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PERSPECTIVE

The relationships between species age and range size

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Abstract

Species range size is a central topic in macroecology, biogeography and conservation biology. Species age has been frequently regarded as a contributor to range size in previous studies on range size, but this has rarely been specifically examined. Using global data from four living terrestrial vertebrate classes (birds, mammals, reptiles and amphibians) as a case study, we examine how species range size might be related to species age at a global scale. We found statistically significant positive, albeit weak, species age–range size relationships for all four species groups. However, although the age–range relationships were positive, species with young ages had very different range sizes (both large and small), and those with very old ages always had small ranges. The observed age–range relationships were more complex than expected. The weak, rather than strong, species age–range relationships could be because our data set included all living species with different stages of their life spans (durations) that are either expanding or fluctuating or contracting, which would necessarily have minimized or cancelled species age–range relationship when all species in a group are considered collectively. Our findings shed new light on temporal dimension and macroecological correlates of species ranges.

KEYWORDS

dispersal, habitat availability, latitude, phylogenetics, species duration, species life span

To all this it is obvious that age must be added – the older a species is, the more area will it have had time to cover.

—Willis (1922)

1 | INTRODUCTION

What determines a species' range size, a key subject in ecology and biogeography, is still far from clear. Previous studies show that species range size is influenced by multiple natural factors such as dispersal,

climate shifts and geological history such as plate tectonics and land-mass changes due to sea-level fluctuation after speciation (Brown et al., 1996). Some recent studies also show that species richness is strongly associated with species range size (Guo et al., 2022; see also Shipley & McGuire, 2023). Recently, species' age has been increasingly cited as a possible major factor that may have contributed to determining species range size (Alzate et al., 2023; Guo et al., 2022; Webb & Gaston, 2000), but its contribution has rarely been examined with empirical data, especially for large species groups (e.g. vertebrate classes) and at a global scale (Gaston & Blackburn, 1997; Webb & Gaston, 2000).

A century ago, Willis (1922) proposed that species range (or distribution area) increases with species age. To date, few studies have specifically tested this hypothesis or the general positive age–area relationship, mostly due to the following two factors: (1) lack of reliable data, especially age data, and (2) the lack of clear distinction between relative and absolute age (see below) that may lead to inconsistent results. As a result, related studies have examined relatively small species groups or selected species from specific large groups of species (e.g. Jablonski, 1987; Miller, 1997; Paul et al., 2009; Taylor & Gotelli, 1994; Weber et al., 2014).

Species' age can be either relative (i.e. young vs. old) or absolute (i.e. the number of years since species formation). Most species that once lived on Earth (>99%) have now gone extinct (Taylor, 2004). After a species is formed (after speciation events), it usually expands in terms of population size and range size. Although the exact rates and trajectories are different among species (e.g. exponential vs. logistic; Vance et al., 1988), each one goes through five main phases, that is, speciation, expansion, fluctuation (some say stationary), contraction and final extinction through their entire life spans or durations (Jablonski, 1987; Liow & Stenseth, 2007). Thus, if the ages of species considered are scaled from 0 to 1 (i.e. 'relative age'), a rise–peak–decline (or unimodal age–range size) relationship could be expected (Figure 1a). However, for certain species, the temporal changes in range size through a species duration (i.e. speciation–peak–extinction) might reflect the spatial patterns across species range (e.g. the front edge–core–the rear edge) which can be gradual, asymmetrical or sometimes truncated (e.g. at the land or ocean boundaries) (Brown, 1995; Brown et al., 1996).

In contrast, if we use 'absolute age', since the number of years living on Earth after speciation can vary enormously among species, and some species may be in their late stages of senescence, the resulting age–range size relationship remains largely unknown and difficult to predict. If most extant species on Earth or in a particular region are still relatively 'young' and spreading their ranges, we might expect a positive relationship (Figure 1b). Empirical observations seem to show that most species may not need a very long time relative to their full durations on Earth (Jablonski, 1987) to occupy the places they can occupy. However, a species' range size is also determined by many other interacting factors that could alter the absolute age–range size relationship. These factors include (1) catastrophic events that could cause a drastic reduction in range size or even extinction, (2) species' life-history or genetic traits, for example, competition ability and dispersal capacity (Lester et al., 2007) and (3) habitat availability: for example, some species may be strong competitors and can disperse far but if they can only occupy mountain tops or caves, they can never have very large ranges (Ricklefs et al., 2008).

Not only is the species age–range size relationship itself interesting, but it also has several important implications. For example, if the rise–peak–decline scenario of species' ranges occurs over time, the absolute age–range size relationship could show whether

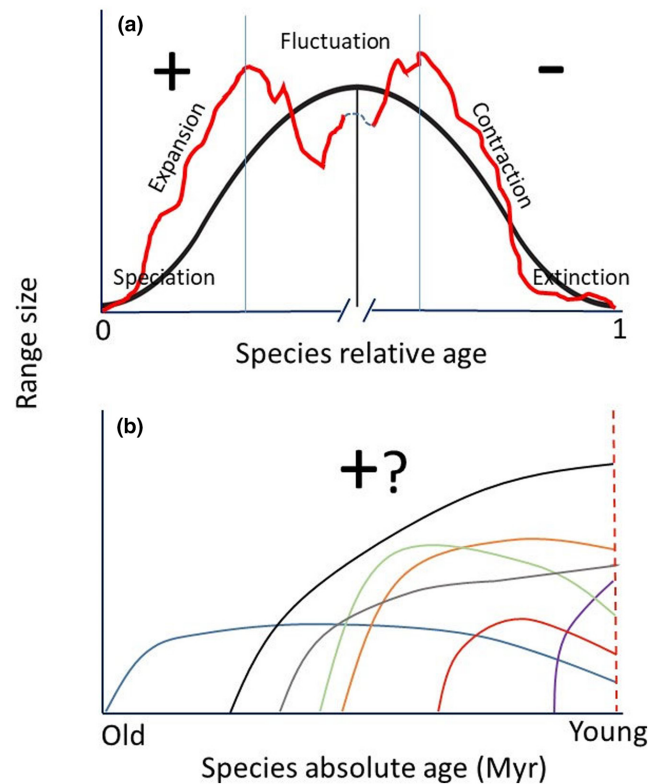


FIGURE 1 (a) The hypothesized trajectory of range dynamics over a species' lifetimes on Earth from speciation to extinction (although many exceptions occur due to catastrophic or disruptive events). The bell-shaped line roughly reflects the mean trajectory of all species in the assembly (ages scaled from 0 to 1) (Pigot et al., 2012). The age–range relationship would be positive right after speciation (on the left) but negative when approaching extinction (on the right). Although the exact trajectories could be very different among species, each one goes through five main phases, that is, speciation, expansion, fluctuation (some say stationary), contraction and extinction. The temporal patterns might also reflect the spatial patterns across species' range which can be gradual, asymmetrical or sometimes truncated (e.g. at the land or ocean boundaries). (b) Range trajectory when absolute age is used (each line represents a species), that is, in this study. Species have very different life spans on Earth.

the current living species in a region or across the globe are still young or old. For example, a positive monotonic relationship between age and range size of extant species would tell us that most extant species are currently in the expansion phase of their life cycles. Here, we first outline a few critical issues related to species' age and its roles in range size. We then perform a case study examining the age–range size relationships in world terrestrial vertebrates at a global scale. Since a unimodal age–range size is expected when relative age (varying from 0 to 1) is used and for most species, we do not have such data, we mainly focus on the absolute age–range size relationships, which are largely elusive. Finally, we discuss the implications and limitations that could shed new light on macroecological and biogeographical patterns in biodiversity and distribution.

2 | THE RELATIVE VS. ABSOLUTE AGE: WHY AGE MATTERS?

Relative to species range, which has received much attention and discussion in the past, the use of a species' age has not been clear and specific in existing literature. As briefly mentioned above, here, we suggest that, in the future, a species' age needs to be clearly defined as 'absolute age', which is the time since the species is formed, and as 'relative age' which could be determined as the absolute age divided by the potential duration on Earth (Figure 1a).

For relative ages, we could scale all species' ages from 0 to 1 (i.e. from the youngest to the oldest, or from speciation to extinction). Using relative age, the temporal range dynamics would resemble a bell-shaped pattern (Liow & Stenseth, 2007). This bell-shaped relationship between age and range size, in most cases, happens to spatial bell-shaped curves related to the 'abundance center' (Brown, 1995; Fristoe et al., 2023) as observed by Webb and Gaston (2000). But similar to many exceptions to the spatial bell-shaped abundance (or range) patterns (Brown, 1995), major disruptive forces (e.g. due to drastic climate fluctuation, land use in modern times) may exist over time from speciation to extinction (e.g. what happened to dinosaurs or spatial disruptions due to land edges). The limitation of using relative age is that it requires fossil data, which are largely unavailable.

However, for living species, we could only estimate how long they have been living on Earth using fossil and molecular data (Figure 1b) but unfortunately, we cannot estimate and predict how much longer a species may continue to live, which depends on how physical (e.g. climate) may change in the future (Farnsworth et al., 2023; Taylor, 2004) and whether it can adequately adapt. With the rapid development in phylogenetic studies (Alzate et al., 2023; Ramirez-Barahona et al., 2020), absolute age data are easier to be estimated (although extinct species are missing from the analysis) and we could examine how their current range sizes might be related to their absolute ages (times since species formation), which is also important for understanding many macroecological and biogeographical patterns and processes (Gaston & Blackburn, 1997). For example, all living species are a 'mixed bag' that includes species' ranges either expanding or contracting, but their relative fractions remain unknown. If there is a general positive age-range relationship, we might be able to say that more species (among all living species) are still expanding their ranges. Below, we use the absolute age and current range size data to explore the age-range relationships.

3 | OUR CASE STUDY OF WORLD TERRESTRIAL VERTEBRATES

The species' age-range size relationship continues to be highly debated as inconsistent findings have been reported from a few recent studies focusing on specific species groups or particular regions. In contrast to most previous studies that examined how physical and life-history factors may have affected species' global range sizes (Brown et al., 1996; Gaston, 2009; Guo et al., 2022), here, we

examine whether species age (i.e. time since species emergence) is related to range size in all global extant terrestrial vertebrates (i.e. birds, mammals, reptiles and amphibians). If a species' range size indeed increases with the species' age, then age should be included as a major factor in predicting species range dynamics, which is important for predicting species extinction and for conservation purposes. Following Willis' (1922) original claims, we specifically test the hypothesis that species range sizes are positively related to their ages.

3.1 | The data

We compiled the age and range size data of all living (extant) species in four terrestrial vertebrate classes around the world (i.e. birds, mammals, reptiles and amphibians; a total of 24,236 species whose distribution and age data are available). We obtained the species range maps of birds from BirdLife International (2021) and the species range maps of mammals, amphibians and reptiles (the order Squamata) from IUCN (2022). Only breeding ranges were used in this study. We downloaded distributional data from the aforementioned sources and used the R package U.Taxonstand (Zhang & Qian, 2023) to standardize species names according to The Integrated Taxonomic Information System (<https://itis.gov>) for birds and Catalogue of Life (<https://www.catalogueoflife.org/>) for mammals, amphibians and reptiles. We then calculated the range size for each species based on the species range maps.

We define the age of a species as the time since it has been formed (birth), that is, the time since the species has been living on Earth (i.e. after origination; Figure 1b). This was measured based on the branch length of the species in a phylogenetic tree, which is a commonly used approach to estimate taxon age (e.g. Lu et al., 2018; Ramirez-Barahona et al., 2020). We obtained time-calibrated phylogenetic trees from the VertLife website (<https://data.vertlife.org>) for birds (Jetz et al., 2012), mammals (Upham et al., 2019), reptiles (Tonini et al., 2016) and amphibians (Jetz & Pyron, 2018). We used the same procedure with the species range data to standardize species names in the phylogenetic trees. We matched standardized names in the phylogenetic trees with standardized names in the aforementioned species distributional data and excluded those species that occurred only in either the distributional data set or only in the phylogenetic trees. As a result, 8251 bird species, 4661 mammal species, 6918 reptile species and 5418 amphibian species were analysed in this study. For each of the four groups of vertebrates, VertLife provides multiple posterior phylogenetic trees. For a given species, we derived its age from each of the first 1000 trees and used the mean value of the ages of the species from the trees as the age of the species in this study.

3.2 | Data analysis

While we examined the age-range relationship for each of the four vertebrate groups at a global scale, because species range

size tends to increase with increasing latitude (i.e. Rapoport's rule; Stevens, 1989), particularly in the Northern Hemisphere (Stevens, 1989) whereas land area decreases with increasing latitude in the Southern Hemisphere, analyses based on the whole globe are likely biased. To account for the effects of these two factors, we conducted a set of analyses in which we first excluded the Southern Hemisphere and then divided the Northern Hemisphere into latitudinal zones each with 10 degrees (e.g. 0–10° N). We assigned a species to a latitudinal zone based on the location of the mean latitude of the range of the species, regardless of how much of the range of the species is constrained within the latitudinal zone. We examined the relationship between species range size and species age for each latitudinal zone. Because species ranges at high latitudes may be constrained by the availability of land at high latitudes on the one hand and may be influenced by the 'Mid-Domain effect' (i.e. species ranges overlap increasingly towards the centre of the domain; see Colwell & Lees, 2000) on the other hand, we focused on the five latitudinal zones south of 50° N in the analyses. The main conclusion of this study is based on this set of analyses with a total of 24,236 species of the Tetrapoda.

We used Spearman's rank correlation coefficient to assess the relationships between species ages and species range sizes using R v 4.2.0 (R Core Team, 2022). We conducted various analyses using raw and $\log_{10}$ -transformed data on age, range or both. We should point out that, here we only focused on the possible role of age in range size. We did not attempt to include many other potential factors, such as climate, species richness and dispersal, among others, as such comprehensive analyses would involve using different analytical approaches, which could yield complicated results (Gould et al., 2023).

3.3 | Our findings

For each of the four groups of vertebrates, when data were analysed across the globe, visual inspection of bivariate plots of species age against species range size revealed complex age–range relationships because there were many 'newer' species with young ages (i.e. newly formed species with short divergence times or branch lengths) had both small and large ranges while ancient species with very long divergence times (branch lengths) were very few and almost always had small ranges (Figure 2). The substantial overlapping of data points in the lower left part of each plot in Figure 2 makes it difficult to visually determine the direction and strength of the relationship in each bivariate plot. However, our correlation analyses showed that species range sizes were positively correlated with species ages in all cases (Figure 2), with the strongest positive correlation found among mammals, followed by amphibians, birds and reptiles. These positive age–range relationships were statistically significant ($p < 0.001$ in three cases, $p = 0.002$ in the other case; Figure 2), albeit the correlation coefficients were relatively small.

When data were analysed for each of the five individual latitudinal zones selected in this study, the age–range correlations tended

to be more positive at lower latitudes (Table 1). For example, the correlations between species range size and species age at the latitudinal zone of 0–10° N were significant for all four groups of vertebrates ($p < 0.0001$ in all cases; Table 1). At the latitudinal zone of 10–20° N, the positive correlation was significant for three of the four vertebrate groups (i.e. birds, mammals, amphibians, $p < 0.0001$ in all cases) and was marginally significant ($p = 0.051$) for reptiles (Table 1). For two of the four vertebrate groups that have better dispersal capability (i.e. birds and mammals), the positive correlation between species range size and species age was significant or marginally significant ($p < 0.10$) in seven out of the 10 cases across the five latitudinal zones (Table 1).

