Biological Conservation 241 (2020) 108323

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Turtle biogeography: Global regionalization and conservation priorities

Joshua R. Ennen[a,*], Mickey Agha[b], Sarah C. Sweat[a], Wilfredo A. Matamoros[c], Jeffrey E. Lovich[d], Anders G.J. Rhodin[e], John B. Iverson[f], Christopher W. Hoagstrom[g]

[a] *Tennessee Aquarium Conservation Institute, Tennessee Aquarium, 175 Baylor School Rd., Chattanooga, TN, 37405, USA*
[b] *Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, CA, 95616, USA*
[c] *Facultad de Ciencias Biológicas, Universidad de Ciencias y Artes de Chiapas, Museo de Zoología, Tuxtla Gutiérrez, Chiapas, México Apartado Postal 29000, Mexico*
[d] *U.S. Geological Survey, Southwest Biological Science Center, 2255 North Gemini Drive, Flagstaff, AZ, 86001, USA*
[e] *Chelonian Research Foundation, 168 Goodrich St., Lunenburg, MA, 01462, USA*
[f] *Department of Biology, Earlham College, 801 National Road West, Richmond, IN, 47374, USA*
[g] *Department of Zoology, Weber State University, 1415 Edvalson, Department 2505, Ogden, UT, 84408, USA*

ARTICLE INFO

Keywords:
Asian turtle crisis
Beta diversity
Conservation
Endemism
Hotspots
Priority areas

ABSTRACT

Defaunation in the Anthropocene has created a need to focus limited conservation resources on geographically-explicit areas with high conservation significance. Priority conservation areas are often defined as those with high biodiversity – hotspots. While these conservation areas are critical to securing global biodiversity, prevailing approaches for their delineation are often qualitative. Here, we demonstrate the benefits of a clade-specific approach that improves conservation. We use the distinct, imperiled clade of turtles (tortoises and freshwater turtles) to delineate biogeographical regions and characterize their comparative levels of biodiversity and conservation values. We produce a quantitative, revisable map of 63 global turtle regions and identify several turtle regions, mostly in the Indomalayan turtle realm, that are high-priority conservation regions. While our high-priority turtle regions include those previously reported in the literature as turtle hotspots, we also describe a new priority conservation region in Southeast Asia (Yangtze-Huang He-Xi Yiang) which has both high species and endemism richness. Although not considered a high or intermediate conservation priority, our analyses delineated another previously unidentified turtle hotspot – the Kalahari Basin-Rift Valley. Additionally, we identify several turtle regions, largely in Central America, with intermediate conservation priority. Our results reveal that many turtle hotspots represent complex biogeographical areas with high inter-regional β-diversity, and several of these turtle-hotspots occur in transition zones with high biogeographical complexity. In these cases, inter-regional conservation efforts will be necessary to ensure turtle biodiversity conservation.

1. Introduction

Human-caused, post-industrial defaunation has reached global proportions, creating a sixth mass-extinction (Barnosky et al., 2011) and inspiring the term ‘Anthropocene’[1] for the modern geological age (1950 to present; Dirzo et al., 2014). Global-scale efforts to halt or at least reduce the rate of anthropogenic extinctions include characterizations of distributional patterns to focus conservation efforts in geographically-explicit areas where they are most needed or most beneficial (Funk and Fa, 2010; Hoffmann et al., 2010; Mittermeier et al., 2011). Popular approaches include identification of hotspots and ecoregions, which have successfully focused conservation efforts, but often lack rigorous assessment (Ladle and Whittaker, 2011). Furthermore, these methods often use predetermined regions delineated by data from other taxonomic groups (i.e., surrogate taxa) and not the group of interest. Often patterns of biodiversity are not correlated among taxonomic groups, leaving uncorrelated groups without protection (Roll et al., 2017).

Objective delineation of regions for major taxonomic groups (e.g., Lissamphibia, Mammalia, Aves, Squamata, etc.) is critical for conservation because each taxon embodies unique evolutionary and ecological properties that create their own legacies of speciation, dispersal, and extinction (Whittaker et al., 2005; Richardson and Whittaker, 2010; Holt et al., 2013). These alternative legacies shape distinct

---

* Corresponding author.
E-mail addresses: jre@tnaqua.org (J.R. Ennen), magha@ucdavis.edu (M. Agha), sch@tnaqua.org (S.C. Sweat), wilmatamoros@yahoo.com (W.A. Matamoros), jeffrey_lovich@usgs.gov (J.E. Lovich), rhodincrf@aol.com (A.G.J. Rhodin), johni@earlham.edu (J.B. Iverson), christopherhoagstrom@weber.edu (C.W. Hoagstrom).

[1] The term ‘Anthropocene’ is not formally recognized by the U.S. Geological Survey as a description of geologic time. We use it here informally. The origins of the term are discussed in Zalasiewicz et al., 2008

https://doi.org/10.1016/j.biocon.2019.108323
Received 24 May 2019; Received in revised form 15 October 2019; Accepted 28 October 2019

biodiversity patterns (e.g. Roll et al., 2017; Leroy et al., 2018) with implications for conservation. Thus, a biogeographic framework that facilitates recognition of these taxon-specific patterns may improve identification of high conservation priority areas and improve representation of previously underrepresented taxonomic groups (De Klerk et al., 2002).

Non-marine turtles (i.e., freshwater turtles, tortoises, and terrapins; henceforth 'turtles') provide an opportunity to discern robust, quantitative, clade-specific conservation regions because their relatively low taxonomic richness (≈360 species), detailed fossil record, and well-studied phylogenetic relationships (Joyce et al., 2013) make the group particularly tractable for study. In addition, they are conspicuous and influential within a myriad of ecosystems (Catano and Stout, 2015; Lovich et al., 2018), and sometimes indicate the quality of habitat (Battisti and Luiselli, 2011; Basile et al., 2011). Nevertheless, turtles are one of the most imperiled major clades of all vertebrates (~60% of species extinct or threatened compared with Lissamphibia, Squamata, Aves, Crocodilia, and Mammalia; Turtle Taxonomy Working Group [TTWG], 2017; Rhodin et al., 2018). This largely reflects ease of harvest for food and the pet trade (TEWG, 2015Turtle Extinctions Working Group [TEWG], 2015), which is unsustainable because many species are long-lived with delayed maturity (Heppell, 1998; TTWG, 2017). Despite their relative ecological and commercial value along with severe imperilment, turtles are often overlooked because they are traditionally grouped with other 'reptiles' (Fa and Funk, 2007; Mittermeier et al., 2011).

Previous assessments of turtle-specific biogeography (Angielczyk et al., 2015; Mittermeier et al., 2015; Roll et al., 2017; Ennen et al., 2016, 2017; Rodrigues and Diniz-Filho, 2017) revealed that areas of high turtle diversity often do not align with hotspots of global biodiversity and ecoregions (Olson et al., 2001; Olson and Dinerstein, 2002; Abell et al., 2008; Mittermeier et al., 2015). For instance, the tropics represent the center of species richness for numerous vertebrate groups, while turtle biodiversity is concentrated in extratropical regions, such as southern Asia and the southeastern United States of America (Roll et al., 2017; Rhodin et al., 2018). Similarly, montane regions are centers of endemicity for many vertebrate groups (Fa and Funk, 2007), whereas turtle biodiversity is mainly concentrated in lowlands (Buhlmann et al., 2009; Mittermeier et al., 2015).

Despite these readily apparent mismatches of turtle biogeography with other vertebrate groups and ecoregions, surrogate- or assemblage-based biogeography has been used in the past to identify overall species conservation regions, potentially resulting in misidentified or underrepresented identification of priority turtle-regions (Roll et al., 2017). Here, we investigate this issue by developing a biogeographical framework that facilitates recognition of clade-specific regions based on turtle distributions, and identifies region-specific conservation value. All of these analyses are repeatable, free from *a priori* bias, and applicable to any taxonomic clade.

2. Methods

2.1. Turtle-region delineation

2.1.1. Data collection

We used species-level taxonomy and distribution maps generated by the TTWG (2017). TTWG has developed the most up-to-date, accurate, and comprehensive study of turtle distributions, which is already being used for global-scale studies of turtle macroecology and evolution (Rodrigues and Diniz-Filho, 2017; Rodrigues et al., 2017). Seven extinct species (genera *Cylindraspis* and *Chelonoidis*) were excluded from the analyses. The two families of sea turtles (Cheloniidae and Dermochelyidae) were also excluded (for their regional conservation assessment, see Wallace et al., 2011).

We created a presence/absence matrix using turtle distributions and our spatial sampling unit (i.e., HydroBASINs; Lehner and Grill, 2013) with the *lets.presab.grid* function (R package letsR, Vilela and Villalobos, 2015). Our final data matrix included presence-absence data of 342 species arranged among 9029 Level-6 HydroBASINs units. We recognized that some units contained better distributional data than others and that distributions of rare, cryptic, or understudied species were not always well-defined. For instance, TTWG (2017) listed 9 species (< 3.0% of the dataset) with "general approximations of their potential distributions". Nevertheless, most of these occupied small distributions, reducing potential influence on our conclusions. In any case, this analysis represents a step forward in understanding regionalization of turtle faunas and is developed with recognition that it can be revised as available information increases or changes.

2.1.2. Turtle biogeographical realms and turtle-region delineation

We followed common statistical approaches to delineate turtle biogeographical regions and describe relationships among them (Matamoros et al., 2012; Hattab et al., 2015; Ennen et al., 2017) using R v. 3.3.2 (R Core Team, 2016). From our presence-absence matrix of HydroBASINs (Lehner and Grill, 2013), we calculated compositional beta diversity using the turnover component of Jaccard's dissimilarity index (βjtu; Baselga, 2010, 2012) along with the *beta.pair* function of the R package betapart (Baselga et al., 2018). We used an unweighted-pair group method with arithmetic mean (UPGMA) clustering analysis using the *hclust* function in βjtu to create a dendrogram of HydroBASINs based on their faunal similarity. A UPGMA was selected because Kreft and Jetz (2010) reported its superior performance with broad-scale biogeographical datasets. We calculated a cophenetic correlation coefficient (Farris, 1969) as a measure of fit of our modeled data (i.e., UPGMA) to the original data.

We used the Kelley-Gardner-Sutcliff penalty function (KGS) of the R package maptree (White and Gramacy, 2015) and visually assessed the UPGMA dendrogram to determine unique HydroBASIN clusters of turtle assemblages, which represented faunally distinct biogeographical regions for turtles (hereafter, turtle regions). The KGS analysis objectively determined the number of clusters by maximizing inter-cluster dissimilarities at all levels of the dendrogram, while retaining intra-cluster homogeneity. Next, we used the number of clusters determined by the KGS function and applied it in the *cutree* function. The end result was a dendrogram of quantitatively delineated turtle regions, themselves consisting of one or more HydroBASINs. We considered the relationship among the turtle regions within the dendrogram as informative for understanding global structure of turtle biodiversity. One of these relationships corresponds to a broader geographical scale – biogeographic realms for turtles (hereafter, turtle realms). That is, we defined turtle realms using broader relationships among groups of turtle regions from the UPGMA dendrogram. Finally, we used ArcMap v. 10.6.1 to spatially map the turtle realms and regions of the globe.

2.2. Turtle-region biodiversity and conservation assessment

2.2.1. Biodiversity and conservation variables

Biodiversity metrics calculated for each turtle region were: (1) species richness, (2) species density (number of species/km^2; Myers et al., 2000), (3) mean number of species per HydroBASIN, (4) endemic-species richness, (5) endemic-species density (number of endemics/km^2; Myers et al., 2000), (6) mean endemic-species richness based on the inverse range-size method (Kier and Barthlott, 2001), and (7) empirical logit transformation of endemism (logit endemism). According to Kier and Barthlott (2001), the inverse range-size method is a better metric of the restrictedness of distributions and it scales linearly with area, unlike other metrics of endemic-species richness. The logit endemism metric gives higher conservation value to turtle regions with relatively high endemism, regardless of species richness, and is superior to proportional endemism for characterizing patterns of endemism across turtle regions (Fa and Funk, 2007). Because species and endemics do not accumulate linearly with area (Arrhenius, 1921), we applied a transformation (natural log +1) to species and endemic densities.

We calculated four conservation metrics for each turtle region. The first was a mean IUCN Red List Index (RLI, Bubb et al., 2009) excluding extinct species. We used IUCN Red List categories reported for turtles by Rhodin et al. (2018) as a qualitative index of faunal imperilment. The RLI uses the following IUCN Red List categories and weighted values: least concern (0), near threatened (1), vulnerable (2), endangered (3), critically endangered (4), and extinct (5). Because this assessment focused on living species and we previously removed all extinct species from our biogeographical analyses, we also excluded them from this metric, creating a modified RLI. We used the modified RLI to provide a comprehensive measure of living faunal imperilment for entire regional turtle fauna. We used similar weighted values as the RLI (excluding extinct category) and modified the formula as follows:

$$RLI = 1 - \frac{\sum W_{sp1} + W_{sp2} + W_{sp3}\ldots}{W_{CR} * N}$$

where W_{sp} is the weight of the IUCN category for a species within a turtle region, W_{CR} is the weight for the critically endangered category, and N is the number of speices assessed in the turtle region excluding the data deficient species. Turtle regions with low RLI values contained more threatened species than non-threatened species.

The second conservation metric was human footprint (Global Human Footprint Dataset; WCS and CIESIN, 2005), which used data collected from 1995-2004. The human footprint variable was calculated as a percentage of the turtle region that was impacted by humans. The third conservation metric was percent area within each turtle region predicted to be inundated by an unmitigated 1-m sea-level rise (Agha et al., 2018). We considered a high human footprint and sea-level rise as surrogate metrics for contemporary and future habitat loss and degradation.

The fourth conservation metric was mean economic value of land (US dollar per ha) for each turtle region (Naidoo and Iwamura, 2007). We considered turtle regions with low-economic-value areas to have greater conservation potential due to increased feasibility for purchasing habitats dedicated to preservation and restoration in developed countries along with increased potential for incentivized systems and ecotourism (McNeely, 1998; Taylor et al., 2009; Hüber, 2019).

All biodiversity and conservation metrics were calculated using means within each turtle region. There were no data for human footprint or economic value of land for the Galápagos Islands and Aldabra Atoll/Seychelles Islands. Therefore, these turtle regions were excluded from the conservation classification tree analysis.

2.2.2. *Classification tree*

We evaluated the descriptive relationship between turtle-region biodiversity, conservation parameters (i.e., explanatory variables), and turtle realms (i.e., response variable) using classification-tree analyses (i.e., recursive partitioning, function *rpart*, package rpart; Therneau et al., 2018). Classification trees are often used to construct predictive models with biological data; however, they can also be used to present a simple descriptive structure for complex data (De'ath and Fabricius, 2000). The classification-tree analysis (McCune and Grace, 2002) is nonparametric and recursively divides (i.e., dichotomizes or subdivides) data using the best explanatory variable producing two homogeneous groups (i.e., decrease in deviance) at each branching. This subdivision continues, growing the tree, until additional branches fail to decrease deviance. At each dichotomous split, the analysis provides a value (i.e., threshold) for the specific variable that separates the data into two groups. Each threshold divides the data into two subsets with higher and lower values of the discriminating variable.

We conducted two classification-tree analyses, one evaluating biodiversity metrics as explanatory variables and another evaluating conservation metrics as explanatory variables. By using multiple metrics in each analysis, we aspired to produce a comprehensive assessment of relative conservation concern among realms (*sensu* Price, 2002; Funk and Fa, 2010). Because optimization occurs at each branching within a classification tree, rather than for the entire dataset, classification-tree models are often statistically over-fit and need to be pruned through cross-validation. We used a *V*-fold cross-validation method, where *V* equaled 20, to prune both classification trees (De'ath and Fabricius, 2000).

2.2.3. *Conceptualization of turtle regions as priorities*

We combined the results from the two classification-tree analyses in a two-dimensional matrix to assess preliminary conservation priorities among turtle regions and provide a framework to support future attempts at more detailed assessments. The matrix provides a straightforward visualization of how biodiversity and conservation metrics interface among turtle regions across the globe.

Based on this matrix, we propose that a turtle region should have highest conservation priority if it was classified as high in logit endemism or range restriction within the biodiversity classification tree (Fig. 3A branches 2, 8, and 9), while at the same time also classified as highly imperiled (RLI) in the conservation classification tree (Fig. 3B branch 2). This follows the tradition of conservation biology that emphasizes endemism, range restriction, and imperilment in conservation actions (see Myers et al., 2000; Kier and Barthlott, 2001; Price, 2002; Fa and Funk, 2007; Funk and Fa, 2010; Rhodin et al., 2018). It is also consistent with efforts to conserve global biodiversity (Myers et al., 2000; Buhlmann et al., 2009; Hoffmann et al., 2010; Mittermeier et al., 2011, 2015).

Following this logic, we further propose that turtle regions have intermediate conservation priority if classified as high in logit endemism or range restriction within the biodiversity classification tree (Fig. 3A branches 2, 8, and 9) and, although not classified as highly imperiled, nevertheless suffering from a high human footprint (Fig. 3B branch 7). This follows the convention that habitat destruction and other human disturbances (e.g., harvest) threaten species with restricted ranges (Purvis et al., 2000; Cardillo et al., 2008). Additionally, we propose that turtle regions with low endemism, low range restriction, and low species richness (Fig. 3A branch 6), but high imperilment (Fig. 3B branch 2) could also be considered of intermediate conservation priority, based simply on the level of imperilment of the resident fauna, which is presumably due to regional factors.

Finally, we propose that other turtle regions be classified as relatively low conservation priorities, from a global perspective. Relatively low range restriction and endemism, imperilment, and human footprint suggest global extinction is less likely for species of these regions than those in the aforementioned categories.

3. Results

3.1. *Turtle-region delineation and hotspots*

3.1.1. *Description and relationships of turtle-regions*

The global distribution of non-marine turtles covers ~77.6 million km^2 (57.5%) of ~135.0 million km^2 of the total global landmass in our dataset. Modeled data from the UPGMA analysis fit the original data well (cophenetic coefficient = 0.862). The UPGMA dendrogram revealed the biogeographical organization of turtle regions (Figs. 1 and 2; Appendix A). The KGS analysis revealed 6 turtle realms and 63 turtle regions nested within these realms. The land size of these turtle regions were highly variable ($\bar{x}$ = 1.23 million km^2, standard deviation = 2.01 million km^2). Turtle realms correspond closely to biogeographical realms defined using freshwater turtle species (*sensu* Bour, 2008) and other taxa, with an exception. The Palearctic turtle-realm was limited to Europe and western Asia, while the eastern portion of the traditional Palearctic biogeographical realm (*sensu* Bour, 2008) was occupied by three turtle regions (i.e., Songhua Jiang-Liao He-Amur-Korea [ID7],

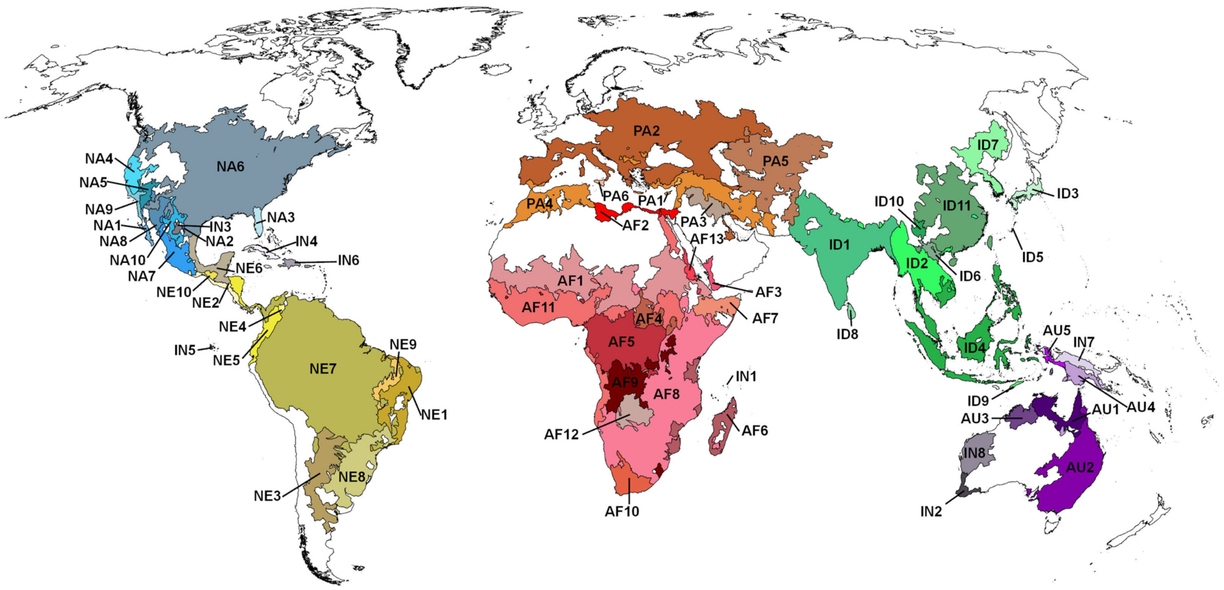


Fig. 1. A map of 63 turtle regions of the world using 342 turtle species and 9029 individual HydroBASINS. Each three-digit code (two letters and a number) represents a turtle-region ID that identifies each turtle region by name (Appendix A; Supplemental Tables A and B). Turtle regions of similar color have relatively similar species composition and comprise turtle realms as follows: Blue (Nearctic), Green (Neotropical), Red (Afrotropical), **Brown** (Palearctic), Yellow (Indomalayan), and Purple (Australasia). Turtle regions shaded grey represent independent, singleton branches that each shares no species with any other turtle region (Fig. 2). Finer resolution maps of each turtle realm are available in the supplemental materials (Supplemental Figures A–F) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

Yangtze-Huang He-Xi Yiang [ID11], and Japan [ID3]) that are contiguous with the traditional Indomalayan (ID) biogeographical realm (Fig. 2). This biogeographical pattern could arise by the lack of eastern dispersal or extinction from Siberia of Palearctic turtles, leaving this area open to colonization from the Indomalayan turtle realm (Barth et al., 2004). That is, the Songhua Jiang-Liao He-Amur-Korea, Yangtze-Huang He-Xi Yiang, and Japan turtle regions represented northward extensions of the Indomalayan turtle realm, east of the Tibetan Plateau, and exemplify the unique and diverse turtle radiation represented in this turtle realm.

The Nearctic (NA) and Neotropical (NE) turtle realms (10 turtle regions each) correspond to the traditional biogeographical realms of the same name and are sister realms for turtles (Figs. 1 and 2). Similarly, the Australasia (AU) turtle realm (five turtle regions) corresponds with the traditional Australasia biogeographical realm and is unaffiliated with other turtle realms (Fig. 2). Singleton (or independent [IN]) branches on the UPGMA dendrogram that did not correspond to any biogeographical realm and were unaffiliated with major turtle realms included islands (e.g., Cuba [IN4], Hispaniola [IN6], Galápagos Islands [IN5], and Aldabra-Seychelles [IN1]) and isolated turtle regions (e.g., Australian Southwestern Coast [IN2] and Pilbara Coastal Drainages [IN8]) of Western Australia (Fig. 2).

We recognize the limitations of displaying all the turtle regions at the global scale in Fig. 1. We provide access to regional maps in the supplemental materials (Supplemental Figures A–F), and online data at https://bit.ly/2GAGCq0; including an interactive map of the turtle-regions with complete summaries of metrics used in this study by turtle-region. As distributional and phylogenetic data for turtles improve, turtle-region boundaries can be updated. Revisions could coincide with future publications of the Turtle Taxonomy Working Group's updated status and distribution compilations.

3.1.2. Turtle hotspot comparison

Our biogeographical approach for delineating turtle regions revealed two categories of the turtle hotspots identified by Mittermeier et al. (2015). The first category consisted of contiguous turtle hotspots that represent individual turtle regions with high α-diversity. Seven of our turtle regions, including Orinoco-Amazon Basin-Tocantinus [NE7], Congo Basin [AF5], Indian Subcontinent [ID1], Tropical Wet/Dry Forest [AF11], East Africa Coast-Madagascar [AF6], Lower Mekong-Malaysia-Indonesia-Philippines [ID4], and Northern Great Karoo-South Africa [AF10], either fully or nearly encompassed an entire turtle-hotspot of Mittermeier et al. (2015). These turtle regions all have high species and endemic-species richness (Supplemental Table A) centered in the hotspot portion of the region. Importantly, we identified two new, previously unrecognized turtle hotspots—Yangtze-Huang He-Xi Yiang [ID11] and Kalahari Basin-Rift Valley [AF8] —each with high α-diversity.

The second hotspot category consisted of nine turtle hotspots (*sensu* Mittermeier et al., 2015) each comprised by multiple turtle regions, which indicates the biodiversity of these turtle hotspots actually reflects inter-regional β diversity. These biogeographically complex turtle hotspots exist within every turtle realm and include the North American Desert Wilderness Area, Southeastern United States, Mesoamerica, north and east Australia, New Guinea, Indo-Burma, and Mediterranean Basin as mapped by Mittermeier et al. (2015). Finally, one turtle hotspot - Tumbes-Chocó-Magdalena – was nearly encompassed by the Mosquitia-Isthmus-Río Atrato-Magdalena [NE5] turtle region. This turtle region substantially overlapped (i.e., shared land area) to the north with another turtle hotspot – Mesoamerican indicating high β diversity between these two Mittermeier et al. (2015) turtle hotspots.

3.2. Turtle-region biodiversity and conservation assessment

3.2.1. Classification tree analysis

The biodiversity classification-tree analyses (Fig. 3a) identified five terminal branches that partition turtle regions by biodiversity metrics: biodiversity nodes 2, 5, 6, and 8-9. Dominant biodiversity metrics useful for classification were logit endemism (used in two nodes), inverse-range endemic (one node), and species richness (one node; Fig. 3a; Table 1). The first partition was dominated by logit endemism (i.e., threshold value of 0.255), partitioning turtle regions into two groups (higher and lower logit endemism). One branch from this first node was terminal with no further branching (terminal branch 2),

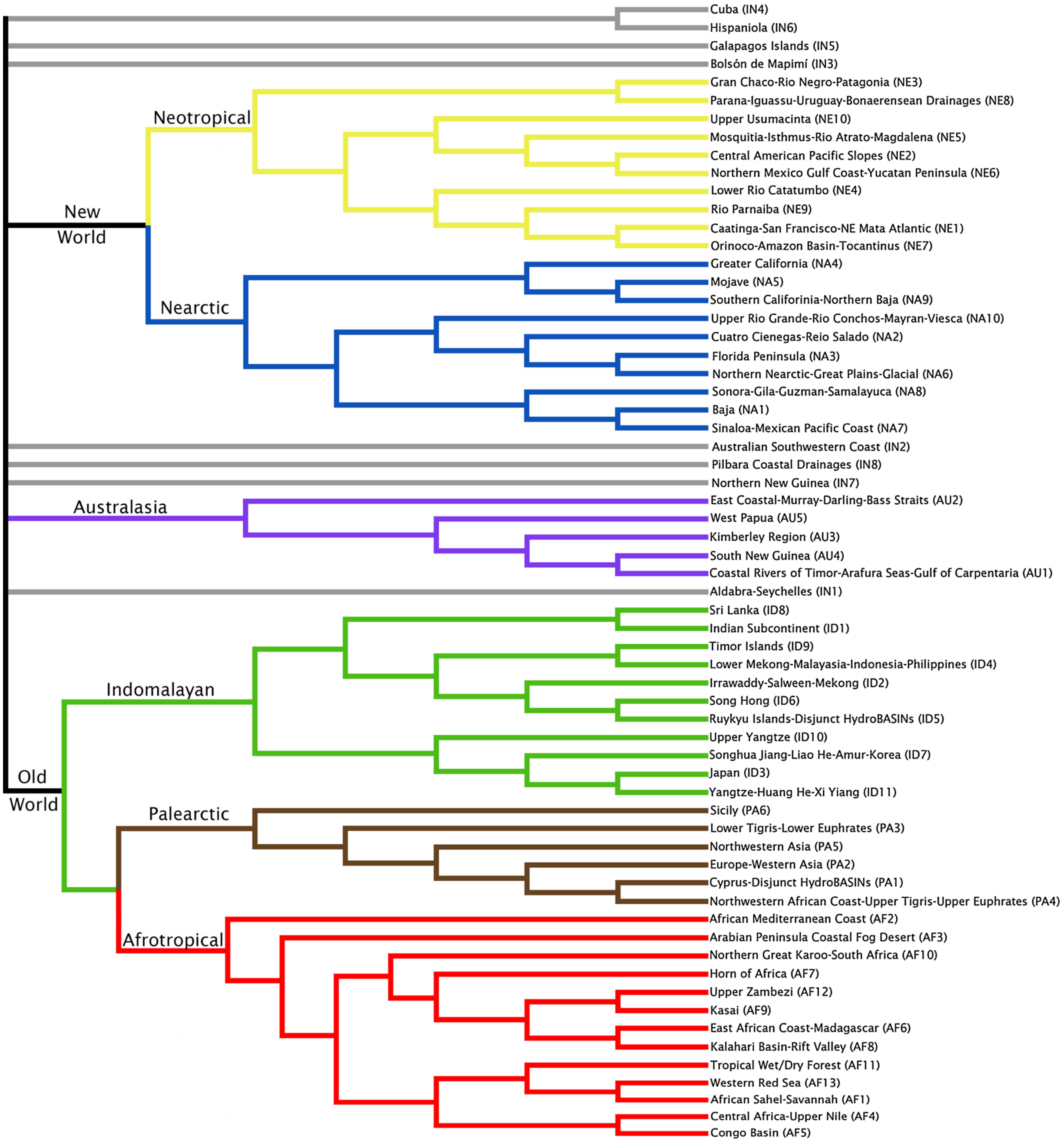


Fig. 2. A simplified dendrogram of overall turnover using unweighted pair-group method with arithmetic averages analysis based on the turnover component of Jaccard's dissimilarity index (βjtu; Baselga, 2012) matrix of 342 turtle species by 9029 HydroBASINS. Each individual branch indicates a unique turtle region identified with a turtle-region name and ID. Defined turtle-region IDs can be found in (Appendix A; Supplemental Tables A and B). Turtle regions of similar color have relatively similar species composition and each broad color classification comprises a turtle realm. New and Old World branches in black are also labeled. Singleton turtle regions (independent branches) in gray share no species with other turtle-regions.

representing seven turtle regions with highest logit endemism (≥ 0.255), predominately from the Independent (or singleton branches) and Australasia turtle realms (Figs. 3a).

The other branch from the first node included remaining turtle regions with logit endemism < 0.255, which were next subdivided based on values of inverse-range endemism (threshold value of 0.023). The branch from this node having lower inverse-range endemism (< 0.023) was further subdivided into regions with higher and lower species richness (threshold value of 9.5). This produced terminal branch 5 consisting of 11 turtle regions with higher species richness (≥ 9.5) dominated by turtle regions from the Afrotropical realm. The other branch from the species-richness node was terminal branch 6, consisting of nine turtle regions with lower species richness (< 9.5), dominated by turtles regions from the Palearctic.

The remaining 36 turtle regions were on the branch from the inverse-range endemic node having higher inverse-range endemism (≥ 0.023), which was further partitioned by logit endemism at a threshold value of -1.533. This logit-endemism node forked into two terminal branches (Fig. 3a). One terminal branch included 21 turtle regions with moderate logit endemism (≥ -1.533, but < 0.255), largely within the Afrotropical and Neotropical turtle realms, but all realms were represented to some degree (Fig. 3a). The other terminal branch included 15 turtle regions with low logit endemism (< -1.533), largely from the Nearctic turtle realm (Fig. 3a).

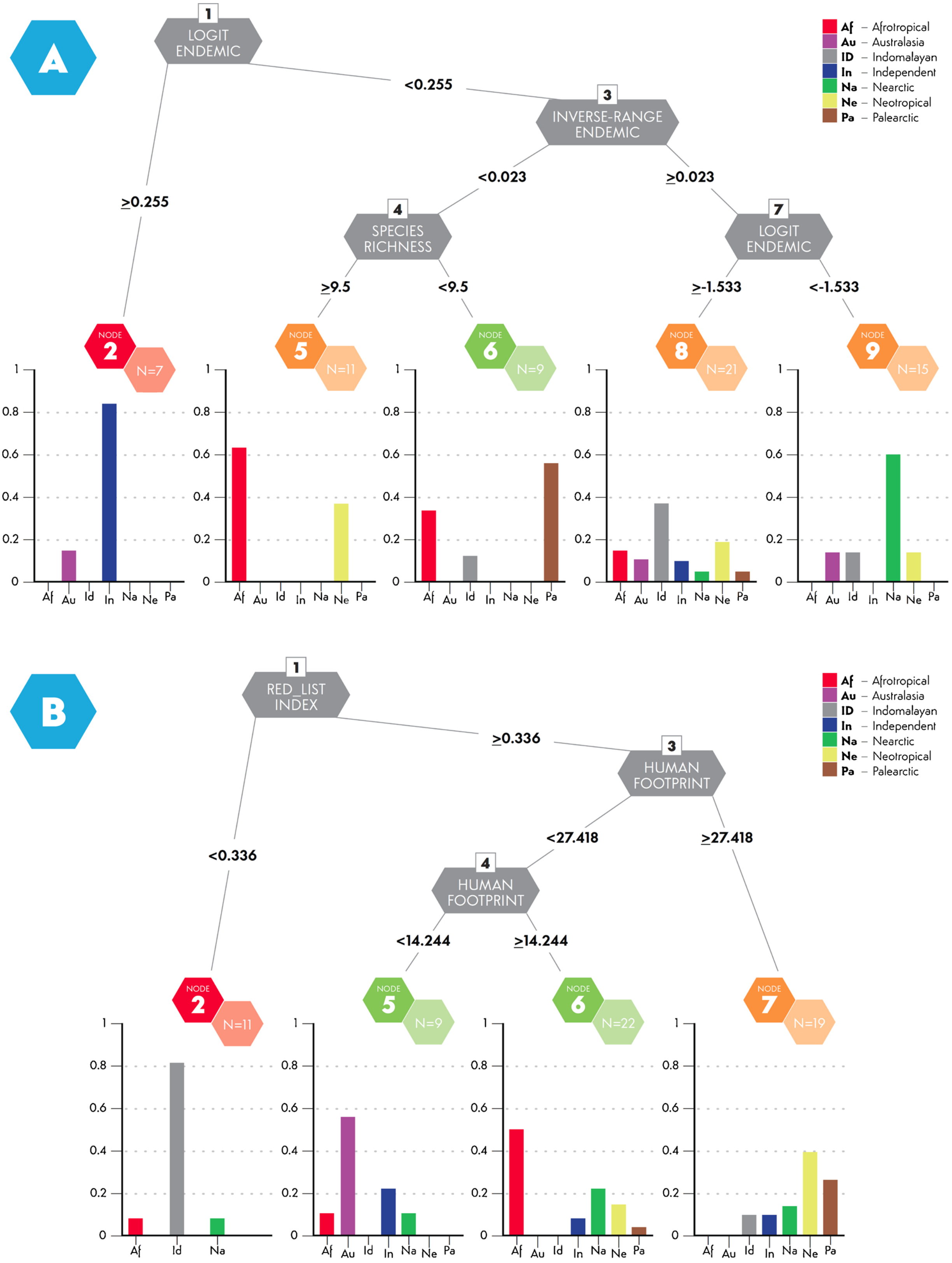


Fig. 3. Results of the classification-tree analyses for turtle-region biodiversity (a) and conservation (b) parameters. The barplots represent the proportion of each branch (y-axis) represented by turtle regions of each turtle realm (x-axis; color scheme corresponds with Figs. 1 and 2). Note, species-density and endemic-density values were multiplied by 1000 to reduce significant digits for display in the figure. Color of the branch tips corresponds to colors of cells within Fig. 4 because results of the classification-tree analyses were used to determine conservation priorities. Also, the numbers within the hexagons correspond with the numbered hexagons in Fig. 4.

Table 1
The mean and standard deviation for five biodiversity metrics by terminal node based on the classification tree analysis. Acronyms are defined as follows: species richness (SR), endemic richness (ER), logit endemism (EN), species density (SD), endemic-species density (ED), species richness per HydroBASIN (SRH), and inverse-range endemism (RE).

Biodiversity node	SR	ER	EN	SD	ED	SRH	RE
Node 2	5.00 ± 5.20	4.29 ± 4.64	1.31 ± 0.93	0.001 ± 0.002	0.001 ± 0.002	0.45 ± 4.00	3.04 ± 0.42
Node 5	15.64 ± 6.33	0.82 ± 1.08	−2.70 ± 0.64	1.35E-05 ± 9.94E-06	3.45E-07 ± 4.52E-07	0.01 ± 0.84	3.343 ± 0.006
Node 6	5.22 ± 2.77	0.33 ± 0.50	−1.85 ± 0.99	1.79E-05 ± 3.18E-05	6.23E-07 ± 1.03E-06	0.01 ± 0.36	1.66 ± 0.006
Node 8	13.86 ± 15.45	4.43 ± 5.92	−0.56 ± 0.57	5.31E-05 ± 8.38E-05	1.50E-05 ± 1.59E-05	0.12 ± 2.28	3.68 ± 0.12
Node 9	12.07 ± 11.76	0.93 ± 1.91	−2.28 ± 0.70	7.16E-05 ± 9.79E-05	2.54E-06 ± 5.77E-06	0.06 ± 3.37	4.02 ± 0.05

The conservation classification-tree analysis (Fig. 3) identified four terminal branches (i.e., conservation branches 2, 5, 6, and 7). The IUCN Red List Index (RLI) was the dominant conservation metric partitioning turtle regions into two main branches. At this first node, turtle regions subdivided at an RLI threshold of 0.336. One fork was a terminal branch, conservation branch 2, including 11-highly-threatened turtle-regions with RLI values < 0.336, predominately in the Indomalayan turtle realm.

The other fork from the RLI node represented turtle regions with fewer threatened species (RLI values ≥ 0.336). This fork branched based on human footprint (Fig. 3b; Table 2) at a threshold value of 27.418. The branch from this node representing higher human footprint (≥ 27.418) was a terminal branch including 19-turtle-regions (conservation branch 7), representing regions in mostly the Neotropical and Palearctic realms, but also the Indomalayan, Independent, and Nearctic realms to a lesser degree (Fig. 3b). The other branch representing lower human footprint (< 27.418) included the remaining 31 turtle regions, which were further split by a second human-footprint threshold, this time of 14.244. This node forked into two terminal branches: terminal branch 5 representing 9 turtle regions with lowest human-footprint (< 14.244), largely including the Australasia realm; and terminal branch 6 representing 22 turtle regions with moderate human-footprint (≥ 14.244 but < 27.418), largely including Afrotropical realms.

3.2.2. *Conservation prioritization of turtle regions*

According to our preliminary conceptualization of prioritization proposed above (Section 2.2.3), turtle-regions with highest conservation priority have high logit endemism values (≥ 0.255) or high inverse-range endemic values (≥ 0.023) (terminal biodiversity branches 2, 8, and 9) combined with low RLI terminal conservation branch 2; Fig. 4). These proposed high-priority turtle regions include Irrawaddy-Salween-Mekong [ID2], Arabian Peninsula Coastal Fog Desert [AF3], Upper Yangtze [ID10], Timor Island [ID9], Ryukyu Island-Disjunct HydroBASINs [ID5], Indian Subcontinent [ID1], Lower Mekong-Malaysia-Indonesia-Philippines [ID4], Yangtze-Huang He-Xi Yiang [ID11], Song Hong (Vietnam/China) [ID6], and Southern California-Northern Baja [NA9] (Table 3). Although removed from the conservation analysis for missing data (i.e., human footprint and economic value of land), Galápagos Islands [IN5] had the highest logit endemism value (3.22) and a very low RLI (0.187) and thus we believe should also be considered a high-priority turtle region for conservation.

Notably, this analysis revealed two previously overlooked global turtle hotspots that also have high α-diversity and highest conservation concern. First is the Yangtze-Huang He-Xi Yiang turtle region in China (turtle-region ID 11, Appendix A, Fig. 1). This turtle region harbors 24 turtle species, four of which are endemics. Second is the Kalahari Basin-Rift Valley turtle region (ID AF8). This turtle region harbors 30 turtle species, three of which are endemics.

Turtle regions with intermediate conservation priority also have high logit endemism values (≥ 0.255) or high inverse-range endemic values (≥ 0.023) (terminal biodiversity branches 2, 8, and 9), but have relatively high RLI values (≥ 0.336) that indicate lower imperilment, but nevertheless suffer from high human footprint (≥ 27.418, terminal conservation branch 7; Fig. 4). For example, several island turtle regions, including Cuba [IN4], Hispaniola [IN6], Japan [ID3], Sri Lanka [ID8], and Sicily [PA6], were considered intermediate conservation priorities because all had high or moderate logit endemism (i.e., biodiversity node 8 and 9) and high human footprint (i.e., conservation node 7). Similarly, nine continental turtle regions had intermediate priority, all of which had high or moderate logit endemism and human footprint (Table 3; Fig. 4). Most of these turtle regions were in the complex biogeographical area encompassing the transition zone between the Nearctic and Neotropical turtle realms. Finally, we also propose the Songhua Jiang-Liao He-Amur-Korea turtle region [ID7] as an intermediate conservation priority. This turtle region was highly threatened (i.e., conservation branch 2), which elevated its overall priority even though it has relatively low values for logit endemism (< 0.255) and inverse-range endemic (< 0.023) and species richness (< 9.5) metrics (i.e., biodiversity node 6).

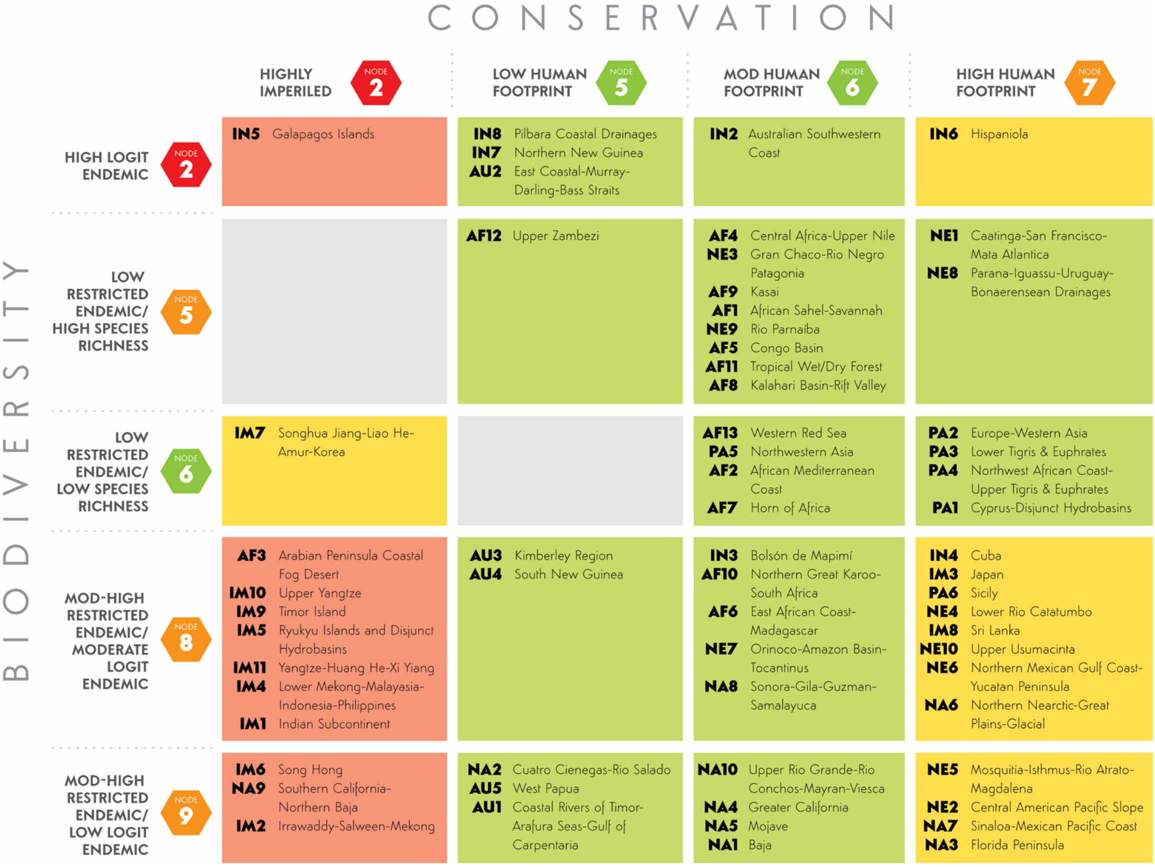
4. Discussion

4.1. *Turtle regions versus turtle hotspots*

The regional perspective provided by this study reveals two distinct categories of turtle hotspots, which suggests a modification is needed for the framework presented by Mittermeier et al. (2015). On one hand, this study identifies several turtle regions with high α-diversity, seven of which fully encompass previously described turtle hotspots (*sensu* Mittermeier et al., 2015). For all of these high α-diversity turtle regions, hotspot-focused conservation should effectively preserve regional turtle diversity. However, global warming and sea-level rise threaten to alter suitability and spatial extent of hotspots, in which case, identification of adjacent regional boundaries associated with hotspots identifies areas naturally available for species responding to these stressors. