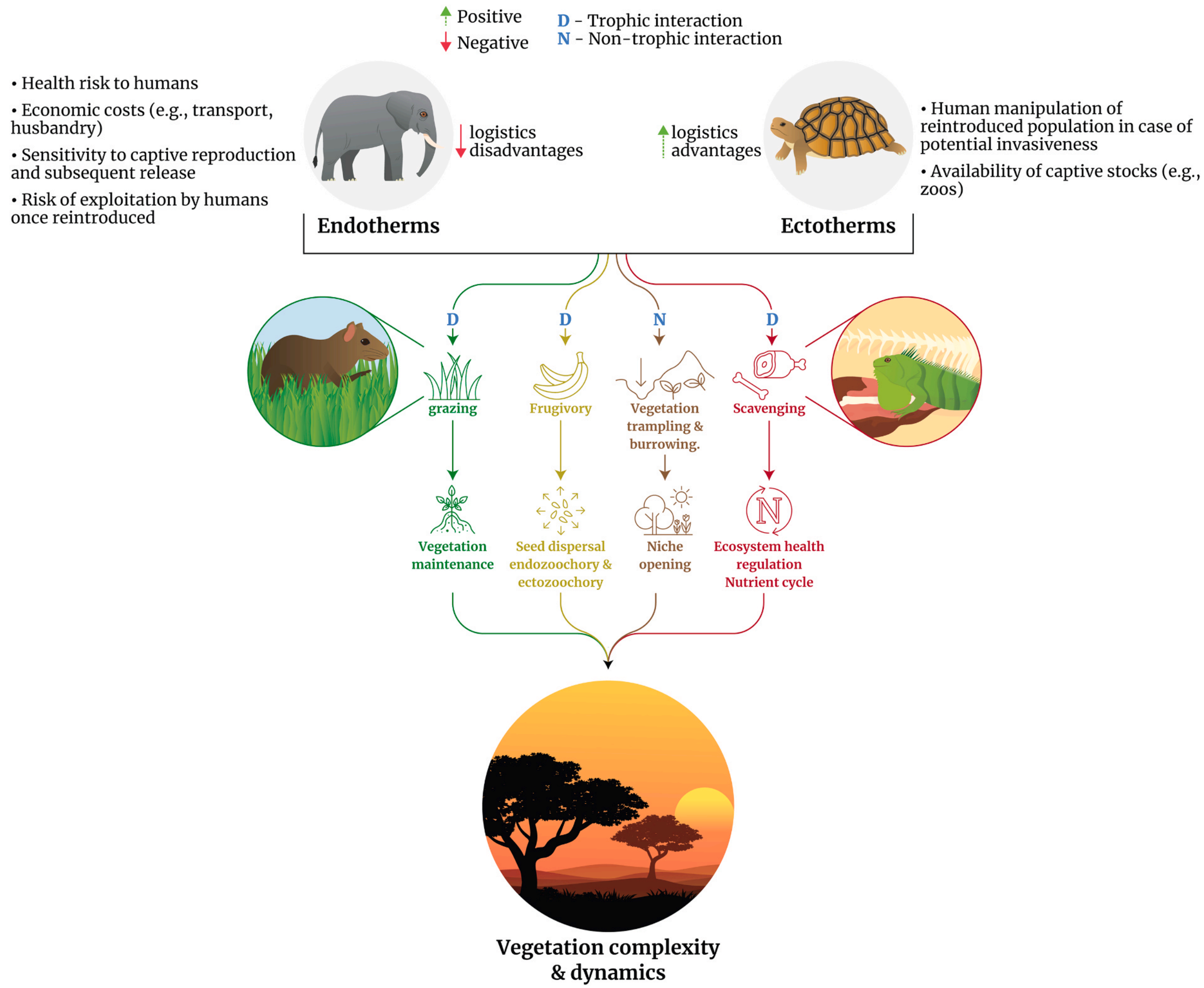

Fig. 1. The ecosystem contributions through the trophic and non-trophic interactions, shaping vegetation communities among designated rewilding candidates: Endotherm represents by The agouti; *Dasyprocta* spp. from Central-South America and the African elephant; *Loxodonta africana*, while among ectotherms, the giant tortoise; *Aldabrachelys gigantea* from the Seychelles and the green iguana; *Iguana iguana* from Central-South America play the role of ecosystem engineers (e.g., via epizoochory, endozoochory or grazing) in their environment. Logistics consideration for (re)introduction vary across each taxon.

scientific literature on rewilding using reptiles as our main focus group, while emphasizing the emerging taxonomic bias in rewilding initiatives. We also suggest that (re)introducing reptiles as addition to mammals, in various ecosystems around the world (from islands to continents) can complement and enhance ongoing rewilding initiatives and help build better conservation strategies that encompass a wide range of animal groups (both ectotherms and endotherms) that can serve as ecosystem engineers and restore functionality and resilience to impoverished ecosystems under climate change (Fig. 1).

2. Taxonomic-based rewilding

The Union for Conservation of Nature defines the reintroduction of species as: “An attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct” (IUCN/SSC, 2013). These critical projects constitute intensive, costly, species-targeted efforts designed to help restore biodiversity (Seddon, 2010). Unfortunately, there is a large taxonomic bias in reintroduction programs around the world, with vertebrates, especially mammals and birds, being greatly over-represented (> 70% for both groups) relative to their species numbers (Clark and May, 2002; Seddon et al., 2005; Bajomi et al., 2010; Donaldson et al., 2016; Bubac et al., 2019). The nature of trophic rewilding initiatives globally, which emphasize the (re) introduction of species as their main conservation strategy for ecosystem restoration (Svenning et al., 2016), has led to taxonomic bias, reflected in the ongoing (or potential) rewilding projects worldwide of certain vertebrate groups.

2.1. Data collection and categorization

We performed a comprehensive search for articles based on English-language scientific papers published over the last 18 years (between 2005 and 2023), using the research engines Web of Science, Google Scholar and ResearchGate, as well as gray literature (e.g., technical reports, graduate theses, and non-peer-reviewed articles). We identified articles using the topic search terms “Rewilding”, “Trophic rewilding” and “Re-wilding” in conjunction with one of five vertebrate groups of animals: mammals, birds, amphibians, reptiles, fishes. To ensure that the systematic review focuses on publications on rewilding in the sense of trophic rewilding, we have only included articles engaging with conservation translocations/reintroductions/introductions explicitly aimed at restoring ecological functions, while excluding articles detailing extreme forms of rewilding strategies (de-extinction). We have also covered all websites related to rewilding initiatives worldwide (with an emphasis on Rewilding Europe: https://rewildingeurope.com/) and digitized in Excel their ongoing and potential projects (for instance the Refauna Project in Rio de Janeiro– Fernandez et al., 2017a). In order to avoid pseudo data-points of similar conservation initiatives into the same specific habitat, we have filtered out and removed duplicates, books, book reviews, conference abstracts, editorials and irrelevant literature, according to rewilding criteria. Throughout this study, we used definitions as provided by the IUCN Species Survival Commission (SSC) (2013), with “introductions” serving as the overarching term and, as such, encompasses reintroductions, reinforcements, assisted colonizations, and ecological replacements. We focused our attention on studies made available in and after the year 2005 in an attempt to resume describing research trends during almost 20-year period following major reviews by Seddon et al. (2005), Seddon et al. (2007), Bajomi et al. (2010) and Bubac et al., (2019). Finally, we retained only studies for analysis with the sole purpose of restoring or reinforcing a species in the hopes of establishing a self-sustaining population, while concomitantly increasing resilience and functionality in their ecosystem. While some articles may have been missed by our search method, we believe our study collection is thorough and representative of the rewilding literature. Furthermore, while we acknowledge the importance of other non-vertebrate species (e.g., insects) or plant reintroductions in the restoration of a functioning ecosystem, including these groups was beyond the scope of this review. Overall, we focused on 70 scientific publications specifically concerning the impact of rewilding on ecosystems.

2.2. Statistical analysis and map generation

We summarized the following information for all species combined for each of the taxa individually (mammals/birds/reptiles/amphibians/fish): 1) general rewilding projects; 2) geographical locations of rewilding projects; 3) the number of studies that focused on species’ diet. We ran Two Sample t-test among physiologically different groups (endotherms and ectotherms), while we ran One-way Anova for the difference among all taxonomic groups (n=5) in our analysis according to each category described above (1−3). We collected latitude and longitude data using Google Earth (Mutanga and Kumar, 2019) for each species, using the rewilded areas’ location (or potential location) noted in each conservation initiative in the database. In RStudio, we created global maps using Geom Map function in ggplot2 package (Wickham, 2011) and uploaded the GPS coordinates and embedded them on a map.

3. Results

We observed a major taxonomic gap in studies concerning rewilding in the last 18 years (See Fig. S1 in supporting information). Most references (number of studies concerning rewilding) in the scientific literature have primarily focused on endothermic species (~84%, n=196, $t = -39$, $df = 39$, $p<0.0001$), with special emphasis on the importance of reintroducing mega-herbivores (e.g., the European bison *Bison bonasus*) or mammalian carnivores (e.g., the grey wolf *Canis lupus*) in rewilding initiatives ($p<0.0001$ between these two groups to the rest of the mammalian groups, e.g., Rodentia). In contrast, only ~16% (n=40) of references to such projects emphasize the use of reptiles, with the main focus primarily on Testudines. Among the ectothermic taxa, the predominant order used or suggested for rewilding was that of the Testudines (95% of the references, n=38, $p<0.0001$), with a major emphasis (~45%, n=17, $p<0.0001$) on giant tortoises (primarily for island ecosystems). The mammalian class was the most represented and referenced group