4 | MECHANISMS AND CONSEQUENCES

The findings of our study that the four terrestrial vertebrate groups exhibit positive, albeit weak, age–range relationships generally support the age–area hypothesis proposed by Willis (1922), which posits that area (range size) should increase with time (after a species is formed) (Webb & Gaston, 2000). Although this hypothesis is well known, our study is the first to use a comprehensive data set including extant species of all four terrestrial vertebrate classes to test this hypothesis at a global scale.

However, the interpretation of our findings needs some caution. Particularly, the observed positive relationships for the four species groups were much weaker than we originally perceived based on existing literature. Also, the strength of the positive age–area correlations (mammals > amphibians > birds > reptiles; Figure 2) did not seem to follow any order based on overall age or range size in the four groups (Figure 3). The high statistical significance level (p -value) for the positive but fairly weak age–range relationships may or may not indicate practical significance in the real world as it is clearly influenced by the large sample size in the study (the number of species included) (Schober et al., 2018).

When we focused on much smaller data sets (i.e. species in each 10°-latitudinal zone near the equator) that avoided potential effects of biases (e.g. declining area towards the pole in the Southern Hemisphere), we obtained stronger correlations with p -values remaining very small. The latitudinal pattern needs to be cautiously interpreted with the following facts and recent discoveries. First, temperate zones appear to exhibit higher speciation rates than lower latitudes, possibly (and partly) due to frequent glaciation cycles in the recent past, which might have restricted the range sizes of certain species (Freeman & Pennell, 2021). Second, there might be variation in species definition a potential taxonomic bias across latitudes; that is, more species are yet to be discovered and recognized in the tropics (Freeman & Pennell, 2021). Third, latitudinal variation in species' age could be important, that is, species in the Northern Hemisphere are sometimes younger on average than tropical species (Marin & Hedges, 2016). Fourth, stronger age–area correlations at lower latitudes may be linked to higher species richness, which affects species range size (Guo et al., 2022). Despite these potential

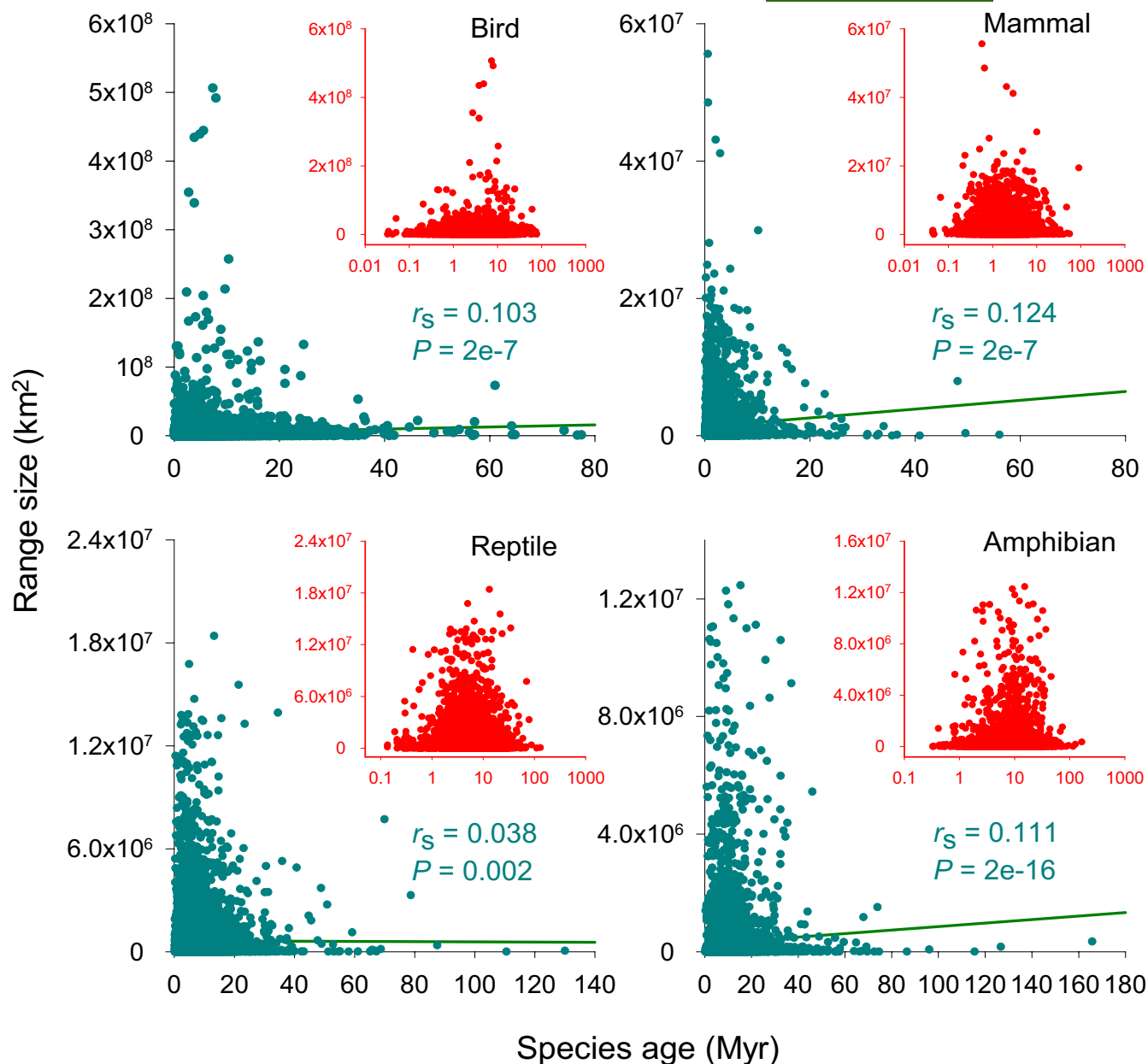


FIGURE 2 Relationships between species ages and species range sizes for terrestrial vertebrates across the world. Each dot represents a species. It seems that most young species (those on the left) can have both small (most) and large ranges while the ranges of very old species are almost always small. Also, many young species expand their ranges relatively quickly after emergence (relative to their life span or duration on Earth). Insets show the relationships between $\log_{10}$ -transformed species age (Myr) and species ranges.

factors, overall, we are confident that our study shows reliable evidence for the positive relationship between species age and species range size.

There are a few possible causes for the generally weak global age-range relationships in terrestrial vertebrates. First, our data set included 'all' living species with different stages of their life spans or durations on Earth. In other words, it contains species that are 'young' and 'old'. Many species expand their ranges relatively quickly after emergence (relative to their life span or duration on Earth). At their late stages, the species ranges will shrink until extinction except in the cases when catastrophic events occur, such

as hits by large bolides (comets or asteroids that lead to dinosaurs' extinctions), and even large ranges could be suddenly lost at once (Chiarenza et al., 2020). Second, our data on both species' age and range size are only a snapshot or one-time observation and thus cannot reflect the history of range dynamics. A species range size usually fluctuates over its duration on Earth but the range size used in this study is only a one-time measure. Such a snapshot of the ranges of the world's living species of all ages cannot indicate whether a particular species' range is expanding, stable or contracting. Most species with the longest life spans on Earth do seem 'relicts' and their ranges are almost always very small. Some become endemic

TABLE 1 Spearman rank correlations between species age (Myr) and range size of the four groups of terrestrial vertebrates across latitudes (Northern Hemisphere only).

Latitude (°N)	Bird			Mammal			Reptile			Amphibian		
	N	r	p	N	r	p	N	r	p	N	r	p
0–10	1498	0.202	<<0.001	857	0.139	<0.001	1090	0.116	<0.001	1254	0.221	<<0.001
20–30	790	0.230	<<0.001	476	0.197	<0.001	1082	0.059	0.051	706	0.233	<<0.001
20–30	869	0.148	<0.001	421	0.018	0.707	846	0.055	0.134	429	0.012	0.797
30–40	486	0.081	0.073	403	0.099	0.048	476	−0.084	0.066	307	0.055	0.337
40–50	308	0.029	0.615	315	0.077	0.176	153	0.137	0.092	123	−0.160	0.080

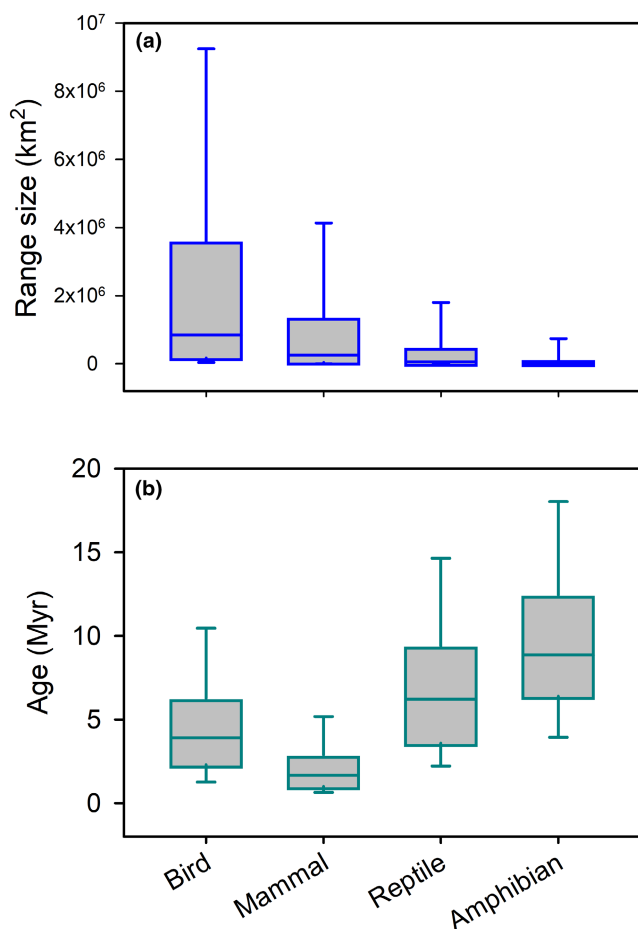


FIGURE 3 Comparison of range size (a) and age (b) among the four classes of terrestrial vertebrates. Across the four classes, it seemed that the group with the “older ages”, such as amphibians had smaller ranges than the classes with “younger ages”, such as birds and mammals. Dispersal capacity and habitat availability could jointly affect the observed pattern.

due to range contraction in the process of extinction if not protected by human actions (Figure 2).

Thus, instead of strong positive age–range (or age–area) relationships as most might have perceived, the observed patterns in our study seem more complex and less consistent. This is evidenced by the facts that (1) most very ‘old’ species have small ranges (Figure 2),

(2) every species goes extinct eventually (Taylor, 2004), (3) many species never occupy their potential ranges during their entire lifetime on Earth (as seen by exotic species invasions) and (4) many endemic species with small ranges are not actually new but relicts.

Age can be an important factor in determining a species’ range size, but it plays different roles during different stages of a species’ lifetime. In one of the earliest investigations of the species age–range relationships, Willis (1922) mostly focused on the early or expanding phase of a species’ history on Earth or the local initial expansion of invading species to a new region (or an island) and found strong positive age–area (or range) relationships.

Willis’s (1922) claim of positive age–area relationships may suit better for (1) the expanding stage of newly formed species when its population starts to grow (short-term), similar to many studies of population biology that mainly focus on initial population growth (expanding) and following up population dynamics (Meiners, 2007), and (2) the spread of newly introduced species to a region or island. However, very few studies focus on the declining/extinction models (Liow & Stenseth, 2007). When an analysis includes species at different lifetime stages in a biological assemblage, as in our study, we hypothesize that the age–area relationship would be weak, as observed in our study, and may be in any direction.

5 | FUTURE CHALLENGES

Even if the effects of species age are confirmed, the relative contribution of age (vs. many other contributing factors such as climate and life-history traits) in range size remains a major task facing ecologists and evolutionary biologists (Guo et al., 2024). This is especially true when its relative contribution may vary among different groups of species, different regions and over geological/historical episodes. In addition, there are several other major issues that need to be addressed.

First, whether and why species in remotely related taxa have similar ages is a complex issue. In some cases, species in the same genus could have very different sizes of ranges (e.g. *Erodium cicutarium* vs. *Erodium texanum*). Closely related sister species often have dissimilar range sizes (Webb & Gaston, 2003). Of course, this is all relative depending on how similar is ‘similar’ (Hunt et al., 2005; Jablonski, 1987; Qian & Ricklefs, 2004; Ricklefs & Latham, 1992). When very large and diverse taxa (e.g. all birds) are included in the

analysis, the magnitude of the difference, on average, may still be smaller than those in remotely related taxa. However, when species across diverse taxa with similar ages have similar range sizes, the underlying mechanisms related to life-history traits (e.g. convergent evolution) deserve further investigation.

Second, when dispersal is not a limiting factor, species range size is then largely constrained by habitat availability (Ricklefs et al., 2008) and time (e.g. after invasions in new regions). However, dispersal capacity and habitat availability could jointly affect the observed pattern. For example, the two endothermic groups (birds and mammals), which possess the better capability of dispersal, support the age-range relationship more strongly, compared with the two ectothermic groups (amphibians and reptiles) in the analysis based on latitudinal zones (Figure 3) (Qian, 2009).

Third, similar to the dynamics in species abundance, species range size fluctuates over its entire life (i.e. species life span or duration) on Earth. Possible causes for dramatic changes in species abundance and distribution over geologic history may include plate tectonics or continental drift (Frisch et al., 2010), climate variation (e.g. glacial-interglacial cycles, drought), diseases (e.g. insect/pathogen infestation), competition and predation, among others. Nevertheless, the changes in range size over the entire species duration on Earth may actually follow what Webb and Gaston (2000) observed in hump-shaped, or unimodal, age-range relationships although exceptions can occur. That is, species first spread or expand after emergence, reach peak abundance and range size, and then contract in population size and go extinct.

Finally, humans have drastically increased some species' ranges (e.g. invasive species, plantations, assisted relocation/migration) while reducing the ranges of many other species. An increasing number of studies are investigating how human activities may have affected species' global range sizes (e.g. Xu et al., 2019). For conservation purposes, many studies focus particularly on 'relicts' that have very small populations and ranges (McGeoch & Latombe, 2016; Ren et al., 2012). Such issues are very complex and have been extensively reviewed elsewhere (beyond the scope of this study). While studies investigating human effects on species ranges are urgently needed, natural causes of range size dynamics should continue to be a focus in future research. Particularly, the species age-range size relationships should be compared between animals and plants and among habitat types such as between terrestrial and marine ecosystems (Dawson, 2012).

6 | SUMMARY

What determines a species' range is a complex issue involving many interactive factors. The relative role of age in species range size is likely to remain debatable before more extensive research on the topic is done. Our case study using global terrestrial vertebrate data shows weak but positive and complex age-range size relationships at the global scale. The positive, albeit weak, age-range relationship may be more common in its early (expansion) stages after a species

emerges. In other words, most extant species are currently in the expansion phase of their entire life cycles on Earth. Caution is needed in using species' age alone as a strong predictor for changes in species range size and for conservation, but relative age (developing stages) should be used instead when data are available.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this study are published data and are available to the public. Specifically, species distribution data are available at the websites <https://itis.gov> and <https://www.catalogueoflife.org/>; and species age data are available at the VertLife website (<https://data.vertlife.org>).

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BIOSKETCHES

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