Title

Demand for small- and large-ranged reptiles in worldwide wildlife trade

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Authors

Zhang, Songqi
Meiri, Shai
Holyoak, Marcel
et al.

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Title: Worldwide endangerment of turtles and tortoises: current extinction risk and future challenges

Abstract: Turtles and tortoises (chelonians) are among the most threatened vertebrates worldwide, yet the factors determining their high extinction risk and their resilience to further challenges are not fully understood. Here, we compile a dataset comprising both intrinsic and extrinsic variables for chelonians to reveal their current risk patterns and vulnerability to future climatic and environmental threats. The results indicate that at-risk species are non-randomly distributed across clades and biogeographical realms, with the Indomalayan region identified as an extinction epicenter. Species that are large-bodied, small-ranged, have higher functional distinctness, or face greater human threats consistently exhibit a higher extinction risk. Furthermore, the projected climatic and environmental changes across the distribution of species are significantly greater than the rates of evolution for traits linked to resilience to climate change and altered environments. Overall, this study provides insights for prioritizing conservation actions and underscores the urgent need to prevent future extinctions of chelonians.

Introduction

Globally, increases in the human footprint have led to a rapid loss of biodiversity, raising concerns about a sixth mass extinction[1]. It is recorded that c. 500 vertebrate species have become extinct in the past 400 years, and 18% of vertebrates are currently at risk of extinction[2]. Nevertheless, not all species are equal in extirpation likelihood since some species decline or disappear while others remain relatively safe and widespread[3]. Understanding the key processes that render certain species highly prone to extinction is an essential first step in preventing future loss of biodiversity[4].

As one of the oldest lineages of vertebrates, turtles and tortoises (chelonians) have survived many devastating mass extinctions, including the Cretaceous–Paleogene extinction event that wiped out more than three-quarters of animal and plant species on earth[5]. In the Anthropocene, more than half of chelonian species are threatened with extinction according to the IUCN Red List assessment, and the populations of many continue to decline at an alarming rate[6]. The conservation of chelonians has been challenging, since turtles generally have long-life cycles, late maturity, and specific habitat associations, which require long-term, multi-faceted conservation efforts. Furthermore, as long-lived and temperature-sensitive ectotherms, chelonians may face an elevated extinction risk when climate change and habitat alteration outpace the adaptive responses of species[6,7]. Nevertheless, previous studies are often species- or region-specific, offering varied and sometimes conflicting strategies for species conservation[8,9]. Hence, we still have a limited understanding of the main factors contributing to the high extinction risk of chelonians both globally and in different regions[10].

Both theory and empirical evidence have long indicated a non-random distribution of extinction risk among species[11]. For chelonians, published studies have shown that species with large body sizes and slow life cycles are particularly at risk of extinction because they are less likely to recover from small population sizes[8]. Additionally, chelonians face a variety of extrinsic threats, such as habitat degradation, pollution, and overexploitation, and species that are particularly sensitive to these threats are often the first to go extinct[7,10]. In this context, unclassifiable species (Data Deficient and Not Evaluated) may have a high risk of extinction in the future because of characteristics shared with congeneric species that have become rare or are already extinct[12]. Understanding how intrinsic traits and extrinsic factors shape the extinction risk of species can help predict the risk for unevaluated species and guide proactive conservation measures, such as evaluating their potential vulnerability to future threats[10].

Chelonians possess various life-history traits (e.g., shells and long lifespans) that have promoted survival and adaption to past environmental changes[13]. Yet, very little information exists on whether the macroevolution of species traits can mitigate species' risk to future climatic and environmental challenges [6,8]. Some studies have shown that the ecological niches of certain chelonians could shrink in the next century due to a substantial decrease in their distributions and habitat suitability[14]. Additionally, due to their temperature-dependent sex determination and limited dispersal ability, human threats, such as future climate change, habitat encroachment and alteration may individually or collectively endanger chelonians[15]. Critically, global extreme weather events are becoming more frequent and pose a significant threat to species' survival[7]. However, species may alternatively mitigate the influences of climate warming through phenological or range shifts[16]. Therefore, it is imperative to ascertain whether chelonians can survive and adapt to or whether they face extinction from forecast future conditions.

This study describes a comprehensive analysis of the factors influencing extinction risk across the whole chelonian phylogeny and explores whether species are capable of adapting to further challenges. For this purpose, we amassed extensive data on species' ecological, environmental, and anthropogenic factors, along with a time-calibrated phylogeny. We use an updated threat status by combining information from the Tortoise and Freshwater Turtle Specialist Group (TFTSG)[10], the IUCN Red List, and regional assessments as indicators of species extinction risk. We address the following three questions: (1) Do chelonians show equal extinction risk among families and biogeographical realms? (2) If not, which suite of traits and extrinsic factors best explains the differences in extinction risk of chelonians worldwide? (3) Are rates of trait evolution alone sufficient for chelonians to compensate for anticipated shifts in climates, population, and habitat? Based on the above findings, we estimate the extinction risk for the Data Deficient and Not Evaluated species in the combined Red List. Our research contributes to the understanding of the factors contributing to high extinction susceptibility and enables more effective planning of conservation actions for these ancient species under global change.

Results

Overall, we retained for analysis 378 chelonians with species-level identification, of which 335 were data-sufficient species (ranging from Least Concern to Extinct, Figure 1, Table S1). When mapping the threatened species listed in the combined Red List, the Indomalayan region exhibits a high diversity of chelonians and a high proportion of threatened species (84.9%, n = 73), followed by the northern Neotropics and the eastern Nearctic (Figure 1).

Non-random extinction risk

The binomial distribution tests on these 335 species showed that the proportion of extinct or threatened species was higher in some chelonian families (Figure 2A, Table S2). The families with more extinct or threatened species than the average of 58.5% were Testudinidae (86.2%, n = 65) and Trionychidae (83.3%, 30) ($p < 0.05$; Figure 2A). In contrast, families of Pelomedusidae (12.5%, 16), Kinosternidae (13.3%, 30), and Chelidae (27.5%, 51) contained significantly fewer extinct or threatened species than the all-family average based on the combined Red List assessment ($p < 0.01$; Figure 2A, Table S2). Although the binomial distribution results for five small families (e.g., Podocnemididae) were not significant ($p > 0.05$; Figure 2A, Table S2), we classified them as high-risk because 100% of the family's species are threatened or extinct.

The geographical realm with the highest proportion of threatened species was the Indomalayan region (84.9%, 73), whereas the least threatened one was the Nearctic (41.5%, 65) ($p < 0.05$; Figure 2B, Table S2). Overall, 56.6% of the species in Trionychidae and 71.0% of Geoemydidae were from the Indomalayan region (Figure 2C, Table S1). Species belonging to the Testudinidae are predominantly found in the Afrotropical (46.2%) and Neotropical (26.2%) regions (Figure 2C, Table S1). However, all six species of Testudinidae in the Indomalayan region are threatened (Table S1).

Correlates of extinction risk

In the univariate correlative analyses, of the 17 ecological factors, the following were related to the threat status of species: extinction risk was strongly and positively correlated with island endemicity, body length, functional distinctness, year of description, and number of human threats, and negatively related to activity time, geographical range size and extreme droughts (SPEI) for most of the groups (all $p < 0.1$; Figure 3, Table S3).

For all 335 data-sufficient chelonians, when ranking all combination of these variables based on AICc values, there were four competing models with ΔAICc ≤ 2 (Table S4). We hence employed a model-averaging approach. The analysis showed that the variables with a higher importance in the 95% confidence set included endemicity (estimate value = -0.50), maximum body length (0.21), geographical range size (-0.67), functional distinctness (0.21), and the number of human threats (0.28) ($p < 0.05$ in all cases; Figure 4, Table S5). Hence, species characterized by island endemicity, large body size, small geographical range size, higher functional uniqueness or under greater human threats have a greater risk of extinction. Notably, with binary threat status as the response variable, the latter three factors mentioned above showed strong correlations with extinction risk ($p < 0.05$; Figure 4, Table S5).

For the 254 aquatic and 81 terrestrial species, geographical range size (estimate value = -0.92, -0.42, respectively, $p < 0.01$) and number of human threats (0.24, 0.63, $p < 0.001$) showed strong correlations with extinction risk (Figure 4, Table S5). However, for aquatic species, body size (0.57) and functional distinctness (0.25) were additionally significant predictors of extinction risk (all $p < 0.05$; Figure 4, Table S5). At the biogeographical realm level, geographical range size (-1.16 – -0.61) and the number of threats (0.25 – 0.54) were significantly related to the extinction proneness of species in all regions ($p < 0.05$), except for Indomalaya (Figure 4, Table S5). Additionally, body size significantly influenced the extinction risk of species in the Australasian (0.76) and Indomalayan (0.88) regions ($p < 0.05$; Figure 4, Table S5).