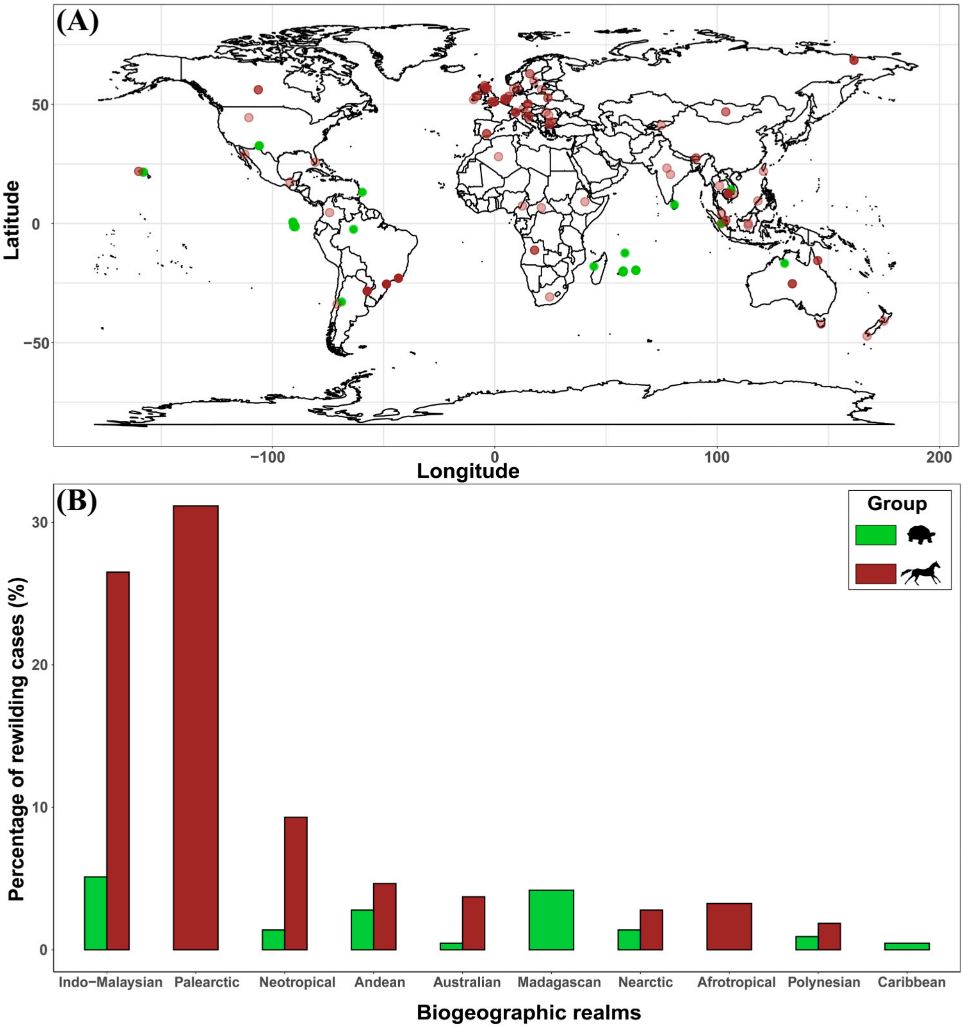

Fig. 2. The distribution of current and potential rewilding projects worldwide according to (A) physiological division (endotherms = birds and mammals, brown circles; ectotherms = reptiles only, green circles); and (B) biogeographical realms [based on Procheş & Ramdhani's (2012) regional analysis]. The percentages in (B) relate to the proportion of each biogeographical group from the pool of all the rewilding projects in our database. Animal icons from PhyloPic.

in rewilding projects around the world, followed by reptiles (almost exclusively Testudines) and birds, with no mentions found for fish or amphibians in any rewilding initiatives (the only reference to amphibians is in the context of studies focusing on restoring the microbiome of amphibians' skin; Kueneman et al., 2022; Korpita et al., 2023). Overall, 32% ($n=70$, $t=-39$, $df=39$, $p<0.0001$) of the published studies relating to rewilding, considered the possibility of using ectothermic species as ecological engineers or creating top-down regulation via herbivory or seed dispersal. In contrast, ~67% of the 70 studies emphasized the importance of using endotherms (mostly focusing on mammals) as top-down regulators (primarily through the action of ungulate grazing and browsing) or ecosystem engineers (see Fig. S2A & B in supporting information).

Geographically, patterns in conservation initiatives worldwide emerged (as also found for reintroductions in general; Bubac et al., 2019). Among the 193 countries of the world, 27% (n=52) of them engage in rewilding projects (encompassing every continent except Antarctica) for the restoration of fully functioning ecosystems (Fig. 2A). The biogeographic distribution (based on the vertebrate zoogeographical analysis by Procheş & Ramdhani, 2012) of reptilian species used in rewilding projects has been limited to the Madagascan, Indo-Malaysian and Neotropical (including the Andean) regions in the equatorial part of the world (Fig. 2B); while endothermic species reveal a global range, especially in the Palearctic region in the northern hemisphere.

There was also bias within the orders of each taxon based on their dietary lifestyle. Among mammalian orders, the majority of rewilding projects involved large-bodied herbivores (~48%, n=78, p<0.0001), with carnivore species making up the second largest group (~41%, n=69, p<0.0001), in addition to a few insectivore (e.g., sloth or echidna species), frugivore (primarily primates) and omnivore (e.g., wild boar *Sus scrofa*) groups (~9%, n=18). In birds, most projects involved carnivorous species (55%, n=17) and a few herbivorous (19%, n=6) or omnivorous (26%, n=8) ones. In contrast, the majority of rewilding initiatives involving reptiles mostly included herbivorous species (~95, n=38, p<0.0001). The only two cases involving carnivores (i.e., the Komodo dragon *Varanus komodoensis* and the Siamese crocodile *Crocodylus siamensis*) include large sized species with specific habitat requirements and behaviours (see Fig. S2 in supporting information).

These regional gaps in rewilding projects specifically and in conservation research in general (Clark and May, 2002), divert precious resources from the protection of highly endangered groups (e.g., giant tortoises; IUCN, 2021), which could constitute their last lifeline in preventing their impending extinctions as a result of the human impacts that are happening around the world. Thus, narrowing the overall research gap between mammals, birds and reptiles concerning rewilding initiatives may facilitate more effective conservation policies, in limiting biodiversity declines and improving ecosystems in certain areas worldwide.

4. Using reptiles for restoring ecosystem functionality

Terrestrial ectotherms (amphibians and reptiles) are disproportionately threatened by human activities relative to other vertebrate groups (Wake and Vredenburg, 2008; Cox et al., 2022). Specifically, reptiles reveal alarming proportions of population decline worldwide (Ceballos et al., 2017), with 21% of species (Cox et al., 2022) threatened and may face extinction risk under the IUCN Red List categories (IUCN, 2021). However, most conservation research disproportionately focuses on birds and mammals, leaving reptiles highly underrepresented, as mentioned earlier (Clark and May, 2002; Di Marco et al., 2017; Stark and Galetti, 2024). Due to this disparity, many studies have proposed the use of reptiles (under the umbrella of rewilding initiatives) to address this growing issue, and have emphasized the importance of specifically reintroducing endangered species in aiding ecosystem restoration in areas where these species might once have played an important role in grazing or dispersing plants (Griffiths et al., 2010; Hansen et al., 2010; Hunter and Gibbs, 2014; Hansen, 2015; Galetti et al., 2017; Sobral-Souza et al., 2017; Tapia et al., 2022; Tapia Aguilera and Gibbs, 2023). Recently, however, a study found that the long-term effects (after 7 years) of reintroducing tortoises into a severely degraded environment have had a low impact on the ecosystem, primarily through grazing. This suggests that additional interventions, such as actively controlling invasive plant species, may be necessary to achieve successful restoration of this specific habitat (Moorhouse-Gann et al., 2022). Although it seems that in some cases reintroducing reptiles may not be a panacea for improving impoverished environments, this group still has potential value for restoring functionality in ecosystems (as described below), similar to the contributions made by mammals in rewilding projects. (Fig. 1).

Overall, there are several advantages to reintroducing reptiles into areas where they have been extirpated. Additionally, introducing species to novel habitats can positively impact their ecosystem. Reptiles (especially tortoises and iguanas) are efficient seed dispersers (Lasso and Barrientos, 2015; Traveset et al., 2016; Falcón et al., 2020), able to digest and excrete different seed sizes from various plant species in large quantities, in addition to accelerating seed germination rates (Laurel et al., 2000; Lautenschlager et al., 2022). Unlike avian and mammalian species, reptiles do not regurgitate/spit the seeds, thereby reducing to a minimum the damage to seeds created by the mouthparts of the various endothermic seed dispersers (Falcón et al., 2020). Tortoise-mediated nutrient cycling and nutrient transporting functions (e.g., defecating and burrowing) are of a magnitude similar to that of large mammals in continental ecosystems, contributing to terrestrial ecosystem functioning that links the above- and below-ground components and influences processes and properties at both the natural community and ecosystem levels (Falcón and Hansen, 2018; Lovich et al., 2018). Furthermore, many testudines control insect populations and keeping aquatic habitats clean and healthy by scavenging on dead animals (Dutt, 2019; Santori et al., 2020; Thomson, 2021). Other reptilian groups, such as iguanas play similar roles to tortoises and contribute to major ecosystem processes in several ways. First, iguanas graze on many plant species (e.g., grasses, herbaceous plants, leaves and floral parts of woody plants), which affect the recruitment of woody plants and thereby mediating woody plant-grass interactions (Kim et al., 2022; Tapia and Gibbs, 2022). Second, iguanas are able to disperse seeds over long distances (Lasso and Barrientos, 2015; Vásquez-Contreras and Ariano-Sánchez, 2016). Third, on islands iguanas can help critical plant species to establish themselves (via long distance seed dispersal), which in turn can act as keystone resource for much of the terrestrial animal community (Traveset et al., 2016; Tapia and Gibbs, 2022). Reptiles represent the highest animal biomass in many tropical, arid (Roll et al., 2017) and island ecosystems (for example, Antilles, New Caledonia and New Zealand: Roll et al., 2017; Cox et al., 2022), which can be important for many plants in contributing to greater dispersal distances and higher rates of seed germination (Gibbs et al., 2008; Falcón et al., 2020). These ecosystem services define reptiles, and particularly Tortoises and Iguanas, as ecological engineers of vegetation community structure and composition worldwide (Fig. 1; Gibbs et al., 2010; Tapia Aguilera and Gibbs, 2023; Tapia and Gibbs, 2022).

In addition to their ecological effects, there are several logistical advantages to reptilian (re)introductions. For example, the tortoises' life history (long-lived species with slow reproduction and relatively small ranges; Stark et al., 2018; Stark et al., 2020; Roll et al., 2017; Bush et al., 2022), enables conservationists to easily monitor (e.g., using radiotelemetry and GPS trackers; Rubke et al., 2019) and manipulate their population size (Griffiths et al., 2010; Hunter et al., 2013; Hansen, 2015; Galetti et al., 2017). Moreover, in cases of tortoise (re)introductions that go awry (over-consumption of native vegetation or the spread of invasive vegetation via seed dispersal), conservationists can easily locate and remove rewilded individuals from the designated area (Hansen, 2015), as opposed to mammalian (re)introductions that can achieve high densities without any human management, causing negative impacts on biodiversity and ecosystem function (Smith, 2005; Ims et al., 2007; Smit et al., 2015). Importantly, herbivorous reptiles do not represent a high health and/or economic risk to humans (e.g., they do not prey on domesticated animals, serving as disease vectors or agricultural pests), making them ideal species for initial (re)introduction into degraded environments in proximity to human settlements (de

Miranda, 2017; Lindell et al., 2018; Mendoza-Roldan et al., 2021). Many reptilian species are available in captive stocks, either in zoos or private captive-breeding programs (Hansen, 2015; Galetti et al., 2017). Using a portion of specific stocks of suitable genetic quality after thoroughly assessed for health considerations can accelerate and improve their post-translocation establishment for rewilding projects (Witzenberger and Hochkirch, 2011; van Zanten and Simpson, 2021). The natural distribution ranges of reptilian taxa span a wide variety of suitable habitats and climates, making them ideal candidates for rewilding projects worldwide (Hansen et al., 2010; Roll et al., 2017).

Main caveats in reptilian rewilding may include the length of time required for these species to reach full maturation size (in the case of tortoises; Griffiths et al., 2012), while also it is difficult to identify their reproductive success (years for observing wild born tortoises) or in some cases their nests or eggs (Germano and Bishop, 2009). These could be a disadvantage in relation to rewilding projects that need a here-and-now approach to restoring ecosystem functioning (Hansen et al., 2010). Another critical caveat for reptilian reintroduction, is their vulnerability to predation by dogs and other non-native mesopredators (Meshaka et al., 2019), while also through high levels of egg poaching that reduce the viability of the population (Stanford et al., 2020). These alterations usually occur in dysfunctional ecosystems that contain high density of mesopredators, which can affect the rewilded herbivores (Prugh et al., 2009, Pires and Galetti, 2023). However, when comparing the advantages against the drawbacks, there is a high potential for herbivorous reptiles in contributing to the conservation of plant–frugivore mutualisms across various habitats, with significant implications for restoring functionality in degraded ecosystems (Fig. 1; Falcón et al., 2020).

The main goal of rewilding using herbivorous reptile lies in restoring plant communities (Griffiths et al., 2012; Hunter et al., 2013), which necessarily constitutes a first priority in establishing a functioning ecosystem (Falcón et al., 2020; Jepson, 2022) where large-bodied vertebrates are pivotal (Donatti et al., 2007). Thus, there should be an appropriate sequence of taxonomic group reintroductions in disrupted environments: first, species from the lower trophic levels (generalist herbivores, such as giant tortoises; Gibbs et al., 2014) should be reintroduced; followed by more specialist species, which would benefit from a richer trophic web; and ending with the (re)introduction of apex predators (carnivorous reptiles; Bowman, 2012; Gray et al., 2019) only after their prey populations have been securely established (Louys et al., 2014).

5. Island rewilding: insular ecosystems shaped by reptiles

On islands around the world there exists a plethora of unique flora and fauna, although many continue to suffer from disproportionally high levels of extinction (Hansen, 2015; Hansford et al., 2021; Bush et al., 2022). The extinction crisis on islands is progressing at a much higher rate than for continental faunas, stressing the need for urgent conservation efforts (Wood et al., 2017; Tapia Aguilera and Gibbs, 2023). Most of our understanding on the effects of herbivore extinction on island ecosystems is based largely on studies of large mammals on continents (Wood et al., 2017). Recently, however, this focus expanded to include extinct reptiles that lived on island ecosystems in the past, and were mostly giant herbivorous species (e.g., tortoises and iguanas) that shaped the plant communities in their environment (Tapia Aguilera and Gibbs, 2023).

Prior to the arrival of humans on certain oceanic islands (e.g., Western Indian Ocean; Cheke, 2010), the largest native vertebrate species were the now extirpated species of giant flightless birds and giant tortoises (Hansen et al., 2010; Hansen, 2015). The extinction event caused by humans to many reptilian families (Fig. S3 in supporting information) worldwide is still ongoing, with ~60% out of the 363 testudines species (Uetz et al., 2023) are in immediate extinction risk in the next few decades (Lovich et al., 2018; Dutt, 2019; Thomson, 2021). The main factors contributing to the testudines' ongoing decline are mainly: habitat destruction, invasive species, extensive hunting (mostly eggs), encounters with domesticated animals, use in traditional Chinese medicine and illegal pet trade (Hailey et al., 1988; Dutt, 2019; Stanford et al., 2020; Thomson, 2021; Araya-Donoso et al., 2022). Even the iconic Galapagos tortoises have been smuggled and trapped in well protected parks (Auliya et al., 2016; Quinzin et al., 2023).

On many islands tortoises were usually the largest, or among the largest, vertebrates in their ecosystems (Hansen and Galetti, 2009; Hansen et al., 2010,). These insular tortoises are functional species that had acted as ecosystem engineers for millions of years on islands around the world (Gibbs et al., 2010). Their presence had several ecological effects, from seed dispersal, which, due to their slow digestion time, enabled the seeds to germinate faster (Falcón et al., 2020), to vegetation trampling and altering plant communities, which in turn positively affected other insular animals (e.g., Telfair's skink *Leiolopisma telfairii* or the waved albatross *Phoebastria irrorata*; Moorhouse-Gann et al., 2022; Tapia Aguilera and Gibbs, 2023). Their roles on islands were equal, on a relative scale, to those of elephants in continental ecosystems (Hansen and Galetti, 2009; Hansen et al., 2010; Hansen, 2015; Kerr, 2022).

One of the most famous examples of successful reintroduction took place in the Galápagos archipelago, involving the Hood Island giant tortoise (*Chelonoidis niger hoodensis*) on Española Island in 1960 (starting with 14 individuals and reaching more than 3000 individuals today; Gibbs et al., 2020; Cayot, 2021; Tapia Aguilera and Gibbs, 2023). This species helped to restore, amongst other things, lost plant-frugivore interactions via effective seed dispersal (Gibbs et al., 2008). One of the earliest examples (mid-1990s) of employing ecological replacement involved the introduction of four Aldabra giant tortoises (*Aldabrachelys gigantea*) into a small enclosure on Île aux Aigrettes Islet (Kerr, 2022). This eventually evolved into a major rewilding initiative in this area, with several more introductions on other Mascarene islands in the Western Indian Ocean (as of 2016, a total of 460 individuals roaming different islands around Mauritius; Hansen et al., 2008; Griffiths et al., 2011, 2012, 2013; Pedrono et al., 2013; Waibel et al., 2013; Jepson and Blythe, 2022). The Aldabra giant tortoises helped to disperse the native seeds on these islands, while also helping to control the spread of invasive plants (Griffiths et al., 2011). The characteristics of this particular species (e.g., successfully reproducing in zoological facilities, low risk of transmitting contagious diseases affecting native species, easily monitored and contained to assess ecological impact) made it an excellent ecological replacement for initial rewilding projects (Hansen et al., 2008; Jepson and Blythe, 2022).

Other successful introductions of ecological replacements involved the saddle-backed hybrids (Edwards et al., 2013), which filled

Table 1
Current and potential (candidate) ectothermic species for ongoing (upper part) or future rewilding (lower part) projects worldwide.

Order	Scientific name	Common name	IUCN status & trend	Distribution	Rewilding	Potential ecological role	Ref
Testudines	*Chelonoidis hoodensis**	Hood Island giant tortoise	CE, Increasing	Española Island	Successful reintroduction on Española Island, and introduction on Santa Fe Island	Herbivory, disturbance and seed dispersal	Cayot, (2008); Gibbs et al. (2014); Tapia et al. (2022)
	*Geochelone gigantea**	Aldabra Giant Tortoise	VU, Unspecified	Seychelles	Successful introductions on Ile aux Aigrettes, Rodrigues, Curieuse, Cousin, and Frégate Islands.	Selective herbivory, dispersing large-seeded fruits	Stoddart et al. (1982); Griffiths et al. (2010); Jones et al. (2022)
	*Astrochelys radiata**	Radiated tortoise	CE, Decreasing	Madagascar	Successful introductions on Réunion & Mauritius. Successful reintroduction on southern Madagascar	Selective grazer, dispersing large-seeded fruits	Griffiths et al. (2010); Griffiths et al. (2013); Randrianjafizanaka, (2014)
	*Chelonoidis carbonarius**	Red-footed tortoise	Unspecified	Amazon Basin	Successful introduction on El Impenetrable National Park in Chaco province, Argentina. Successful introduction on Barbados Island (Caribbean)	Large seed disperser, Herbivory, disturbance	Hansen et al. (2010); Lautenschlager et al. (2022); https://news.mongabay.com/2022/05/a-helping-hand-for-red-footed-tortoises-making-a-comeback-in-argentina/
	*Chelonoidis denticulatus**	Yellow-footed tortoise	VU, Unspecified	Amazon Basin	Successful reintroduction on Tijuca National Park, Brazil	Large seed disperser	Sobral-Souza et al. (2017); https://oeco.org.br/english/in-rio-de-janeiro-a-forest-slowly-returns-to-life-one-species-at-a-time/
	*Gopherus flavomarginatus**	The Bolson tortoise	CR, Decreasing	Mexico (Chihuahua, Coahuila, Durango)	Successful reintroduction on the Southern New Mexico area	Herbivory (weed control)	Truett and Phillips, (2009)
	*Centrochelys sulcata**	African spurred tortoise	EN, Decreasing	Southern edge of the Sahara Desert	Successful introduction of ecological proxy on Makauwahi Cave Reserve, Hawaii	Herbivory (weed control)	Burney et al. (2012); Burney and Burney, (2016)
	Indotestudo elongata	Elongated tortoise	CE, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Diverse diet of fruits and vegetative matter helps in dispersal.	Gray et al. (2019)
	Pelochelys cantorii	Asian giant softshell turtle	CR, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Scavenging and maintaining clean aquatic ecosystems	Gray et al. (2019)
	Heosemys annandalii	Yellow-headed temple turtle	CR, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Diverse diet of fruits helps in dispersal.	Gray et al. (2019)
	Cuora amboinensis	Amboina box turtle	EN, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Seed dispersal & accelerating germination of edible grains	Gray et al. (2019)
	Heosemys grandis	Giant Asian Pond turtle	CR, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Selective diet, scavenging, seed disperser.	Gray et al. (2019)
	Amyda ornata	Southeast Asian softshell turtle	Unspecified	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Selective diet, scavenging, seed disperser.	Gray et al. (2019)

