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Synergistic and Additive Effects of Multiple Threats Erode Phylogenetic and Life History Strategy Diversity in Testudines and Crocodilia

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ABSTRACT

Understanding how multiple threats interact is crucial for the prioritisation of conservation measures. Here, we investigate how interactions between six common threats (climate change, habitat disturbance, global trade, overconsumption, pollution and emerging diseases/invasive species) reduce the life history strategy diversity and phylogenetic diversity of 230 species of Testudines and 21 of Crocodilia. We classify threat interactions into additive, synergistic and antagonistic according to the reduction of life history strategy and phylogenetic diversity. Most threat interactions are antagonistic; the effect of threats jointly is lower than the sum of the effects of threats separately. However, we find that the interaction between emerging diseases or invasive species with other threats has synergistic and additive effects, meaning that the combined effects are greater than or equal to the effects of threats separately. Our work can help target conservation strategies and detect key places to address multiple threats when they appear together.

1 | Introduction

Habitat loss, climate change, pollution and overexploitation for consumption and trade are each placing significant pressure on the persistence of species across the globe (Díaz et al. 2019; Maxwell et al. 2016; Steffen et al. 2011). These threats, however, often interact to affect biodiversity, sometimes amplifying their effects and creating additional challenges for species viability (Côté et al. 2016). For example, habitat loss can make species more vulnerable to the impacts of climate change (Mantyka-pringle et al. 2012), while poaching and unsustainable trade can further exacerbate the impact of habitat loss in species like the jaguar (*Panthera onca*; Romero-Muñoz et al. 2019) or elephants (*Loxodonta* spp.; Breuer et al. 2016). Despite the impacts of these complex interactions, we currently lack a global understanding of where and which threats

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interact, and in what direction, to shape life history strategy and phylogenetic diversity. Life history strategy diversity is defined as the amount of variance in combinations of life history traits (e.g., generation time, age at maturity, clutch size; Healy et al. 2019), while phylogenetic diversity is quantified as the total shared evolutionary history on a phylogenetic tree that connects a group of species to each other (Faith 1992). Crucially, this knowledge is critical for the effective implementation of conservation measures (Craig et al. 2017).

Ongoing biodiversity decline is leading to the erosion of functional diversity, including life history strategy diversity (Carmona et al. 2021; Toussaint et al. 2021). Reduction in functional diversity can reduce the resilience of the ecosystem and may result in the loss of ecological processes (Mouillot et al. 2014; Oliver et al. 2015; Schmitt et al. 2020). In this context, life history strategies describe species' life cycles and their suitability for adaptation to a given environment (Capdevila et al. 2020; Healy et al. 2019; Salguero-Gómez, Jones, Jongejans, et al. 2016; Stearns 1999). We recently examined how the theoretical extinctions of species of Testudines and Crocodilia facing anthropogenic threats would reduce the life history strategy diversity and the vulnerability of specific vital life history strategies (Rodríguez-Caro et al. 2023). In that study, the authors found that different human threats affect specific life histories and therefore differentially risk the life history strategy diversity of the taxonomic group. For instance, species of Testudines and Crocodilia with 'slow' life histories (i.e., late maturity and low numbers of offspring), are particularly vulnerable to threats from invasive species and diseases. However, the effects of interactions among multiple threats on life history strategy diversity loss remains unknown.

In addition to life history strategy diversity, assessing losses in phylogenetic diversity can be key to understanding evolutionary potential (Faith 1992) and to prioritising conservation measures (Faith 2008; Rosauer et al. 2017). Phylogenetic diversity assesses the combined influence of species on the overall Tree of Life, measuring the extent of evolutionary variation within a set of species (Faith 2008). However, to the best of our knowledge, there has been little exploration of the expected effects of anthropogenic threats on phylogenetic diversity. Previous work has evaluated the loss of phylogenetic diversity in reptiles relative to the Human Footprint Index (Venter et al. 2016), across the spatial distribution of the species (Gumbs et al. 2020). However, to date no study has specifically explored the effects of interactions of threats on Testudines and Crocodilia species.

Importantly, the outcome of threat interactions can depend on the spatial context of each threat (Capdevila et al. 2022; Bowler et al. 2020). For example, local threats such as habitat destruction or emergent diseases are directly associated with human populations (Di Giulio et al. 2009; Berry et al. 2015). Consequently, the prevalence of these local threats is expected to vary with human population density regardless of latitude (Santini et al. 2017). Globally, however, other global threats like climate change are distributed unevenly, particularly latitudinally (Harfoot et al. 2021; IPCC 2021). The uneven distribution of certain threats poses challenges in predicting the spatial distribution and the effects of multiple, interacting threats. Moreover, the co-occurrence of threats may endanger the conservation of life history strategy and phylogenetic diversity (Geary et al. 2019).

Testudines (tortoises, terrapins, freshwater and sea turtles) and Crocodilia (crocodiles, alligators and gharials) have recently been identified as the groups whose life history strategy and phylogenetic diversity are most at risk of being lost due to extinction. (Rhodin et al. 2018; Colston et al. 2020; Gumbs et al. 2020; Rodríguez-Caro et al. 2023). Indeed, 50%–60% of species in both groups are threatened with extinction (Cox et al. 2022; IUCN 2020). Moreover, the extinction of these species could result in greater-than-expected losses in life history strategy diversity (Rodríguez-Caro et al. 2023). To make things worse, the interactions among multiple anthropogenic threats to these threatened species are exceptionally high. For example, the Roti Island snake-necked turtle (*Chelodina mccordi*), a Critically Endangered species (Assingkily et al. 2019), is threatened by habitat disturbances, which have resulted in its displacement towards more anthropogenic areas where the risk of illegal trade for pet collection is higher (Rhodin et al. 2018). These threats have been compounded by the emergence of exotic species, pollution and climate change, which pose a significant risk to the persistence of this (Rhodin et al. 2004; Eisemberg et al. 2016) and other species (Cox et al. 2022).

Here, we quantify how interactions between different threats may reduce the life history strategy and phylogenetic diversity of Testudines and Crocodilia, and identify the regions around the world with a higher risk of said loss. To do so, we first analyse the loss of life history strategy and phylogenetic diversity by simulating the extinction of species affected by various anthropogenic threats and quantifying the associated loss of life history strategy and phylogenetic diversity. Next, according to Côté et al. (2016), we assess whether the effects of combinations between different threats exhibit different relationships: (i) Additive: the loss of life history strategy or phylogenetic diversity from each threat separately is equivalent to the loss of diversity when both threats act simultaneously. An additive effect would indicate that the threats affect different domains of the life history strategy spectra or disparate evolutionary lineages (Figure 1); (ii) Antagonistic: the loss of life history strategy or phylogenetic diversity of two threats together is lower than the threats separately. An antagonistic effect would indicate that species with similar life history strategies are affected by the same threats. In other words, there is an overlap in the life history strategy spectrum across different threats, resulting in less than a cumulative impact on life history strategies (Figure 1); and (iii) Synergistic: the combined loss of life history strategy or phylogenetic diversity when the two threats act jointly is greater than when two threats affect separately. A synergistic effect would indicate that the threats affect complementary species in the same region of the life history strategy space or phylogenetic tree, completely eliminating this part of the space (Figure 1). We hypothesise that, in general, (H1) the loss of life history strategy and phylogenetic diversity resulting from multiple threats exhibits antagonistic effects. However, we expect that (H2) interactions among threats that are known to affect specific

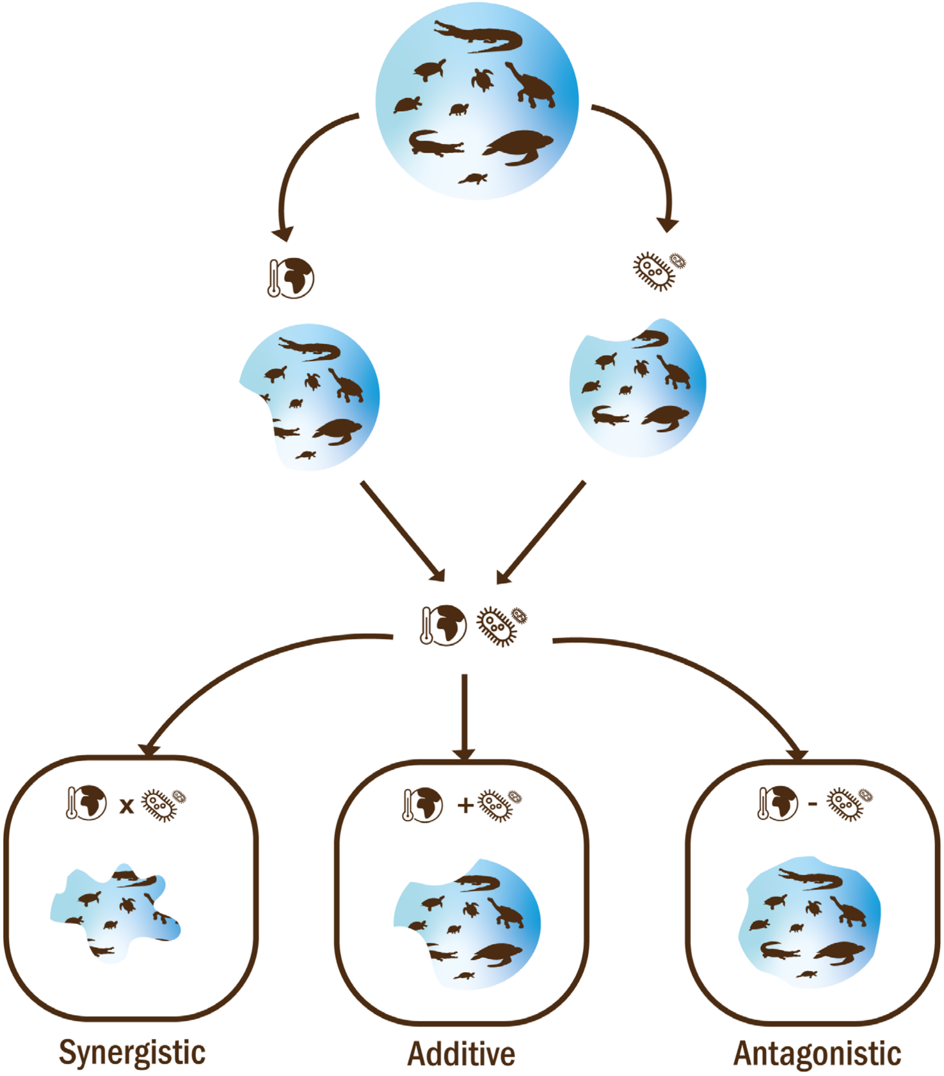

FIGURE 1 | Diagram illustrating the three types of threat interactions observed in our analyses of loss of life history strategy and phylogenetic diversity. The effects of combinations of pairwise threats can in principle exhibit three different outcomes: (1) Synergistic: The combined loss of life history strategy or phylogenetic diversity when two threats act jointly is higher than the loss of diversity of the two threats separately; (2) Additive: The loss of life history strategy or phylogenetic diversity from each threat separately is equivalent to the loss of diversity when both threats act simultaneously; and (3) Antagonistic: The combined effect when both threats act together is lower than the loss of life history strategy or phylogenetic diversity of the two threats analysed separately. The icons refer to two of the threats analysed in the study, namely climate change and emerging diseases.

portions of the life history strategy spectrum of Testudines and Crocodilians, such as local consumption, diseases and invasive species, and pollution (Rodríguez-Caro et al. 2023), may exhibit additive or synergistic effects.

2 | Materials and Methods

2.1 | Life History Strategy and Phylogenetic Diversity

To identify the trait space and examine life history strategy diversity of Testudines and Crocodilia, we quantified their life history strategies using life history trait data. Life history traits define key moments along the life cycle of a species (e.g., age at maturity, maximum longevity; Capdevila and Salguero-Gomez 2021), and are underpinned by the vital rates of survival, development and reproduction (Roff 1993). We obtained these trait data from the published literature, as detailed in Rodríguez-Caro et al. (2023). Briefly, life history traits were obtained from COMADRE Animal Matrix Database v. 4.23.3.1 (2016; Salguero-Gómez, Jones, Archer, et al. 2016), DATLife Database (DATLife Database 2021), Amniote Life History Database (Myhrvold et al. 2015) and published reviews (Allen et al. 2017; Pfaller et al. 2018; Reinke et al. 2022). Missing traits in the dataset (38%, Figure S1) were imputed using the R package *mice* (Van Buuren and Groothuis-Oudshoorn 2011), which uses multiple imputation, and the add-on *phylomice* to include phylogenetic information (imputed data was estimated in Rodríguez-Caro et al. 2023). We used six life history traits that encompass detailed information regarding the timing, intensity, frequency and duration of vital rates across the life cycle of any species: adult survival (Sa), juvenile survival (Sj), maximum lifespan (ML), age at sexual maturity (Lα), mean number of clutches per year (CN) and clutch size (CS). The resulting data encompass 259 species: 236 testudines and 23 crocodilians.

To assess the role of evolution in shaping the life history strategies of our species, we carried out phylogenetic comparative analyses. To that end, we employed a recently published species-level phylogenetic tree for Testudines and Crocodilia (Colston et al. 2020), which allowed us to explicitly consider the influence of evolutionary constraints on the observed life history strategies. The tree was constructed using 14 mitochondrial loci and six nuclear loci from 357 species of turtles and tortoises, as well as 27 crocodilian species (Rhodin et al. 2017). Colston et al. (2020) built Maximum Likelihood trees using RaxML (Stamatakis 2014) and applied phylogenetic multiple imputation to fill gaps in data for 17 out of 384 species. More detailed information on the tree construction methods is available in Colston et al. (2020). To perform the phylogenetic comparative analyses, we selected demographic data for species with available phylogenetic information, which resulted in a final dataset comprising 259 species: 23 Crocodilia and 236 Testudines.

To identify potential differences between the patterns of association among life history traits for Testudines and Crocodilia species, we used a phylogenetically informed PCA (*p*PCA), corrected by adult body mass (data and code from Rodríguez-Caro et al. 2023). This approach allows us to examine life history strategy diversity while also assessing and estimating the strength of non-independence among the examined lineages (Revell 2009) due to their shared evolutionary history, which is particularly important when analysing traits that may have evolved in a correlated manner. Since body mass typically correlates with life history traits (Stearns 1999; Capdevila et al. 2020), we accounted for this effect in our multivariate analyses using residuals from a phylogenetic regression between body size and each trait, a standard step in comparative life history trait studies (Gaillard et al. 1989; Capdevila et al. 2020; Rodríguez-Caro et al. 2023). The *p*PCA considers the correlation matrix of species' traits while accounting for phylogenetic relationships and simultaneously estimates phylogenetic signal via Pagel's λ (Freckleton 2000), which ranges from 0 (trait pattern not explained by phylogeny) to 1 (pattern perfectly explained by the phylogenetic structure of the species). The *p*PCA was estimated using the R package *phytools* (Revell 2012), assuming a Brownian motion model of evolution (Revell 2010), using the consensus tree estimated by Colston et al. (2020). Life history trait data were log-transformed to fulfil normality assumptions of PCA and z-transformed to mean = 0 and SD = 1 (Legendre and Legendre 2012). We used the Kaiser criterion (Kaiser 1960) after optimisation through varimax rotation (Corner 2009) to determine the number of axes necessary to explain a substantial amount of variation. Finally, we kept only two axes, which had an associated eigenvalue > 1. To account for the potential effect of body mass in life history analyses, we used the residuals from a phylogenetic regression of adult body size and each trait using the function 'phyl.resid' from the *phytools* package (Revell 2012). These residual values from the phylogenetic regressions are the ones we have used to model the *p*PCA.

To describe the life history strategy spectra of our study species, we estimated the multivariate kernel density of the trait data. To do so, we used the *TPD* (Trait probability density; Carmona et al. 2019) and *ks* R packages (Duong 2007, 2014) for the two first axes of the *p*PCA (Rodríguez-Caro et al. 2023). The resulting grouped kernels for all species were transformed into the continuous TPD function. Following methods described in detail elsewhere (Carmona et al. 2021; Toussaint et al. 2021; Rodríguez-Caro et al. 2023), we divided the continuous life history strategy space into a two-dimensional grid composed of 200 equal-sized cells per dimension. Next, we estimated the value of the TPD function for the 40,000 cells. In this way, the value of the TPD function represents the density of species in that particular region of the life history strategy space (i.e., species with similar life history strategies).

We used the phylogenetic trees of Colston et al. (2020) to represent the phylogenetic relationships of the species in our study. We sampled 1000 phylogenetic trees from the published set of 10,000 to adequately reflect the variation in phylogenetic placements and divergence time estimates inherent in such a subsample of the posterior distributions of trees (Thomas et al. 2013). The sum of all branch lengths of the phylogenetic tree represents the total phylogenetic diversity of the clade (Faith 1992).

2.2 | Threats to the Studied Species

To identify threats of Testudines and Crocodilia species, we used data collated from three sources, detailed in Rodríguez-Caro et al. (2023). Briefly, these sources are Stanford et al. (2020), Bonin et al. (2006) and the section about threats in the IUCN Red List (IUCN 2020). The main described threats were as follows: (i) habitat loss, fragmentation and degradation (Luiselli 2009), (ii) over-collection of individuals and their eggs for food consumption (Gong et al. 2017), (iii) unsustainable or illegal international trade, as well as over-collection for the trade in medicines (Sung and Fong 2018), (iv) climate change (Gibbons et al. 2000), (v) invasive species and emergent diseases (Jacobson et al. 2014; Tompkins et al. 2015), and (vi) pollution (Hutchinson and Simmonds 1991). We assessed these six threats for 230 (65% of the extant species) species of Testudines, and for 21 (78% of extant species) species of Crocodilia. Due to the lack of data regarding the intensity of threats to each species, here threat variables were categorised as 1 (or 0) if a specific threat was described for the species (or not).

2.3 | Effects of Interactive Threats on Global Life History Strategy and Phylogenetic Diversity

To quantify the effect of the threats on the life history strategy spectra of our 251 species of Testudines and Crocodilia, we simulated threat-specific extinction scenarios. In each scenario, species were classified as extinct if they were reported as affected by the assessed threat. To evaluate the differences between threatened and non-threatened species, we carried out two comparisons: (1) between the TPD function considering all the species (current spectra of life history strategy diversity) and the TPD function after removing the species affected by each of the six threats separately (habitat degradation, trade, local consumption, climate change or interactions with invasive species and diseases), irrespective of their threatened category; and (2) between the TPD function considering all the Red List-assessed species and the TPD function after removing the threatened species (Critically Endangered [CR], Endangered [EN] or Vulnerable [VU]) affected by each specific threat. Next, we estimated the loss of life history strategy spectra using the TPD function considering all the species assessed and the TPD function after removing the species according to specific threats. Here, the comparisons between TPD functions are supported by the fact that they are probability density functions, and as such they integrate to 1 across the whole life history strategy space, regardless of the number of species considered (Carmona et al. 2016). To reduce the potential effect of outliers in the life history strategy space, we applied a quantile threshold of 99%, following Carmona et al. (2016). Finally, we quantified how much of the life history strategy spectra is lost after the extinction scenarios according to the different threats by estimating which life history strategy space cells became empty after our simulated extinctions.

To identify the type of relationship between the different threats (Hypotheses H1 and H2 outlined in our introduction), we estimated the potential loss of life history strategy diversity attributable to each threat and between the combinations of threats. To that end, we use a comparison between TPD functions similar to the one explained above. We then evaluated the differences among single and multiple effects to identify synergic, antagonistic and additive effects (Figure 1). We carried out these comparisons both considering the extinction of all the species affected by each threat and considering only the extinction of threatened species (CR, EN, VU). To provide a spatial description of the interactions between threats, once the relationships between the different threats (antagonistic, synergistic or additive) have been described, we identified on which continents these relationships occur at the species level. We estimated how often synergists, antagonistic and additive effects appear in each continent to assess which ones face higher risks of life history strategy diversity loss in Testudines and Crocodilia species.

We repeated the same scenarios of extinction based on single and pairwise combinations of threats across the 1000 phylogenetic trees. For each phylogenetic tree, the total phylogenetic diversity was calculated prior to the removal of the species affected by each threat or combination of threats. The phylogenetic diversity was then recalculated following the removal of the affected species from the phylogeny, and the difference in phylogenetic diversity values (i.e., the amount of phylogenetic diversity lost) was calculated for each scenario across each of the 1000 trees.

To assess if the impacts of the interaction of threat on the phylogenetic diversity, we also compared the observed changes in phylogenetic diversity to a null model where the extinct species were randomly selected within the pool of species. For each scenario of extinction associated with an interaction of threats, we compared the phylogenetic diversity to 999 losses of phylogenetic diversity where the same number of threatened species were randomly selected among the pool of species, similar to Rodríguez-Caro et al. (2023) with regards to functional diversity. This step allowed us to understand whether the extinction in the different scenarios reduces the phylogenetic diversity more or less than expected. We compared the 5% and 95% percentiles of the random simulation with the value of loss of phylogenetic diversity per each extinction scenario to estimate if the values were significantly different. In this case, higher than expected reductions in phylogenetic diversity would mean that the species that are going extinct in the considered scenario are unique in terms of phylogenetic diversity, whereas lower than expected reductions would imply that the species going extinct are mostly phylogenetic redundant.

3 | Results

3.1 | Effects of Interactions

To assess the differences between the individual effects of threats and their combined effects, we compared the loss of life history strategy diversity in each case. By conducting pairwise combinations of our six different threats, we find that most combinations of threats exhibit antagonistic effects (73.3% of combinations, Figure 2). However, one pairwise combination of threats shows an additive effect (pollution × invasive species/diseases), and 20% of combinations exhibit synergistic effects, such as invasive species/diseases × habitat disturbances, invasive species/diseases × local over-consumption and invasive species/diseases × international trade. This pattern remains largely consistent when analysing threats in three-way interactions: antagonistic relationships are the most common (80%; Table S1). However, additive (5%) and synergistic (15%) interactions also occur in these triads, particularly when one of the threats involves emerging diseases or invasive species. Additionally, while the analysis of the relation between threats remains consistent between the two subsets of data (threatened and total species), differences were found in the combination of unsustainable local consumption × habitat disturbance. In that combination, the relationship is additive in the analyses with all species, but when considering only the threatened species (CR, EN and VU), the relationship becomes antagonistic (Figure 2a). However, when combinations of three or more threats affect threatened species, synergistic effects no longer appear. Detailed results on the loss of life history diversity in combinations of three or more threats are provided in the Table S1.

When examining the effect of interactions of threats on phylogenetic diversity, practically all relationships are antagonistic (Figure 2b). This means that the combined effect of both threats on the reduction of phylogenetic diversity is lower than the effect of threats separately (results about the loss of phylogenetic diversity separately are in Figure S2). However, when the interaction occurs between the threat of emerging diseases and invasive species with unsustainable global trade, the loss of phylogenetic diversity shows additive results. Hence, different threats affect divergent evolutionary lineages. In combinations of three or more threats, all relationships were antagonistic (Table S2).

Finally, to estimate the effect of the pairwise combinations of threats on the loss of phylogenetic diversity, we simulate the extinction of species affected by each combination to calculate the percentage of loss of phylogenetic diversity (Figure 3). We compare the potential loss of phylogenetic diversity by each threat combination, with a simulated scenario where the identity of the species affected by each threat is randomised within the pool of species. All the effects of loss of phylogenetic diversity due to all the combinations for threatened species are similar to those expected by the random models. However, when we explore the loss of phylogenetic diversity for all the species (threatened and

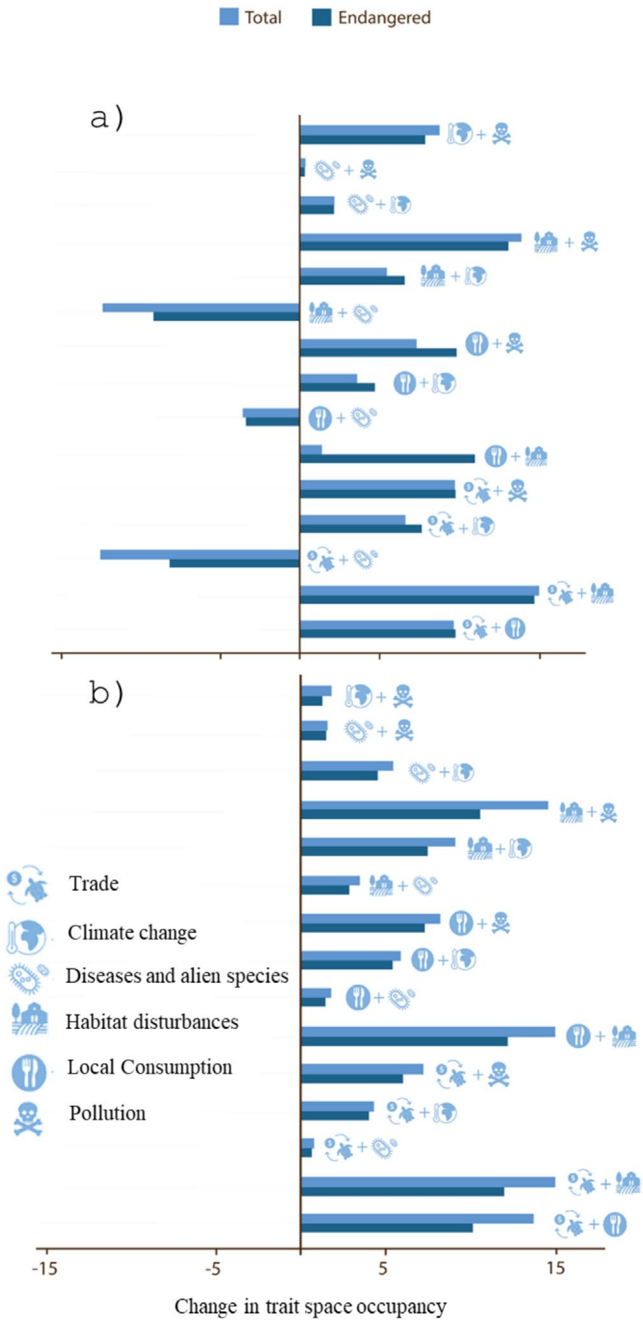

FIGURE 2 | Most of the threat interactions that shape the loss of life history strategy and phylogenetic diversity in Testudines and Crocodilia worldwide are antagonistic. Positives values of loss of life history strategy space is related to antagonistic relationships, negative values are related to synergistic interactions and values near to zero represent additive interactions. However, synergistic or additive relationships are observed when diseases and invasive species are involved for (a) life history strategy diversity and (b) phylogenetic diversity. (a) The bar chart illustrates the effects on life history strategy diversity loss by comparing the individual effects of each threat with the combined effects of all threats acting simultaneously. (b) Bar chart with the loss of phylogenetic diversity with the combined effects of threats. Negative values indicate synergistic effects, positive values indicate antagonistic effects and values close to 0 indicate additive effects. The analysis has been performed twice, once with the entire species set (light blue) and once with the threatened species subset (dark blue).

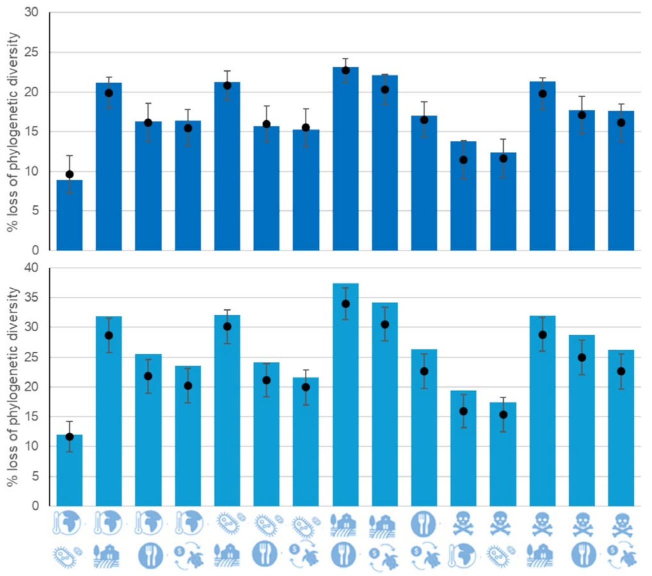

FIGURE 3 | Loss of phylogenetic diversity according to the interaction of anthropogenic threats. Bar chart with the loss of phylogenetic diversity with the combined effects of threats. Simulated loss of phylogenetic diversity of Testudines and Crocodilia under extinction scenarios by the interaction of threats. In dark blue (top), we removed only threatened species (i.e., Critically Endangered [CR], Endangered [EN] and Vulnerable [VU] as per the IUCN Red List) and, in light blue (bottom) removed all the species affected (threatened or not). For each scenario, we compared the loss of phylogenetic diversity with 999 iterations of a null model where the same number of species were randomly selected among all 251 species. The 999 randomisations are represented for each threat as a grey dot for the 50th percentile, with grey whiskers representing the 5th and 95th percentiles.

non-threatened), most of the interactions are greater than expected by random extinctions, whose effect is beyond the 95% percentile for random simulations (Figure 3). Results for the analysis of the single threat are available in Figure S2.

3.2 | Spatial Evaluation of Interactions

To evaluate the spatial distribution of the different relationships among threats, each pairwise combination has been classified into three categories (additive, synergistic and antagonistic). In the spatial results, in most regions, the highest proportion of effects is antagonistic, indicating that the same species are affected by multiple threats. However, synergistic effects are more prominent in species from Oceania, accounting for 20% of the interactions, as well as in marine species distributed worldwide, representing 16% of the interactions. Despite additive effects being observed in only one type of interaction, their representation is as much as 10% of the interactions in North America (Figure 4).