Risk probability of DD and NE species

Among the unevaluated species in the combined Red List, five belonged to high-risk families (binomial distribution test), 13 to families that did not significantly differ from average risk, and 25 to low-risk families (Figure 5, Table S7). Additionally, we assessed the probability of DD and NE species becoming threatened or unthreatened using the logistic regression framework with body size, geographical range size, functional distinctness and number of threats as the predictor variables. The results showed that four and 12 species among 43 DD and NE species had a probability of being threatened by ≥ 0.75 or ≥ 0.50, respectively (Figure 5, Table S7).

A combination of these two classifications revealed that the eight species in high-risk or moderate-risk families and with a risk probability of becoming threatened exceeding 0.50: *Emys trinacris* (Sicilian Pond Turtle), *Natator depressus* (Flatback), *Pelodiscus axenaria* (Hunan Softshell Turtle), *Pelodiscus huangshanensis* (Huangshan Softshell Turtle), *Pelodiscus maackii* (Northern Chinese Softshell Turtle), *Cuora praschagi* (Assam Box Turtle), *Cyclemys enigmatica* (Enigmatic Leaf Turtle), and *Trachemys grayi* (Western Meso-American Slider) (Figure 5, Table S7). Additionally, the Afrotropical species *Pelomedusa gehafie* (Eritrean Helmeted Turtle) and *Pelomedusa somalica* (Somalian Helmeted Turtle) have tiny, fragmented distributions and are expected to face a high future extinction risk.

The rates of trait evolution compared to future challenges

To assess whether high-risk species will face intensified threats from projected climatic and environmental changes, we compared the diversification rates of species traits (in felsen units, which represent the variance among *ln*-transformed trait values per million years. We divided the evolutionary rate of each trait by 10,000 to convert the unit to centuries) to the rates of changes in mean temperature, extreme droughts, heatwaves, human expansion, and forest degradation from 2000 to 2100. This analysis tests the macroevolutionary potential of chelonians to mitigate future climatic and environmental challenges. Observed rates of trait evolution ranged from 2.39×10^{-6} (activity time) to 7.48×10^{-6} (maximum lifespan) felsen units per 100 years (Figure 6, Table S6). For comparison, the rates of mean temperature change across species' distribution extents were 3.50×10^{-3} to 4.06×10^{-3} felsen units per 100 years (mean ± se) under the best-case climate-change scenario and 3.82×10^{-2} to 4.32×10^{-2} units under the worst-case scenario (Figure 6A, Table S6). Thus, the future mean temperature change was projected to change by three to four orders of magnitude faster than the fastest-evolving trait of chelonians (Figure 6A, Table S6). Furthermore, the average rates of extreme droughts (0.028–0.468, felsen units per 100 years), heatwaves (2.15–3.87), human expansion (0.157–0.266) and forest degradation (0.021–1.082) across species' distribution extents were projected to change by four to six orders of magnitude faster than the fastest-evolving trait of chelonians (Figure 6BCDE, Table S6). Overall, the rates of trait evolution of chelonian species were much slower than future climatic and environmental challenges.

Discussion

Despite over half of the assessed chelonian species being classified as threatened or extinct, our understanding of the ecological factors that predispose certain species to a heightened extinction risk lags far behind other taxa[10]. We explored the patterns and processes of extinction and threats to chelonians worldwide and across major habitats and regions. These findings consistently showed that species with smaller geographical ranges, larger body sizes, higher functional distinctness or facing higher human threats disproportionately were at a higher risk of extinction than other taxa. We have also found that the projected rates of environmental change across the distribution of species were significantly greater than the rates of evolution for traits linked to resilience to climate change and altered environments. Overall, our findings provide insights into priority taxa and threats meriting conservation action and emphasize the need for increased efforts to prevent future extinctions of chelonians.

High-risk species families and geographical regions

Our binomial distribution test identified the families of Testudinidae and Trionychidae as being at high risk of extinction. For the Testudinidae (tortoises), many species have large body size and face a high risk of human exploitation and consumption[10].The globally widespread and highly aquatic softshell turtles (family Trionychidae) are highly imperiled due to reductions in their ranges and numbers because of human overexploitation, habitat alteration, and pollution[17,18]. Geoemydidae also showed a high risk of extinction, which was primarily due to the high proportion of imperiled species (79.0%) in the subfamily Geoemydinae (Asian and Eurasian species). There were also five evolutionarily distinct and small turtle families (e.g., Carettochelyidae) that have 100% threatened species. These small families deserve special conservation attention because they possess considerable unique life history and evolutionary information[10].

Our study also showed strong evidence of a high risk of extinction for the chelonian fauna in the Indomalayan region compared to others. Therefore, our research further emphasizes the significance of turtle conservation in this region[10, 19]. In addition, we should also give greater attention to turtle conservation in the Afrotropical region, where there has been a disproportionate lack of scientific and conservation attention despite the high extinction risk of chelonians[20]. Additionally, of the 43 species currently listed as Date Deficient or Not Evaluated species in the combined Red List, 25.0% are found in Africa.

Moreover, effective conservation of at-risk families must also take their geographic distributions into account. Specifically, by associating high-risk families with their respective regions, we highlighted that the Indomalayan region should be designated as a conservation hotspot for the families Trionychidae and Geoemydidae. However, it is also essential to strengthen international cooperation to promote the protection of Testudinidae, as these threatened species are widely distributed across biogeographical realms.

Correlates of extinction risk

Our results showed that body size was an important biological factor in predicting the extinction risk of chelonians, which is consistent with numerous previous studies[11,21]. Larger species tend to have traits associated with high extinction proneness, such as lower population densities, slower life histories, larger habitat requirements, and slower population recovery rates[22]. For instance, the death of "Lonesome George" in 2012, the last purebred Pinta giant tortoise (*Chelonoidis abingdonii*), marked the extinction of the Pinta species of tortoise[10]. Being slow, terrestrial, and defenseless, larger species are also easy targets for early and recent hominids to obtain meat or eggs[6].

The small geographical range was another predictor of extinction risk. Small-ranged species are more likely to face threats from demographic stochasticity, environmental fluctuation, sex-biased populations, and inbreeding. Moreover, a restricted geographical range size, such as on islands, could also expose species to risks from habitat destruction, human collection, and species invasion[11,21]. For instance, the range of the large Burmese roofed turtle (*Batagur trivittata*) in Myanmar, as well as the habitat of the Flattened musk turtle (*Sternotherus depressus*), have shrunk by at least 90 percent. Therefore, protecting natural habitats and connecting fragmented habitats are crucial strategies for increasing their survival possibilities[23].

The number of human threats is an important extrinsic factor influencing the extinction risk of species[6]. Notably, the impacts of various threats were widespread across families and geographical realms, indicating that most species, regardless of their life histories and locations, are vulnerable to human pressure. Furthermore, we demonstrated that 68.1% of chelonians were affected by at least two threats, raising great concern about more species becoming imperiled in the future.

We also observed that species with a higher functional distinctness were more likely to be threatened. For instance, the leatherback sea turtle (*Dermochelys coriacea*) is the most functionally distinctive chelonian species, characterized by large body size, large clutches and comparatively long lifespan. Unfortunately, this species is experiencing alarming declines in many regions[24]. The Asian Giant Softshell Turtle (*Pelochelys cantorii*) is the most functionally distinctive chelonian species on land, and its populations have been heavily depleted and severely fragmented[25]. Species with high uniqueness often face heightened human pressures and are less likely to recover from population declines.

Extreme droughts emerged as another important variable influencing extinction risk, although their effects were secondary in magnitude compared to geographical range size and human threats in the model-averaging analyses. Droughts have been linked to declines in survival rates, habitat loss, and changes in predation pressure for turtles[26,27]. In Southeast Asia, for instance, extreme drought can lead to significant habitat loss for freshwater turtles[28]. Droughts may have greater biological consequences than those caused by changes in climate means, a pattern that has been revealed in studies of various taxa worldwide[29,30]. However, such research on turtles remains limited, underscoring the need for further studies to investigate the increasing frequency and severity of these conditions affecting chelonians.

The risk probability of DD and NE species

Since our findings showed the non-randomness of threatened or extinct species in specific clades and with specific traits, we combined family-level extinction risk and species-level risk probability and found that eight species in high-risk or moderate-risk families and with a risk probability of becoming threatened of exceeding 0.50. For instance, the flatback turtle only nests on the north coast of Australia and is threatened by the loss of nesting sites and by climatic variability[31]. The flatback turtle is protected by being listed as Vulnerable under the Western Australia Biodiversity Conservation Act 2016 and the Commonwealth Environment Protection and Biodiversity Conservation Act 1999[32]. Additionally, we identified the Sicilian Pond Turtle, Hunan Softshell Turtle, and Assam Box Turtle as potential at-risk species in the future. These species have either small geographical range sizes or low population densities, yet all face multiple threats including habitat loss and fragmentation, hunting, and climate change. Overall, our prediction for DD and NE species could help identify other species that currently share many characteristics with at-risk species and assist assessors in reconsidering the status of these species.