(*continued on next page*)

Table 1 (*continued*)

Order	Scientific name	Common name	IUCN status & trend	Distribution	Rewilding	Potential ecological role	Ref
	Malayemys subtrijuga	Mekong snail-eating turtle	NT, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Selective diet & scavenging	Gray et al. (2019)
	Stigmochelys pardalis	Leopard tortoise	LC, Unspecified	Eastern and Southern Africa	Potentially in Makauwahi Cave Reserve, Hawaii	Herbivory (weed control)	Burney et al. (2012)
	Chelonoidis niger	Galápagos tortoise	CR, Unspecified	Galápagos	Potentially in Oceanic Islands	Herbivory, disturbance and seed dispersal	Hansen, (2015)
	Manouria emys	Asian forest tortoise	CR, Decreasing	Southeast Asia	Potentially in Oceanic Islands	Herbivory and seed dispersal	Hansen, (2015)
	Chelonoidis chilensis	Chaco tortoise	VU, Unspecified	South America	Potentially in Oceanic Islands and Argentina/Brazil	Herbivory and seed dispersal	Hansen, (2015)
	Geochelone elegans	Indian star tortoise	VU, Decreasing	India, Pakistan and Sri Lanka	Potentially in Oceanic Islands	Herbivory and seed dispersal	Hansen, (2015)
Crocodilia	*Crocodylus siamensis*	Siamese crocodile	CR, Decreasing	Southeast Asia	Potentially in Laos, Cambodia and Vietnam	Regulation of prey control and landscape of fear in freshwater ecosystems.	Gray et al. (2019)
Squamata	*Conolophus subcristatus*	The Galápagos land iguana	VU, Decreasing	Ecuador (Galápagos)	Potentially in Oceanic Islands	Ecosystem engineering shaping the structure of terrestrial plant communities.	Tapia and Gibbs, (2022)
Squamata	*Varanus komodoensis*	Komodo dragon	EN, Stable	Indonesia	Potentially in Australia	Regulation of prey control and landscape of fear	Bowman, (2012)

* Reptilian species that were rewilded into natural areas for ecosystemic restoration purposes worldwide, as indicated in Fig. 3A.

the gap in the ecological niche of a closely-related extinct species (*Chelonoidis nigra abingdonii*) on Pinta Island (Hunter et al., 2013). The success of tortoise rewilding on islands reached a level at which even the unusual introduction of the large African spurred tortoise (*Centrochelys sulcata*) was carried out at the Makauwahi Cave Reserve on the island of Kauai, Hawaii, as an ecological substitute for the extinct endemic frugivore-herbivores (giant flightless ducks and geese) that had been extirpated from the island (Burney et al., 2012). This 'extreme' introduction in the Makauwahi Cave Reserve, helped to remove 98% of the non-native plant species in the areas where the African spurred tortoise where released, while their dung helps in enhancing soil nutrients, and seed germination of native plant species (Burney and Burney, 2016). Another interesting example of "extreme" introduction of tortoises on islands occurred in Barbados, with the naturalized *Chelonoidis carbonarius* tortoises reported as de facto taxon substitutes for an extinct giant tortoise species ("Geochelone'' Genus; Fig. S3) that occurred on the island (Hansen et al., 2010). More than 12 species of Giant *Chelonoidis* tortoise species were known from the Caribbean archipelago (Kehlmaier et al., 2017; Steadman et al., 2020; Rhodin et al., 2015) and many plant species may be under severe population decline due to dispersal failure (Kim et al., 2022; Vollstädt et al., 2022). Ongoing efforts to rewild Caribbean islands by reintroducing tortoises as a substitute for extinct species can help restore the vegetation community through seed dispersal. These endeavors offer valuable insights for future tortoise rewilding projects in this impoverished archipelago (Kemp, 2023). The overall contribution of rewilding with tortoises draws the attention to the fact that grazing is an important ecological process on islands as well as in continental ecosystems, while also reframing these species and potentially others (e.g., land iguanas; Tapia and Gibbs, 2022) as megaherbivores in the context of islands and on other ecosystems (Hansen and Galetti, 2009; Jepson and Blythe, 2022).

The role of reptiles in grazing upon and dispersing seeds of endangered native plant species, and thus in aiding island ecosystem restoration, has paved the way for future (re)introduction of reptiles from various taxa (Gibbs et al., 2008, 2014, 2010; Griffiths et al., 2010, 2011, 2012; Hunter et al., 2013; Pedrono et al., 2013; Hansen, 2015; Gray et al., 2019; Moorhouse-Gann et al., 2022; Tapia and Gibbs, 2022). Recently, several studies have discussed the effects of reptilian reintroduction into non-insular ecosystems, such as tropical regions (e.g., Brazil or Cambodia), and their aid in ecosystem restoration, primarily via seed dispersal (Sobral-Souza et al., 2017; Gray et al., 2019; Lautenschlager et al., 2022). These studies have emphasized the roles of various species, such as the yellow-footed and red-footed tortoises (*Chelonoidis denticulatus* and *Chelonoidis carbonarius*, respectively), and how they might act as seed dispersers of large-seeded plants (matching the success of the rewilding efforts of the Aldabra giant tortoises on islands; Falcón et al., 2020), in fragments of the northern Atlantic Forest, which in turn can mitigate the negative cascading effects of defaunation. Another ambitious study suggested the rewilding of degraded ecosystems in South-East Asia with several groups of reptiles (including carnivorous species; Gray et al., 2019). This proposed species list (Table 1) includes Testudines that can contribute to ecosystem

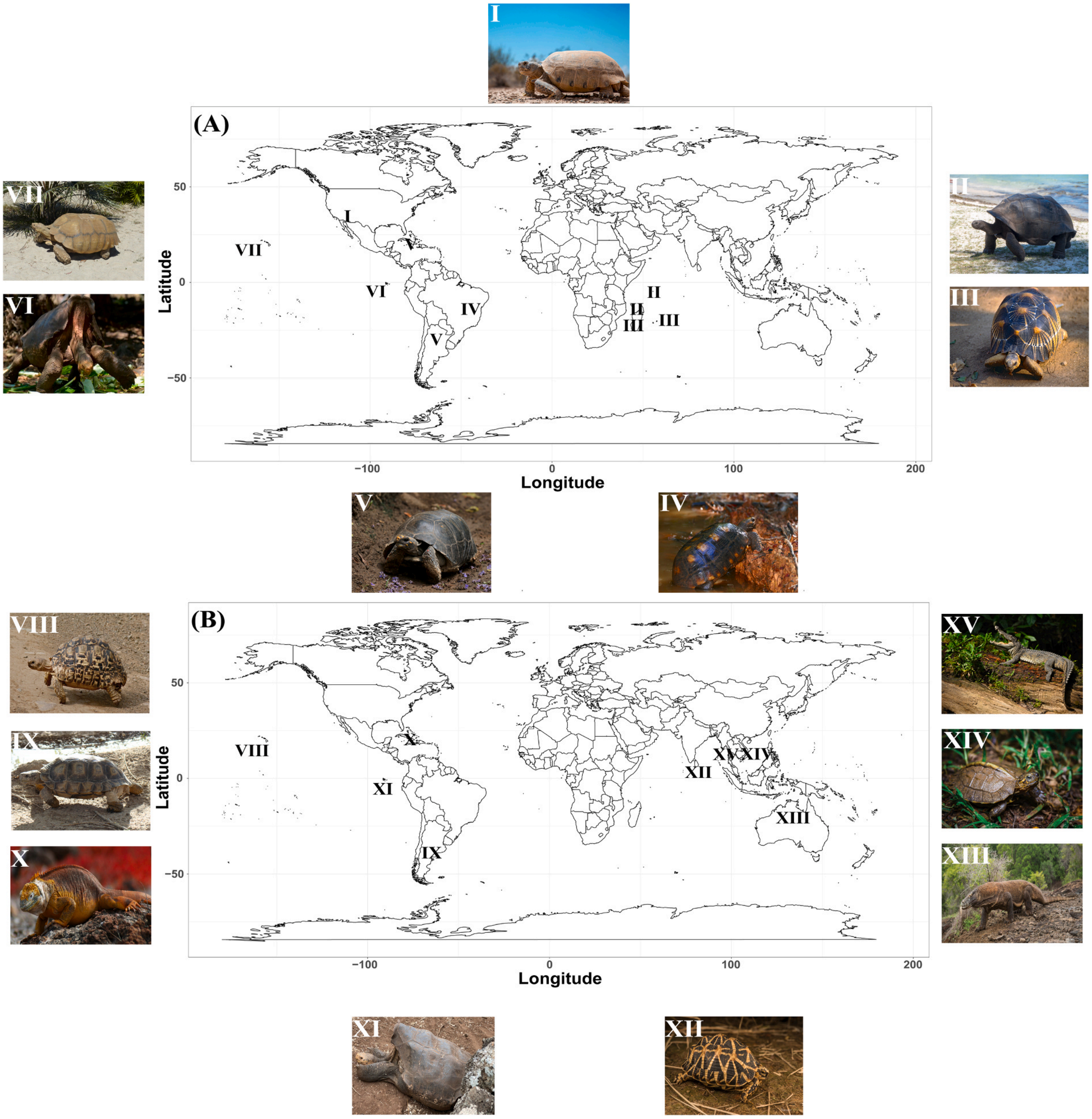

Fig. 3. Reptilian species in current (A) and potential (B) rewilding projects worldwide. All species are marked by Roman numerals. Upper panel: I (reintroduced *Gopherus flavomarginatus*, photograph: Peter Paul van Dijk); II (introduced *Geochelone gigantea*, photograph: www.seychelles.org); III (introduced *Astrochelys radiata*, photograph: Bernard DUPONT); IV (reintroduced *Chelonoidis denticulatus*, photograph: Bernard DUPONT), V reintroduced *Chelonoidis carbonarius*, photograph: Matt Grube); VI (reintroduced *Chelonoidis hoodensis*, photograph: Rodrigo Buendía); VII (reintroduced *Centrochelys sulcate*, photograph: Bernard DUPONT). Lower panel: VIII (*Stigmochelys pardalis*, photograph: Bernard DUPONT); IX (*Chelonoidis chilensis*, photograph: melba0127); X (*Conolophus subcristatus*, photograph: Peter Wilton); XI (*Chelonoidis niger*, photograph: Elias Rovielo); XII (*Geochelone elegans*, photograph: Scott Trageser); XIII (*Varanus komodoensis*, photograph: Christina Zdenek), XIV (*Heosemys grandis*, photograph: Thai National Parks); XV (*Crocodylus siamensis*, photograph: Tontan Travel). All images are published online on Flickr attributable to licence: CC BY 2.0.

restoration in several ways from selective herbivory (controlling weeds) to scavenging (reducing the prevalence of diseases in ecosystems) and long-distance seed dispersal (Gray et al., 2019). Moreover, this diverse group (four families) is composed mostly of endangered species, making their reintroduction a double victory: both reinforcing their declining populations and helping to restore functionality in their ecosystem, located in a north-eastern Cambodia wildlife sanctuary that has experienced the extirpation and decline of several populations of animals (Gray et al., 2019). The implementation of ongoing and potential rewilding projects concerning reptiles, specifically Testudines, is widespread, particularly in the regions around the equator (Fig. 3). Consequently, it is important to highlight the potential success of reptilian rewilding in restoring ecosystem functionality (Table 1). Finally, it is important to look beyond island rewilding, and also to support emerging rewilding projects in critical regions worldwide, such as in the tropics (where the greatest biodiversity decline occur worldwide, Clarke et al., 2017; Barlow et al., 2018),

6. Reptilian reintroductions under climate change

Addressing taxonomic biases alone may not lead to direct conservation action but understanding the suggestive biases uncovered in our review, may become increasingly valuable given the likelihood of taxa- and region-specific differences in animal responses to global climate change (Winter et al., 2016). Unlike endothermic megafauna, ectothermic terrestrial animals depend on access to an adequate range of environmental temperatures for efficient thermoregulation and on adequate precipitation to regulate their water balance, making them vulnerable to changing climatic conditions, particularly higher temperatures and lower precipitation (Deutsch et al., 2008; Kearney et al., 2009; Böhm et al., 2016).

Given that reptiles are ectothermic, they are likely to be influenced strongly by current and future climate warming, with desert species already experiencing body temperatures above their physiological optima (Sinervo et al., 2010; Vale and Brito, 2015; Stark et al., 2022, 2023). In addition, temperate species are also likely to be vulnerable, assuming that their physiological adaptations for living in cold environments might hinder their ability to cope with hotter climates (Kearney et al., 2009). The effects of climate change on the physiology of reptiles are direct and can alter their body temperature and consequently their performance and vulnerability, leading to altered energy and water balances (Huey et al., 2012), in contrast to endotherms, which possess a high physiological capacity to buffer environmental fluctuations. In ectotherms across all ecosystems, from the tropics to deserts, their thermal safety margins could be breached, leading to a negative energy balance and driving the risk of heat stress and their eventual extinction worldwide (Deutsch et al., 2008; Sinervo et al., 2010; Huey et al., 2012).

As mentioned in previous studies, tortoises can fundamentally influence their ecosystem using two main behavioural factors: activity and movement (Griffiths et al., 2010; Falcón and Hansen, 2018). Among other, these factors are known to be strongly affected by temperature and precipitation (Lovich et al., 2014; Nowakowski et al., 2020; Blake et al., 2021). Due to changes in these abiotic parameters, the activity and movement patterns of tortoises may be negatively impacted by rapid temperature increases and precipitation decreases caused by climate change. These changes can in turn affect the timing and magnitude of tortoise activity levels, potentially resulting in longer periods of inactivity (Falcón and Hansen, 2018). As tortoise activity diminishes, it will also cause a reduction in the extent of tortoise-mediated ecosystem engineering. This, in turn, will result in the fragmentation and clustering of the vegetation community within their ecosystem (Falcón and Hansen, 2018). To counter these climate-related negative impacts under stressful conditions, tortoises are able to move long distances to reach water or favoured feeding grounds (these species can survive for months without food or water in harsh arid zones; Kerr, 2022), which can lead to an increase in the long-term genetic connectivity of plant populations; while in larger-scale rewilding projects tortoises can even facilitate plant range shifts (Falcón and Hansen, 2018).

In rewilding initiatives involving reptiles it is important to consider which species is most likely to provide long-term, sustained ecosystem functions for a given site (Falcón and Hansen, 2018; Gray et al., 2019). This entails an in-depth analysis and literature review of the life history of the targeted rewilding candidate, while also highlighting the specific habitat or site that needs to be rewilded (Segar et al., 2022). In addition, it is necessary to acquire detailed knowledge of the thermal and hydric ecology of the species under consideration (Falcón and Hansen, 2018). These preliminary assessments can contribute to ensuring more efficient, science-based, successful (re)introductions of ectothermic species, able to restore ecological functionality and ecosystem dynamics.The current bias inherent in global conservation initiatives, emphasizing mostly mammalian reintroductions as a natural climate solution (Cromsigt et al., 2018; Sandom et al., 2020; Schmitz et al., 2023), is shifting the focus of conservationists from rewilding reptiles on large scale that may equally influence and help shaping vegetation structure (Nori et al., 2020; Yang et al., 2023), leading to stronger ecosystem resilience, which can help to mitigate the effects of rapidly increasing temperatures under climate change (Schmitz et al., 2023).

7. Conclusion

Currently, reptiles are prominent as one of the most threatened group worldwide (Cox et al., 2022), with habitat loss (Powers and Jetz, 2019; Cordier et al., 2021; Stark et al., 2023), alien species invasions (Kraus, 2015) and climate change (Alford et al., 2007; Lal and Nadim, 2021; Stark et al., 2023) implicated as the major factors involved in their decline. It was recently demonstrated that protected areas worldwide act as refugia for many reptilian species, helping to reduce the impact of climate change, as opposed to unprotected areas (Mi et al., 2023). There is thus an urgent need for additional pragmatic solutions in order to protect this endangered taxon. Therefore, if we are to alleviate the current dire condition of reptilians around the world, we need immediate solutions that will incorporate urgent and radical introductions, with the goal of boosting their declining populations while simultaneously helping to restore functioning ecosystems in their protected (and unprotected) areas. To overcome our ongoing biodiversity crisis, much more ambitious and far-reaching efforts are needed in order not only to protect but also to re-expand the natural world. Conservation biology has moved well past discussions of what is 'natural', with preservationist ideals having become replaced by the more pragmatic 'novel ecosystems' paradigm, which involves the introduction of species for the purpose of restoring ecological functionality, processes and dynamics (Watson and Watson, 2015; Svenning et al., 2016; Svenning and Faurby, 2017; Perino et al., 2019). The inclusion of other ectothermic vertebrates (e.g., amphibians and fish) and even invertebrates (e.g., Dung beetles or Partula snails) in emerging trophic rewilding initiatives has the potential to become an important conservation strategy for biodiversity and ecological restoration across the world, transcending borders and countries.

CRediT authorship contribution statement

Galetti Mauro: Writing – review & editing, Writing – original draft. **Stark Gavin:** Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Competing interest statement

One of the authors is the Editor-in-chief of the journal.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02834.

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