The additive effects found in the loss of phylogenetic diversity occur mainly in two regions, North America and Africa. In these regions, the threats of emerging diseases and invasive species with unsustainable trade have a higher occurrence (42% occur in North America and 33% are Africa), with the remaining continents showing lower representation.

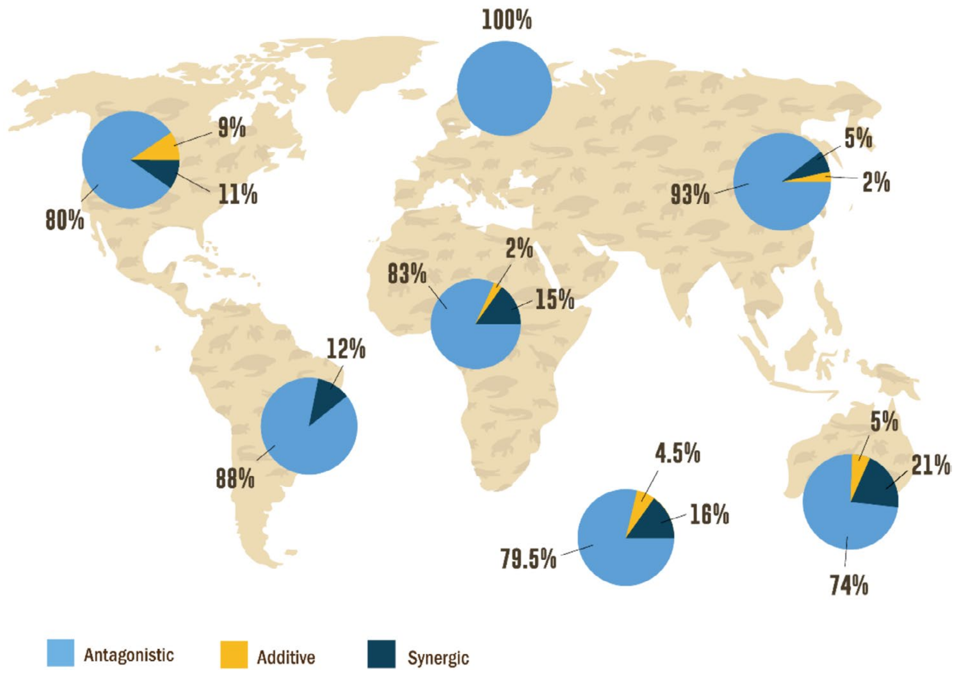

FIGURE 4 | Despite the high occurrence of antagonistic effects of human threats on the reduction of life history strategy diversity of Testudines and Crocodilia worldwide, synergistic effects are quite common in Oceania. The pie chart is the description of the proportion of each interactive pairwise threat effect in different continents. The threats (not shown) are habitat degradation, unsustainable consumption, illegal trade, climate change, interaction with invasive species and diseases and pollution. The bottom centre pie chart represents worldwide distributed marine species.

4 | Discussion

Here, we analysed the interaction of multiple threats on the life history strategy and phylogenetic diversity of two groups of high conservation interest: Testudines and Crocodilia (Colston et al. 2020). We report a wide disparity in the effect of threats on both groups, with prevalent antagonistic interactions between threats (73.3% of threat combinations), whereby the impact of two threats together is lower than the reduction in diversity when these threats are considered individually. Additionally, we found differential distributions of the threat interactions across the globe, with a high proportion of synergistic interactions in Oceania. Finally, our analyses show that variability in said interacting effects is greater concerning life history strategy diversity than phylogenetic diversity.

The fact that most threats present antagonistic relationships (Hypothesis H1) reflects the high redundancy in life histories in reptiles (Carmona et al. 2021; Rodríguez-Caro et al. 2023). Our results indicate that the same species are indeed affected by several threats simultaneously. For instance, in the case of the genus *Testudo*, species are mainly threatened by habitat loss, climate change and illegal trade (Graciá et al. 2020). In fact, in our results, 43% of our examined species for which threats have been described are at risk from at least three different threats. In our database, species such as the Olive Ridley sea turtle (*Lepidochelys olivacea*) and the Roti Island snake-necked turtle (*Chelodina mccordi*) face risks from all six threats examined in this study. Both species are long-lived threatened species, and the population trend is decreasing according to the Red List (IUCN 2020). However, the occurrence of additive or synergistic relationships in our study indicates that threats affect complementary life history strategy groups, which points to greater risks of extinction and loss of diversity (Côté et al. 2016). Synergistic relationships described for other taxonomic groups such as neotropical primates, affected by habitat fragmentation and hunting, have helped focus attention on holistic conservation efforts; for example, restoring connectivity can indirectly reduce hunting impacts if human access is restricted to local communities (Mancini et al. 2023). In our case, conservation policies aiming to preserve testudines and crocodilians should be directed not towards specific species, but towards key threats to the conservation of functional diversity. For example, the management of invasive species must accompany habitat restoration, as we have found a synergistic relationship among these threats.

In our study, synergistic relationships usually are found when one of the threats is invasive species/emerging diseases, thus providing support for our Hypothesis H2. Emerging diseases and invasive species affect slow testudines and crocodilians (i.e., species with long generation length and maximum lifespans such as terrestrial tortoises) more than fast ones (Rodríguez-Caro et al. 2023). However, when Testudines or Crocodilia species are also affected by other more generalist threats, such as habitat loss or unsustainable trade, the loss in functional diversity is much greater than expected (Cox et al. 2022; Rodríguez-Caro et al. 2023). Here, emerging diseases, such as diseases in the respiratory tract in tortoises (Origgi and Jacobson 2000), interact synergistically with other globally distributed threats like habitat disturbances (Farooq et al. 2023), and together they may pose a high risk to the loss of functional diversity of this taxonomic group.

We found that synergistic interactions of threats occur mainly in Australia and in worldwide seas. In Australia, invasive species are widely recognised as the second largest threat to the local biodiversity (Evans et al. 2011). Australia is one of the most important hotspots of biodiversity in the world (Lindenmayer et al. 2010), but also has one of the highest rates of species extinction (Woinarski et al. 2015). Previous studies have described that the co-occurrence of threats to biodiversity in Australia jeopardises species conservation (Allek et al. 2018). In fact, Australian vertebrates face an average of six threats, with habitat fragmentation and invasive species being the most common ones (Hobbs 2002; Allek et al. 2018). On the other hand, our results show that marine species are also affected by synergistic effects of threats; for sea turtles, the first life stages are particularly sensitive to invasive species (Stokes et al. 2024), habitat disturbances (Mathenge et al. 2012) and local overconsumption in beaches with human presence (López-Mendilaharsu et al. 2020). Indeed, recent studies have highlighted the importance of considering that threats in marine and terrestrial ecosystems may interact synergistically, such as with loggerhead sea turtles (*Caretta caretta*) in the Mediterranean basin (Mancino et al. 2022). Therefore, establishing measures to control this combination of threats in regions like Australia or in worldwide seas is urgent to halt the loss of life history strategy diversity.

Although the loss of life history strategy diversity shows synergistic or additive interaction, the loss of phylogenetic diversity by multiple threats is mainly antagonistic for Testudines and Crocodilia. Given the hierarchical nature of phylogenetic trees, a large proportion of the phylogenetic diversity of a clade is typically contained along internal branches ancestral to multiple species (Faith 2008). Previous studies have found that phylogenetic diversity correlates with life history strategy diversity when threats are examined in isolation in plants (Tucker et al. 2018), and in mammals (Brodie et al. 2021). These findings support our results for Testudines and Crocodilians because both diversities show similar correlations (Rodríguez-Caro et al. 2023; Figure S2). However, here we identify that the loss of phylogenetic diversity shows additive and antagonistic relationships, whereas the loss of life history strategy diversity also shows synergistic relations. For synergistic effects to emerge from two threats, all species in a given clade must be impacted by at least one of those threats: a single species unaffected by either threat will prevent the loss of all branches from which it descends. Therefore, synergistic effects on phylogenetic diversity are expected to be rare. However, the emergence of synergistic effects would represent a serious risk of tipping points leading to the loss of deep phylogenetic branches (Faith 2015).

Analysing the impact of interactions between threats on species viability is crucial not only to prioritise conservation measures, but also to detect hotspots where conservation efforts are urgently needed (Craig et al. 2017). Our analyses are limited to species for which some threats have been described, but our approach allows us to identify which life history strategies may be affected and extrapolate their effects to other species with less information available, for example, using new databases about the information of threats worldwide in reptiles (such as Farooq et al. 2023). In future studies, it may be valuable to consider other aspects of trait space change, such as trait space density, which could provide a more detailed understanding of the impact of threat interactions. For instance, a smaller trait space with low density is likely more vulnerable than one with high density, making it a key factor for conservation (Guillerme et al. 2020; Mammola et al. 2021). Expanding our approach to other taxonomic groups may be crucial for rapid threat detection and to improve conservation of threatened species for which threats have not yet been described. For example, our approach can be particularly relevant for mammals, where previous authors identified a marked vulnerability in species located at the boundaries of functional space (Carmona et al. 2021). Thus, our approach could help to refine conservation strategies for mammals too. On the other hand, our approach will be of special interest for reptiles and amphibians, for which significant gaps in information exist (Conde et al. 2019). Our study serves as a starting point for assessing the effects of interactions between threats on wildlife.

Author Contributions

R.C.R.-C. and R.S.-G. conceived the original idea. R.C.R.-C. curated the data. R.C.R.-C. and R.G. did the analyses. R.S.-G. supervised the analyses. R.C.R.-C. and R.S.-G. wrote the first draft, and all authors (R.C.R.-C., R.G., E.G., S.P.B., H.C., M.K.G., C.P.C., H.A.P.-M., A.G., K.J.D. and R.S.-G.) reviewed and edited the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code for producing the results in the paper are publicly available at https://datadryad.org/stash/share/HOcooctAEnAgihiz0tmxXmVKvXK5uTujEUDr-Q_ou4g. The data to estimate the life history strategy diversity spectrum is accessible at https://doi.org/10.1038/s41467-023-37089-5 (Rodríguez-Caro et al. 2023).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.