The rates of trait evolution compared to future challenges

Our results showed that even under the best-case climatic and environmental change scenarios, environmental change velocities exceeded the maximum observed trait evolutionary rates by three to six orders of magnitude. This disparity suggests that contemporary environmental shifts may outpace the adaptive capacity supported by the specific traits we analyzed. Of particular concern are the constraints of the Anthropocene on the population sizes of chelonians — at least seven species of chelonians have gone extinct in the past 280 years[6], with many populations in steep declines for decades[10]. Hence, even if any unmeasured traits (e.g., dispersal ability) were evolving at higher rates, the synergistic erosion of adaptive potential in small populations (e.g., the world's 25 most endangered chelonians) would severely limit their responses to ongoing threats such as habitat fragmentation and overexploitation[33,34].

Despite this, it is important to note that species may exhibit behavioral or physiological plasticity, which helps mitigate the effects of future climatic and environmental challenges[35,36]. For instance, both theoretical and empirical studies have revealed that some turtles can show flexibility in behaviors such as nest-building to offset the climatic influences on the sex ratios[37,38]. Additionally, some ectotherms can rely on behavior adaptations to avoid overheating during the warmest periods, particularly in the lowland tropics[39]. In sea turtles, the response to heat shock is heritable, showing that the presence of heritable variation in the expression of key thermotolerance genes is essential for species to adapt to warming[40]. Nevertheless, other studies argue that turtles may not be able to adjust their behavior sufficiently to mitigate the impacts of climate change[41]. For example, an experimental study carried in both the laboratory and the field showed that green turtles were not locally adapted to different thermal conditions experienced during incubation[42].

We acknowledge several limitations in our study on evolutionary rates *vs.* environmental change. First, our analysis focuses on single-trait evolutionary rates rather than multivariate trait complexes that may jointly determine species fitness in the face of future challenges[35]. Second, we did not consider population-level factors, including effective population size and genetic diversity, which may constrain adaptive potential[43]. Third, for widely distributed species that span diverse ecosystems, using range-wide trait averages may obscure locally adapted populations that could serve as evolutionary reservoirs[44]. While our analysis reveals an order-of-magnitude disparity between environmental change velocities and estimated trait evolutionary rates, this should be interpreted as a preliminary indicator of extinction risk. Future integration of population-genetic parameters and data on phenotypic/behavioral plasticity will be essential for developing robust vulnerability assessments.

Altogether, our phylogenetic comparative analyses focused on all chelonians and clearly showed that no single solution exists for proactive conservation. We suggest that we should prioritize conservation efforts for species with extinction-prone traits and prevent human threats, such as human overexploitation and habitat destruction, to effectively preserve chelonians[6,10]. Additionally, we found that the projected rates of environmental change across the distribution of species were significantly greater than the rates of evolution for traits linked to resilience to future climatic and environmental changes. While at this point, the future may not look bright for chelonians, it has been pointed out that many species of sea turtles are showing signs of population recovery, thanks to concerted conservation efforts worldwide[24]. The steady increase in nesting numbers, the protection of critical habitats, and the reduction of bycatch have all contributed to these positive trends[7]. Such conservation achievements offer hope and motivation for ongoing efforts to protect these remarkable creatures, and there is still much that can be saved.

Methods

Data collection

We compiled the species list of global chelonians through a critical synthesis of four authoritative taxonomic frameworks: 1) the paper of Global Conservation Status of Turtles and Tortoises (Order Testudines) published in 2018 (360 species included)[10], 2) Turtles of the World: Checklist and Atlas (9th Ed., 2021; 357 sp.)[45], 3) the Reptile Database (version September 2024; 371 sp.)[46], 4) the IUCN Red List (version 2024-02; 272 sp.). For the *Chelonoidis nigra* complex, the Turtle Taxonomy Working Group[45] and the Reptile Database[46] recognize them as subspecies, whereas TFTSG[10] elevates each to species rank. We adopted the TFTSG classification based on diagnostic morphological, behavioral, and genomic divergence identified by a recent study[47]. Seven recently proposed species (e.g., *Chelodina ipudinapi*, *Elseya auramemoria*) were excluded pending formal validation by TTWG. The final checklist comprises 378 validated species (Table S1), with taxonomic decisions cross-verified through correspondence with Dr. Anders G.J. Rhodin.

The IUCN Red List evaluated the threat status of 272 chelonian species, and among which 138 species (> 50%) were assessed before 2014[10]. Based on the 2018 IUCN Red List, the TFTSG Red List 2018 assessed unevaluated tortoises and freshwater turtles and re-assessed these species with outdated assignments[10]. Overall, the threat status of 360 species was evaluated, including 7 Extinct, 187 threatened, and 136 non-threatened species. When compared, the threat status of 66 Data Deficient (DD) and Not Evaluated (NE) species in the IUCN Red List was evaluated, which included 45 Least Concern (LC) species, 5 Near Threatened (NT) species, 12 Vulnerable (VU) species, 2 Endangered (EN) species, and 2 Critically Endangered (CR) species[10]. Besides, TFTSG reevaluated 32 data-sufficient species assessed by the IUCN Red List, lifting the extinction risk of 16 species[10]. Considering the higher degree of data completeness of TFTSG over the IUCN Red List, we chose the TFTSG Red List as our primary dataset. We assigned the Red List status of species with a score to represent their extinction risk. Following previous studies[11], we categorized the extinction risk in descendent order as Extinct or Extinct in the Wild (EX = 5), CR = 4, EN = 3, VU = 2, NT = 1, and LC = 0.

In addition, since the TFTSG report has not updated the threat status since 2018, we took three additional steps to enhance the dataset. First, we updated the threat status of chelonians based on the TTWG 2021 report. Second, we updated the threat status of species that was revised by the IUCN Red List only after 2018, as these updates were also conducted by the IUCN-SSC TFTSG. Lastly, while the global population of green turtles (*Chelonia mydas*) is reported to be downlisted to LC in 2025[7], the status of other marine turtles recorded in the IUCN Red List is significantly outdated and does not accurately reflect their current risk status. Therefore, we averaged the risk status of their subpopulations as assessed by the IUCN-SSC Marine Turtle Specialist Group. Specifically, the loggerhead turtle (*Caretta caretta*) was assessed as VU (coded as 2) in 2015, with all ten subpopulations ranging in status from LC (0) to CR (4). The average risk status of these subpopulations was 1.7, and hence we rounded this number and assigned the threat status of loggerhead turtle as VU. However, for leatherback sea turtle (*Dermochelys coriacea*), its global threat status was assessed as VU in 2013. We assigned its threat status as CR (4) based on the average values of its seven regional assessments (assessed between 2013 and 2019), which was 3.8. Our assessment aligns with recent studies that leatherback turtles are experiencing declines in several regions[48,24]. Overall, the updated dataset included 335 data-sufficient species and was used in our analyses, comprising 7 Extinct, 73 Critically Endangered, 56 Endangered, 60 Vulnerable, 39 Near Threatened, and 100 Least Concern species (Figure 1, Table S1). (In sensitivity analyses, we used the IUCN or TFTSG Red List assessment, respectively as the response variable and found largely similar results, which are detailed in Table S9).

We collected several traits that were shown by previous studies to be predictors of extinction risk in the studies of chelonians and other vertebrate groups (a summary in Table S8), including activity time, diet, insular endemism, maximum lifespan (years), maximum body length, mean clutch size, and geographical range size. Specifically, we categorized activity time into nocturnal (0), crepuscular (1), diurnal (2), and cathemeral (3, day and night). Diurnal and cathemeral species have activity patterns that closely coincide with human activities. Secondly, previous studies have shown that carnivores are often at a higher risk of extinction than omnivores and herbivores[23]. Based on this, we quantified the chelonians as omnivores (0), herbivores (1), feeding on invertebrates (2), and feeding on vertebrates (3). Insular endemism was classified as either island endemic species (1) or not. Since species with a larger body size and a smaller geographical range size appear to have higher extinction risk[49], we compiled the data on the maximum straight-line carapace length (mm) of adults to represent body size, and geographical range size as the extent of occurrence (km^2). Species with smaller clutch sizes are likely to be prone to extinction due to a weak recovery potential from small population sizes[50]. Accordingly, we quantified clutch size as the mean number of eggs per clutch.

We recorded geographical range size from a recent study[51] and supplemented it with information from the IUCN Red List[2] and the TTWG 2021[45]. Body size was collected from the TTWG 2021[45] and supplemented with the published species traits of chelonians[52,53] as well as related publications[54]. The information on activity time, diet, insular endemism, maximum lifespan and mean clutch size were derived from the two global datasets of the species traits[52,53], the book written by Lovich and Gibbons[55], the Reptile Database[56], the IUCN Red List[2], and related papers[46]. We collected trait data for all 378 species, except for a small proportion of missing values in the following categories: activity time (26 species), diet (66), maximum lifespan (51), and mean clutch size (23). We then imputed missing values using the impute function in R package funspace[57], which fills in missing values (of continuous or categorical ones) using trait–trait correlations through a machine-learning process that accounts for phylogenetic relatedness. This methodology has been recommended in recent papers[58], and this imputation procedure has been shown to produce reliable results with minimal error rates[59]. In this study, we run this gap filling approach 100 times and performed the analyses on each imputed dataset[60]. We then pooled the results at the end using the Rubin's rule[61], which adjusts the standard errors and provides more accurate parameter estimates by incorporating both within-dataset variance and between-dataset variance.

To represent the phylogenetic relationships among chelonians, we constructed a phylogenetic tree for chelonians based on Colston et al.[21]. This tree recognizes 357 species of extant or recently extinct chelonians and contains all 335 data-sufficient species in the combined Red List. However, since we need to impute the missing values in species traits also for data-deficient species (20 sp.), we employed two different methods to address this issue. For species that were previously classified as subspecies or subpopulations, we positioned them alongside their sister species (the vast majority are in this situation. e.g., Galapagos giant tortoises). For some newly discovered species, we used the add.species.to.genus function (phytools)[62] to incorporate the missing species midway along the branches of their respective genera. To assess whether the correlates of species extinction risk differed among habitats, we grouped chelonians into aquatic (freshwater and marine) and terrestrial species based on the classification of the IUCN Red List, the published species traits dataset, books, and related papers, detailed in Table S1. Finally, we used the Reptile Database to align species names (i.e., matched the species names across all datasets) and ensure consistency across all datasets.

To determine the influence of external environmental factors on the extinction risk of chelonians, we collected four climatic variables (mean annual temperature, mean annual precipitation, temperature seasonality, and precipitation seasonality) by calculating the mean values of these bioclimatic data (WorldClim 1, 1970-2000)[63] across species distribution ranges. In fact, many sea turtles have a global distribution across tropical, subtropical, and temperate regions, making it challenging to derive a climate metric[64]. Nevertheless, we measured these variables for sea turtles across their ranges, as temperature can influence the abundance and distribution of food resources in the oceans[65], and to ensure consistency with terrestrial species. We did not consider other climatic variables from WorldClim website (e.g., minimum or maximum temperature) because they are not only highly correlated with the mean values but also highly variable between years. In addition, extreme weather events, such as heatwaves and droughts, are occurring with increasing frequency and intensity, which may lead to even greater biological consequences than those caused by changes in climate means[29,30]. Hence, we measured the Standardized Precipitation

Evapotranspiration Index (SPEI) to represent extreme droughts[66]. This index is one of the most widely used tools for monitoring and quantifying meteorological droughts because it accounts for the impact of evaporative demand on drought severity. We averaged the historical period (1971-2000) of the SPEI raters (0.5° × 0.5°) and transformed it into a 5-km Mollweide projection raster. A lower SPEI value indicates a higher risk of drought exposure to species. Furthermore, we selected the Warm Spell Duration Index (WSDI) to represent heatwaves, which is defined as the annual count of days with at least six consecutive days when the daily maximum temperature exceeds the 90th percentile of maximum temperature for the corresponding calendar day, centered on a 5-day sliding window during the baseline period[67]. We used the same procedure to produce a 5-km WSDI raster. Lastly, we mapped these two extreme climates across species distribution ranges.

Additionally, we obtained the year of description as a variable[45] since species described earlier may have a broader distribution, potentially leading to a reduced risk of extinction[68]. We grouped the chelonians into fourteen families based on the classification of the TTWG 2021[45]. For biogeographic distributions, we made our results comparable to global biogeographical studies on chelonians[69], by including Afrotropics, Australasia, Indomalaya, Nearctic, Neotropics, Palearctic and Marine. We classified species into those realms by intersecting their ranges with the shapefile of the World Wildlife Fund for Nature (WWF) biogeographical realms. We calculated the proportion of species distribution range belonging to each biogeographical realm using ArcGIS 10.7. A species was assigned to a realm when at least 80% of its range overlapped with that realm, which left 14 unclassifiable species without any realm designation due to their widespread distribution (Table S1).

Lastly, we calculated the functional distinctness of species using the functional traits including activity time, body length, clutch size, diet, and lifespan. We computed the function distance matrix of these variables and then employed the distinctness function in the R package funrar[70] in R 4.3.2[71] to quantify the average functional distance from a species to all other chelonians. It is computed as:

$$D_i = \frac{\sum_{j=0, i \neq j}^{N} d_{ij}}{N-1}.$$

Where D_i is the functional distinctiveness of species i, N is the total number of species in the chelonian group and d_{ij} is the functional distance between species i and j. The values range from 0 to 1, indicating the functional distinctness of species from low to high. Following Colston[21], we calculated the evolutionary distinctness of species within the tree using the R package picante ("fair.proportion" metric)[72]. The metric quantifies the weighted sum of the branch lengths along the path from the root of an ultrametric tree to the tip, with weights assigned as the reciprocal of the number of tips that ultimately subtend that branch[72]. This analysis measures the evolutionary isolation of each species, with high values of evolutionary distinctness representing relict lineages on long branches[72].

The populations of chelonians have been heavily threatened by overexploitation and trade, increasing habitat loss and fragmentation, environmental pollution, invasive species, and global climate change[6,15]. We gathered threat information for each species from several sources (Table S1): the IUCN threat classification scheme, which provides a detailed description of the threats faced by each species but only covers ~ 270 species that they assessed; the Biology of Freshwater Turtles and Tortoises compiled by the IUCN/SSC TSTSG, which details the threats for 171 chelonian taxa; trade records from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); the reports by the Turtle

Conservation Coalition (TCC)[73]; and books[55]. We reclassified threat types into five basic and recognized categories, including human exploitation (pet trade, human consumption, medicine), habitat destruction, pollution, invasive species, and climate change (Table S11)[6,8]. Some other threats, such as roadkill or sacrificial purposes, were excluded due to minimal records. We constructed a species-by-threat matrix using these seven threat types, with 1 representing affected and 0 representing not affected. We derived the number of human threats for each species by summing the total records documented for a focal species (0 to 5).

Non-random extinction risk

Based on the extinction risk assessment of the combined Red List, we conducted a binomial distribution test to examine which families have a higher or lower proportion of threatened species than expected by chance alone. Overall, 335 data-sufficient species (from LC to EX) were grouped into two categories: at-risk/threatened species (VU, EN, CR, including EX) and non-threatened species (LC, NT). The null hypothesis posits that threatened species within each family occur randomly, implying that the proportion of at-risk species is equally distributed among families. In this case, the probability of K threatened species in a family with N species should follow a binomial distribution[74], where the total proportion of threatened species in all families is 0.585 (196 divided by 335). Since the binomial distribution test was conducted independently for each family, we used the Dunn-Sidak method to calculate the adjusted critical value[75]. In addition, since the binomial test has relatively low statistical power when the taxonomic family is small[76], we categorized small families into high-risk or low-risk groups when they contained 100% or 0% threatened or extinct species (those with > 0% and < 100% were omitted). To identify the high-risk realms, we also performed the binomial distribution test for species in all biogeographical realms (including species in the unclassifiable group). Lastly, we linked the species families to the realms where they belong to identify the conservation priorities.

Correlates of extinction risk

To test for correlations of biological traits and external factors with the extinction risk of chelonians while accounting for the influence of shared ancestors among species, we conducted Phylogenetic Generalized Least Squares (PGLS) tests with Brownian motion (the Ornstein–Uhlenbeck model gave very similar results, Table S12)[77]. The data analysis followed four steps. First, we employed univariate PGLS to test the effect of each of the twelve ecological factors on the extinction risk category of species. Secondly, we selected the important variables with $p < 0.1$ in the first step and removed the variables with a variation inflation factor (VIF) > 5 to reduce the collinearity among predictor variables (all VIFs < 5; Table S10). Thirdly, we built models using various combinations of these variables and ranked all models using the information-theoretic approach based on Akaike's information criterion corrected for a small sample size[78]. We used the Akaike weight (w_i) to compare model performance. If there were several competing models (ΔAICc ≤ 2), we conducted a model-averaging approach to calculate the relative importance of each variable within a 95% confidence interval[76]. The PGLS analysis was carried out using package caper[79].

We excluded DD and NE species from the univariate and multivariate PGLS analyses and log-transformed the continuous variables to achieve a normal distribution. We conducted the analyses using the combined Red List with categorical threat status ranging from 0 (LC) to 5 (EX). We conducted analyses for aquatic and terrestrial species since they generally show extensive variation in habitat preferences and life-history strategies. We also repeated all the above analyses for each realm using the combined Red List assessment (0-5) due to the availability of more adequate data for the analyses. To minimize the impact of any changes in the threat status of species on our findings, we further categorized the threat status into two groups: threatened (VU, EN, CR, EX, coded as 1) and non-threatened (NT, LC, coded as 0). We employed phylogenetic logistic regression models (PGLM, using the phylolm package)[80] to identify the significant predictors of the probability of a species being threatened. We refrained from performing multivariable PGLS and model selection for species in the Palearctic region due to the limited sample size (15 sp.). We reported the standard errors, within-dataset variance, and between-dataset variance across 100 datasets for both univariate and multivariate PGLS analyses in Table S5.

The risk probability of DD and NE species

To predict the extinction risk probability of DD and NE species in the combined Red List, we combined the results from the binomial distribution test and the model-average analyses. At the family level, we grouped all species into high- (significantly higher than average), medium- (no difference from the average), or low-risk (significantly lower than average) family groups based on the results from the binomial distribution test. We then extracted the lists of DD and NE species belonging to each of the three groups. At the species level, we fitted a logistic regression model on the extinction risk of all data-sufficient chelonians using the significant variables identified through the model-average analysis following Senior[81]. We then used this model fit to predict the probability of DD and NE species becoming threatened (1) or unthreatened (0) status using the predict.glm() function. The model predicted the probability of the DD and NE species having a threatened status (1), which ranged from 0 to 1. We then grouped these value estimates into three categories (0.75~1, 0.5~0.75, < 0.5). The classification is highly artificial, while as suggested by Senior[81], a value > 0.75 suggests that species have a higher probably to be threatened in the future because of characteristics shared with congeneric species that have become rare or gone extinct. Lastly, we integrated the family-level and species-level results and formatted them into a matrix. We considered that the unassessed species belonging to moderate or high-risk families and having an estimated value ≥ 0.50 had a higher extinction risk.

The rates of trait evolution compared to future challenges

To predict how well chelonians can adapt to climate change, human expansion, and forest degradation in the next century, we calculated the rates at which traits were evolving and compared them to the rates of change of these threats, separately. We calculated the rate of trait evolution, which represents the variance among *ln*-transformed trait values per million years[32]. For two species, the evolutionary rate in felsens is:

$$ER = \frac{(x_1 - x_2)^2}{2t}$$

Where x_1 and x_2 represent the *ln*-transformed trait value of two species, t denotes the divergence time of t million years. A higher ER value indicates a faster rate of evolution[32]. The model considers that each trait is evolving at a constant rate with Brownian motion, so we used the BM model for all traits[32].

To measure the rates of climate change, we first extracted historical climate data on mean annual temperature (1981-2000, with a spatial resolution of 2.5 minutes) for all non-marine species across their ranges. We then calculated the projected mean temperatures using three climate change models (ACCESS-CM2, MIROC6, MPI-ESM1-2-HR) for the period 2081-2100, under both the best-case (SSP1-2.6, Sustainability) and worst-case (SSP5-8.5, Fossil-fueled Development Scenario) climate change scenarios for each species. We calculated the rates of climate change per century for both scenarios using the aforementioned equation, and subsequently obtained the average and standard deviation values for each scenario. Similarly, we calculated the projected extreme droughts (SPEI) and heatwaves (WSDI) using the historical extreme climate data (1981-2000) and projected climate data (2081-2100) under the two climate change scenarios. We used the same climate change models and the equation above to determine the changes (Mean and SE) in the intensity of extreme droughts and heatwaves. Furthermore, to represent the change in intensity of human activities, we collected data on the world population and land-use projections of SSP1 (2100) and SSP5 (2100), as well as their base-year raster data of 2000 from the NASA Socioeconomic Data and Applications Center[82] and Land-Use Harmonization[83], respectively (only one model available). The Land-Use Harmonization provides seven land-use states (e.g., proportion of forested primary land, managed pasture, rangeland and urban land) and we only considered the changes in the total fraction of primary and secondary forested land types. We calculated the rate of population change and forest cover change per century in both the best-case and worst-case scenarios, respectively. To standardize all values for comparison, we divided the estimated evolutionary rate of each trait by 10,000 to convert the unit to centuries.

Data availability: The data for this study is provided in Supplementary Table S1. The species list is derived from the most recent taxonomy checklists of the report of the Turtle Taxonomy Working Group[45] and the Reptile database (http://www.reptile-database.org/data/). The extinction risk of species is derived from The IUCN Red List (www.IUCN.org) and the TFTSG Red List[10]. Most of the ecological characteristics are generally derived from three online datasets of the species traits of chelonians (e.g., activity time, diet, insular endemism, maximum lifespan, mean clutch size, and geographical range size)[8,52,55] and the Turtles of the World (e.g., body size)[45], which supplemented with data in the Reptile Database, the IUCN Red List, and related papers[56]. All past and future climate data are freely available from CHELSA (https://chelsa-climate.org/bioclim/). The past and future heatwaves are freely available from Climate Data Store (https://cds.climate.copernicus.eu/datasets/sis-extreme-indices-cmip6?tab=overview). The past and future extreme droughts are collected by consulting the authors of the paper (https://doi.org/10.1029/2022EF003420). The further projection of land-use change is from the Land-Use Harmonization[2] (https://luh.umd.edu/data.shtml). The further projection of population change is from the NASA Socioeconomic Data and Applications Center (https://sedac.ciesin.columbia.edu/data/set/popdynamics-1-km-downscaled-pop-base-year-projection-ssp-2000-2100-rev01).

Code availability

R script and data developed for the analysis are deposited in https://figshare.com/s/9e1784bea9e7287c2b3e.

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Additional information

Table S1. Data on extinction risk, ecological traits, and extrinsic variables in csv format and also in https://figshare.com/s/e2bb7bdfef4bcb73c11b?file=51022458

Table S2. The proportion of threatened species among families and realms

Table S3. The univariate correlations between predictors and extinction risk

Table S4. The relative performance of each candidate model for all species

Table S5. Model-averaged parameter estimates

Table S6. The rates of trait evolution to track future changes

Table S7. The risk probability of non-assessed (DD + NE) species

Table S8. Hypotheses on the relationships between predictor factors and extinction risk

Table S9. Sensitivity analyses using the IUCN or TFTSG as the response variable

Table S10. variation inflation factors for each species group

Table S11. Threat classification based on the IUCN threat classification scheme

Table S12. Phylogenetic Generalized model with the Ornstein–Uhlenbeck process

Figure legend

Figure 1. Phylogenetic tree of 378 species of chelonians worldwide. The colors of the tips represent the species' conservation status based on the combined Red List. The classification of families (branches) was based on the Reptile database 2024. Here, we assigned species to a specific biogeographical realm when more than 80% of their range overlapped with the realm. The bar plots on the left showed the number of species in each realm, Red List, and family category. The inner map shows the species richness and proportion of threatened species for non-marine species based on the combined Red List.

Figure 2. The Indomalaya region is an extinction epicenter. We show the proportion of threatened and extinct species among families or biogeographical realms in subplots A and B. The background colors in subplots A and B indicate significantly higher (red) or lower (blue) values of binomial test levels at 5% or having 100% or 0% threatened species. Since the binomial test has relatively low statistical power when the family is small, we grouped small families into high-risk or low-risk groups when they contained 100% or 0% threatened or extinct species (those with > 0% and < 100% are omitted). Subplot C depicts the origins of species in families from various biogeographical realms.

Figure 3. Results of univariate phylogenetic comparative analyses for predicting the risk of extinction in chelonians using the combined Red List (0-5, from LC to EX). The analyses were further conducted for aquatic and terrestrial species and species in each biogeographic realm using this classification. To minimize the impact of any changes in the threat status of species on our findings, we categorized species

into threatened (1) and non-threatened (0) groups and reformed the analyses (phylogenetic logistic regression). The filled boxes show z values while the blank boxes represent no correlation. The analysis was not conducted for species in marine due to the limited sample size.

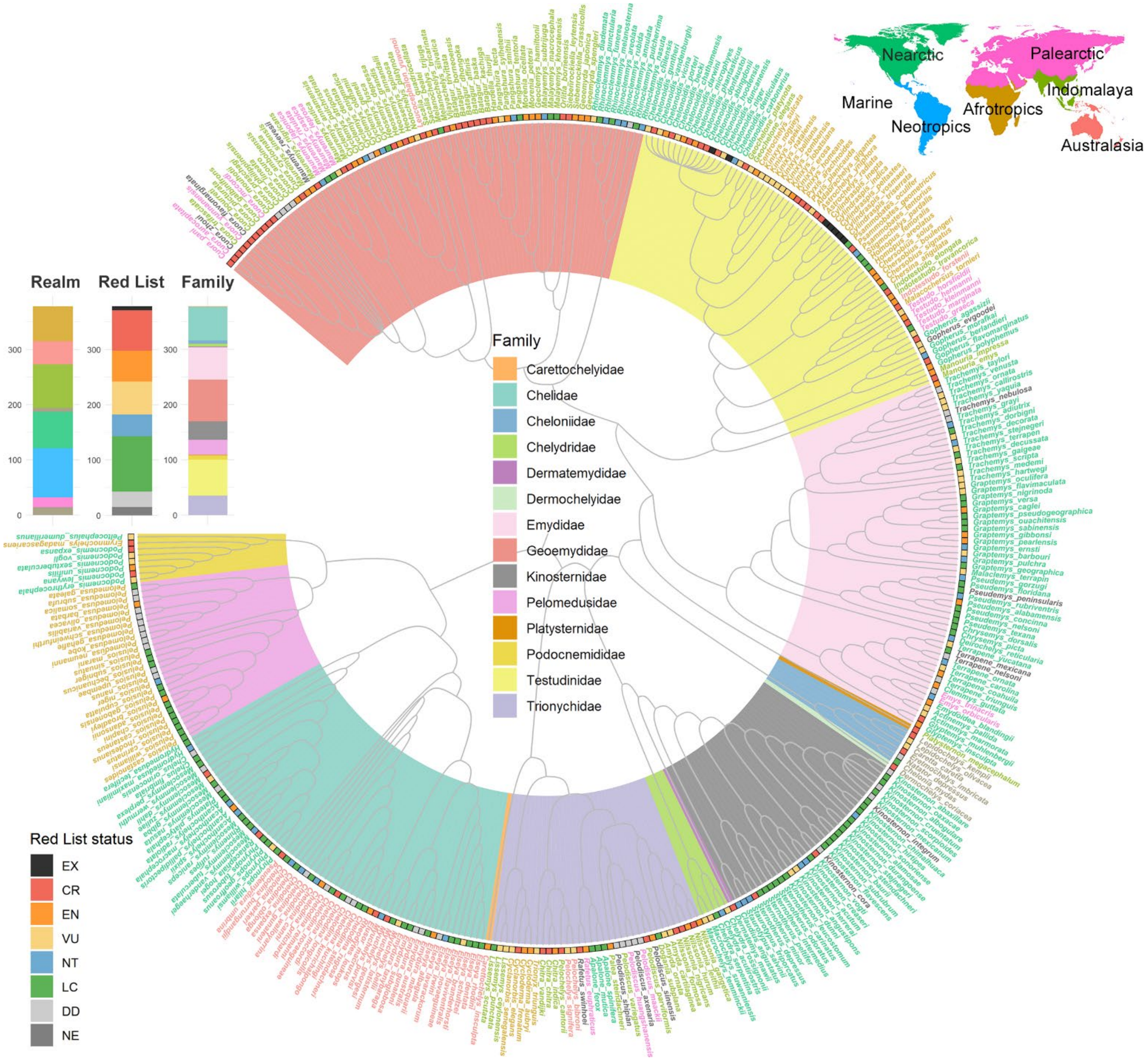
Figure 4. The model-averaged estimates revealed the key correlates of extinction risk (0-5, from LC to EX) in global chelonians. The model-averaged estimates and unconditional standard errors (error bar) for the significant variables ($p < 0.05$) in the 95% confidence set in predicting the extinction risk of all chelonians, species clades and regions. Note that we also carried out the analysis for a binary extinction risk pattern, marked as all species (0-1). The sizes of the dots represent different levels of significance. The analysis was not conducted for species in the Palearctic region due to the limited sample size.

Figure 5. More than half of non-assessed species under future extinction risk. The y-axis categorizes non-threatened species into high-, medium-, or low-risk families based on the results from Figure 2. The *x*-axis represents the risk probability using a logistic regression projection framework on unevaluated species. In this matrix, the dots, colored from blue to brown, represent species that have an increased probability of being threatened in the future.

Figure 6. The rates of trait evolution are three to six orders of magnitude slower than future challenges. We compared rates of trait evolution to mean temperature change (A), extreme droughts (B), heatwaves (C), human population expansion (D), and forest degradation (E). The dots illustrate the rates of

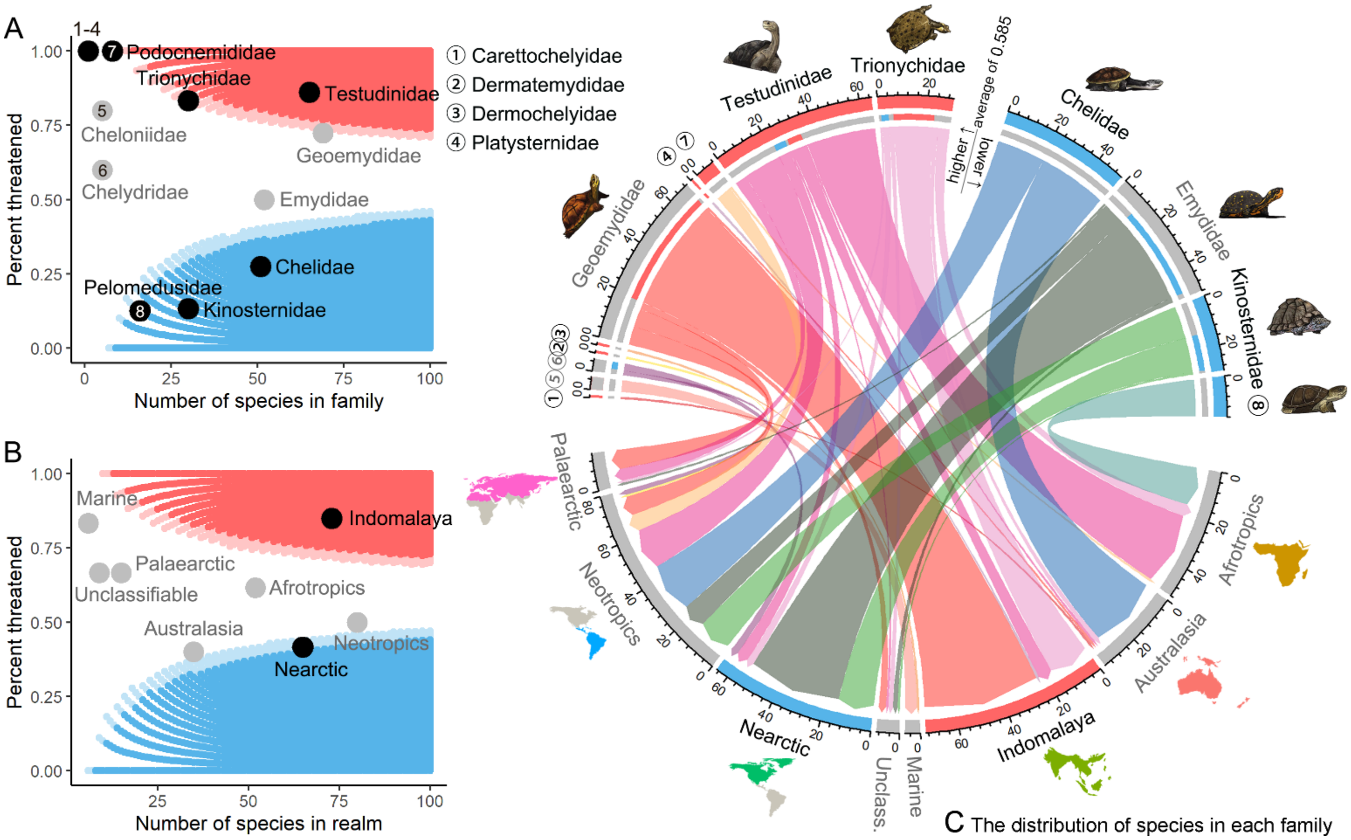
evolutionary change (felsen unit) for each species trait. The lines represent the projected rates of climatic and environmental changes under the best-case (SSP1) and worst-case (SSP5) scenarios. The graphic symbols are downloaded from Pixabay under “Use Content for free”.

Figure 1



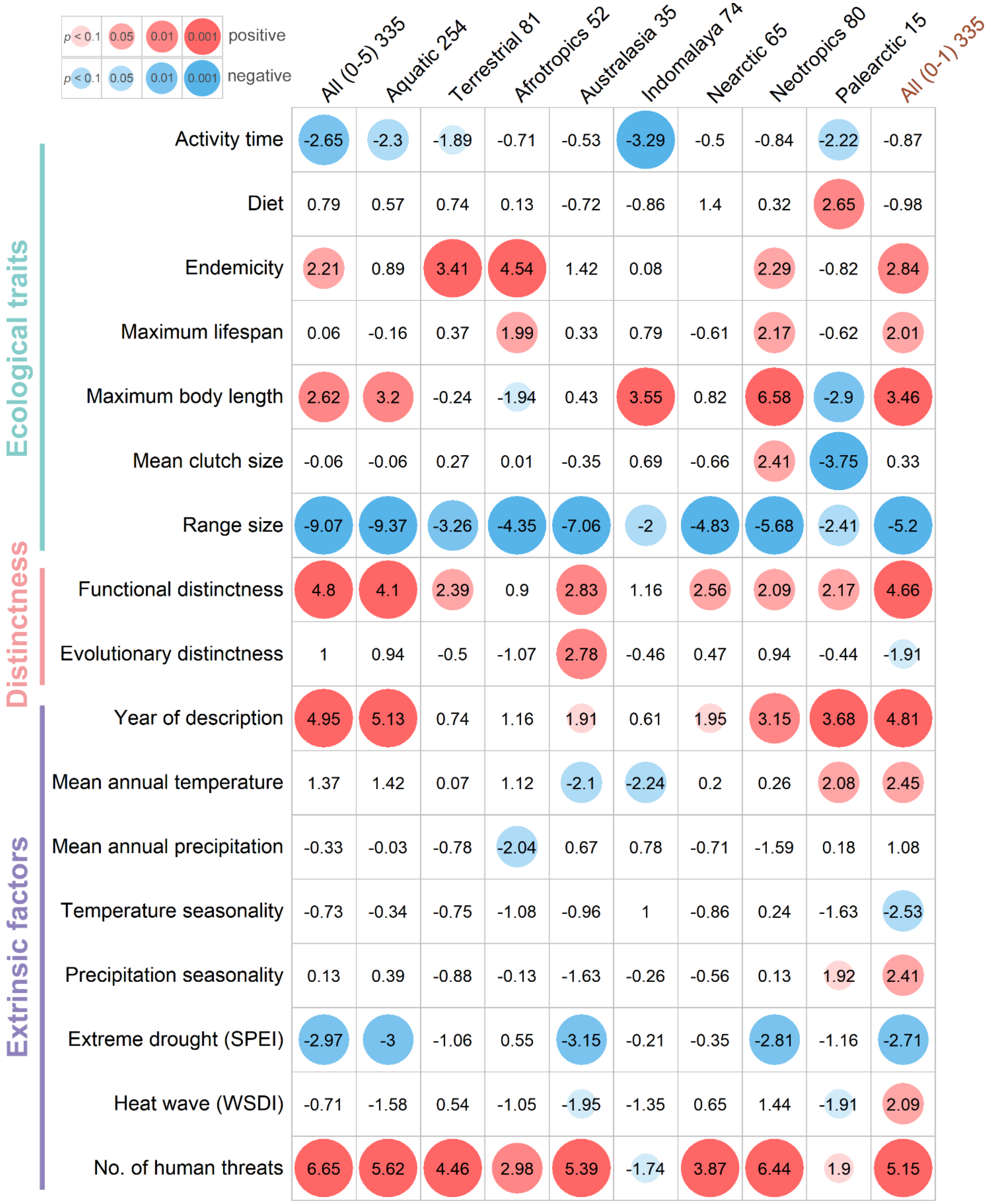
Nearctic
Palearctic
Marine
Indomalaya
Afrotropics
Neotropics
Australasia
Realm
Red List
Family
0
100
200
300
Family
Carettochelyidae
Chelidae
Cheloniidae
Chelydridae
Dermatemydidae
Dermochelyidae
Emydidae
Geoemydidae
Kinosternidae
Pelomedusidae
Platysternidae
Podocnemididae
Testudinidae
Trionychidae
Red List status
EX
CR
EN
VU
NT
LC
DD
NE

Figure 2



A
1-4
⑦ Podocnemididae
Trionychidae
Testudinidae
⑤ Cheloniidae
Geoemydidae
⑥ Chelydridae
Emydidae
Chelidae
Pelomedusidae
⑧ Kinosternidae
① Carettochelyidae
② Dermatemydidae
③ Dermochelyidae
④ Platysternidae
Percent threatened
1.00
0.75
0.50
0.25
0.00
0
25
50
75
100
Number of species in family
B
Marine
Indomalaya
Palaearctic
Unclassifiable
Afrotropics
Australasia
Neotropics
Nearctic
Percent threatened
Number of species in realm
higher ↑ average of 0.585
lower ↓
Testudinidae
Trionychidae
Chelidae
Emydidae
Kinosternidae ⑧
Geoemydidae
Palaearctic
Neotropics
Nearctic
Unclass.
Marine
Indomalaya
Australasia
Afrotropics
C The distribution of species in each family

Figure 3



	All (0-5) 335	Aquatic 254	Terrestrial 81	Afrotropics 52	Australasia 35	Indomalaya 74	Nearctic 65	Neotropics 80	Palearctic 15	All (0-1) 335
Activity time	-2.65	-2.3	-1.89	-0.71	-0.53	-3.29	-0.5	-0.84	-2.22	-0.87
Diet	0.79	0.57	0.74	0.13	-0.72	-0.86	1.4	0.32	2.65	-0.98
Endemicity	2.21	0.89	3.41	4.54	1.42	0.08		2.29	-0.82	2.84
Maximum lifespan	0.06	-0.16	0.37	1.99	0.33	0.79	-0.61	2.17	-0.62	2.01
Maximum body length	2.62	3.2	-0.24	-1.94	0.43	3.55	0.82	6.58	-2.9	3.46
Mean clutch size	-0.06	-0.06	0.27	0.01	-0.35	0.69	-0.66	2.41	-3.75	0.33
Range size	-9.07	-9.37	-3.26	-4.35	-7.06	-2	-4.83	-5.68	-2.41	-5.2
Functional distinctness	4.8	4.1	2.39	0.9	2.83	1.16	2.56	2.09	2.17	4.66
Evolutionary distinctness	1	0.94	-0.5	-1.07	2.78	-0.46	0.47	0.94	-0.44	-1.91
Year of description	4.95	5.13	0.74	1.16	1.91	0.61	1.95	3.15	3.68	4.81
Mean annual temperature	1.37	1.42	0.07	1.12	-2.1	-2.24	0.2	0.26	2.08	2.45
Mean annual precipitation	-0.33	-0.03	-0.78	-2.04	0.67	0.78	-0.71	-1.59	0.18	1.08
Temperature seasonality	-0.73	-0.34	-0.75	-1.08	-0.96	1	-0.86	0.24	-1.63	-2.53
Precipitation seasonality	0.13	0.39	-0.88	-0.13	-1.63	-0.26	-0.56	0.13	1.92	2.41
Extreme drought (SPEI)	-2.97	-3	-1.06	0.55	-3.15	-0.21	-0.35	-2.81	-1.16	-2.71
Heat wave (WSDI)	-0.71	-1.58	0.54	-1.05	-1.95	-1.35	0.65	1.44	-1.91	2.09
No. of human threats	6.65	5.62	4.46	2.98	5.39	-1.74	3.87	6.44	1.9	5.15

Figure4

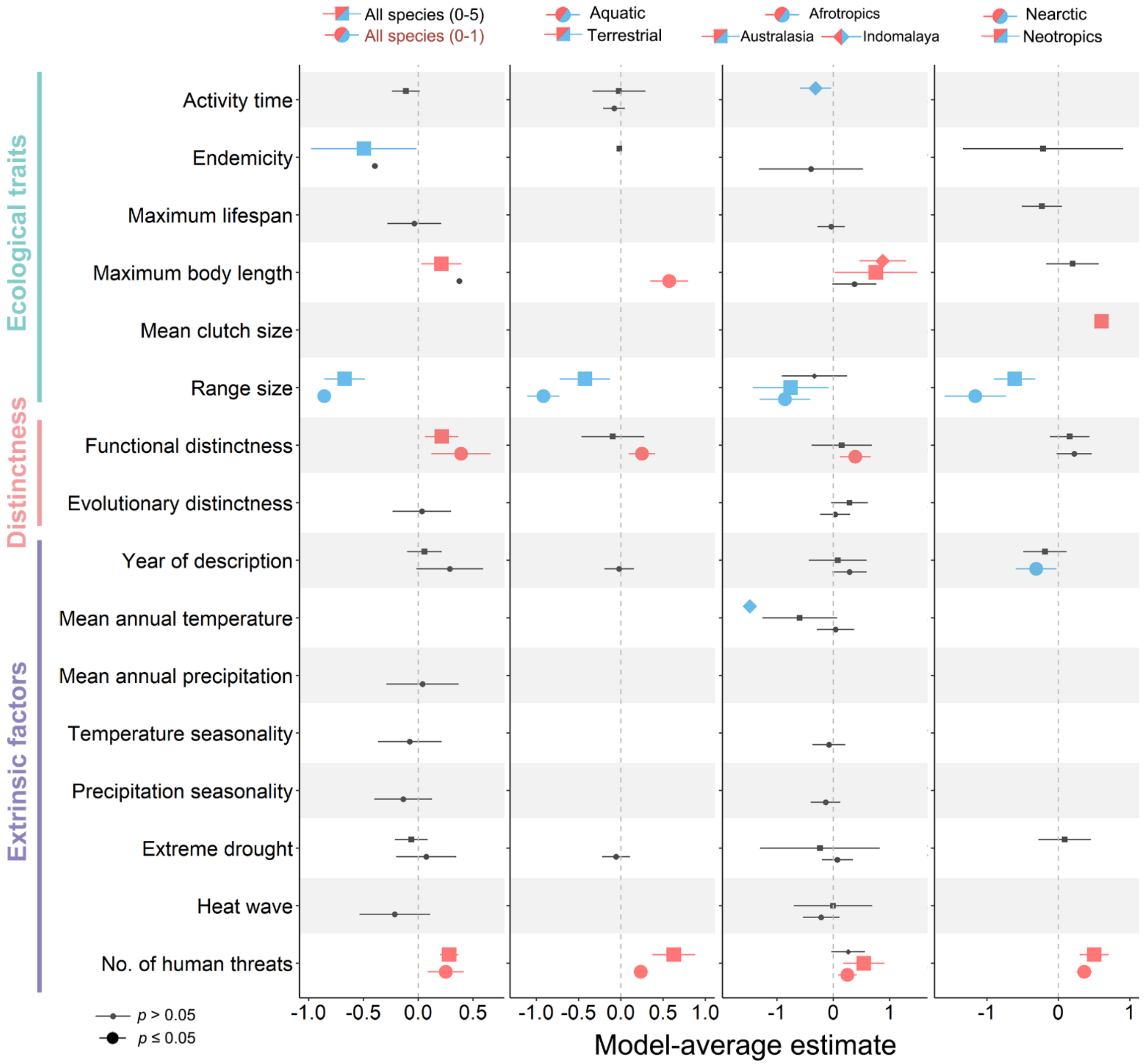

All species (0-5)
All species (0-1)
Aquatic
Terrestrial
Afrotropics
Australasia
Indomalaya
Nearctic
Neotropics
Ecological traits
Distinctness
Extrinsic factors
Activity time
Endemicity
Maximum lifespan
Maximum body length
Mean clutch size
Range size
Functional distinctness
Evolutionary distinctness
Year of description
Mean annual temperature
Mean annual precipitation
Temperature seasonality
Precipitation seasonality
Extreme drought
Heat wave
No. of human threats
-1.0 -0.5 0.0 0.5
-1.0 -0.5 0.0 0.5 1.0
-1 0 1
-1 0 1
$p > 0.05$
$p \leq 0.05$
Model-average estimate

Figure 5

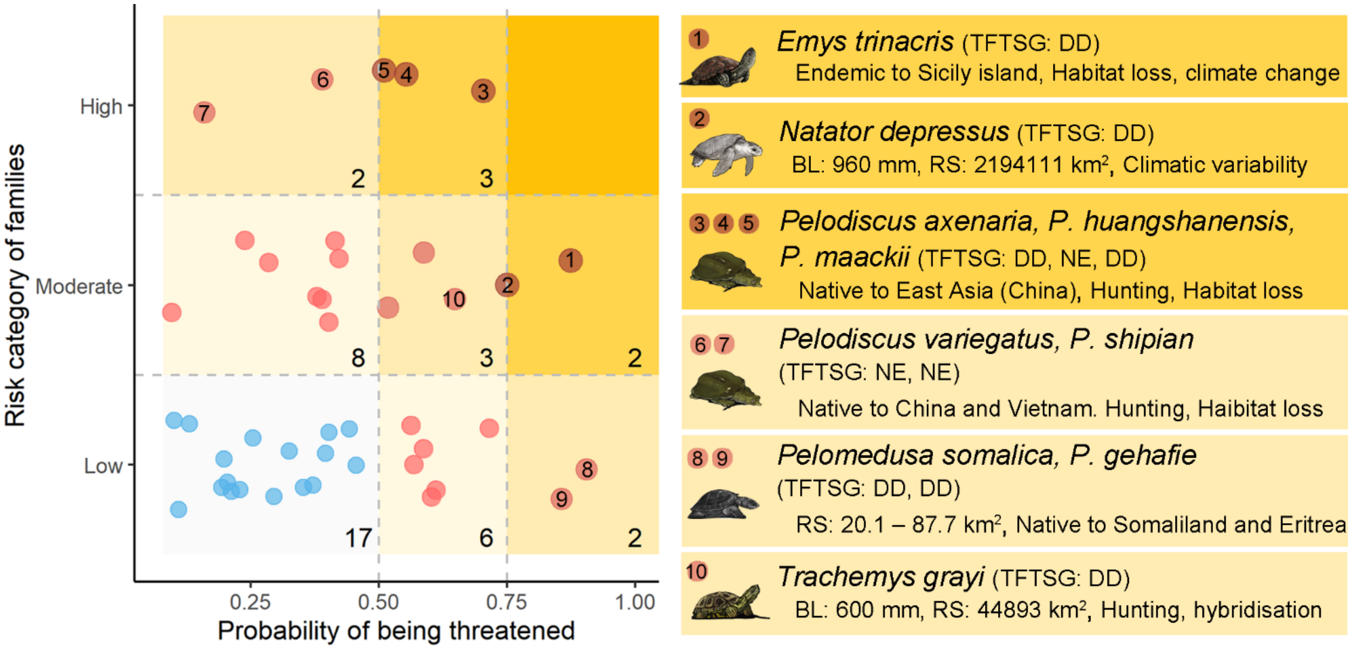
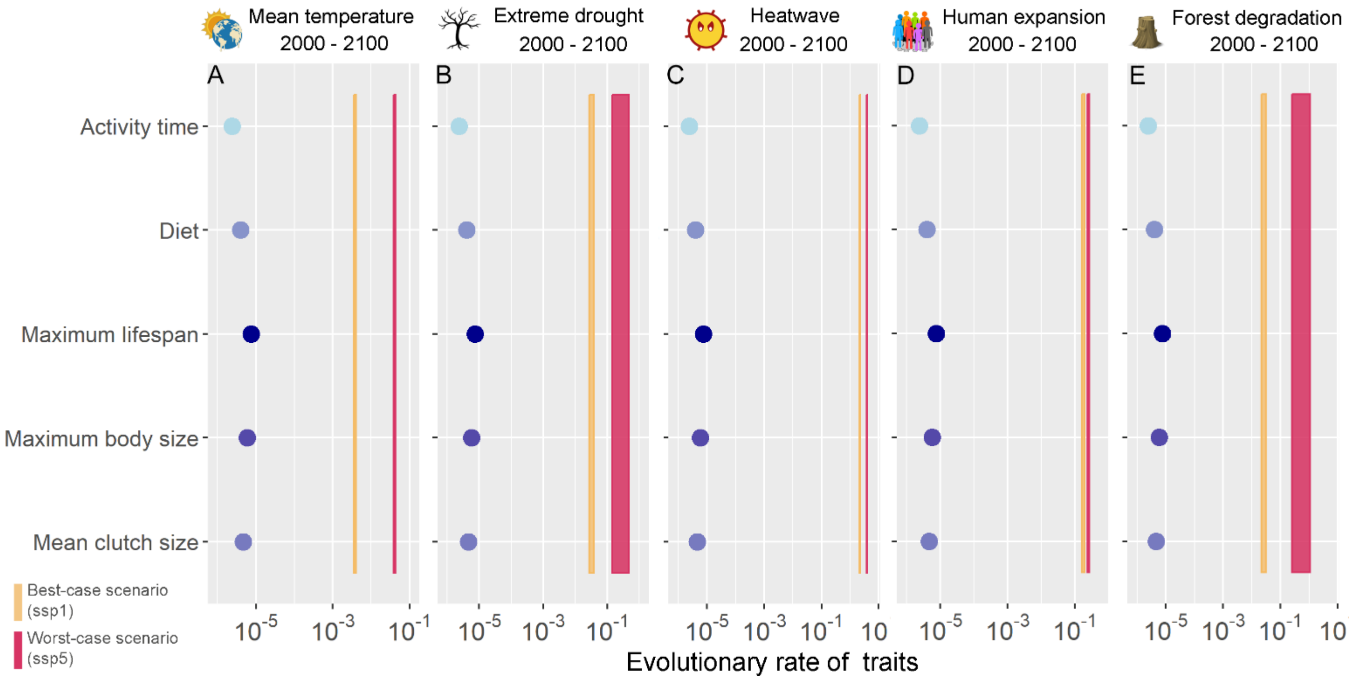

Risk category of families
High
Moderate
Low
Probability of being threatened
0.25
0.50
0.75
1.00
2
3
8
3
2
17
6
2
1 2 3 4 5 6 7 8 9 10
1 Emys trinacris (TFTSG: DD)
Endemic to Sicily island, Habitat loss, climate change
2 Natator depressus (TFTSG: DD)
BL: 960 mm, RS: 2194111 km², Climatic variability
3 4 5 Pelodiscus axenaria, P. huangshanensis, P. maackii (TFTSG: DD, NE, DD)
Native to East Asia (China), Hunting, Habitat loss
6 7 Pelodiscus variegatus, P. shipian
(TFTSG: NE, NE)
Native to China and Vietnam. Hunting, Haibitat loss
8 9 Pelomedusa somalica, P. gehafie
(TFTSG: DD, DD)
RS: 20.1 – 87.7 km², Native to Somaliland and Eritrea
10 Trachemys grayi (TFTSG: DD)
BL: 600 mm, RS: 44893 km², Hunting, hybridisation

Figure 6


Mean temperature
2000 - 2100
Extreme drought
2000 - 2100
Heatwave
2000 - 2100
Human expansion
2000 - 2100
Forest degradation
2000 - 2100
A
B
C
D
E
Activity time
Diet
Maximum lifespan
Maximum body size
Mean clutch size
Best-case scenario (ssp1)
Worst-case scenario (ssp5)
10^{-5}
10^{-3}
10^{-1}
10
Evolutionary rate of traits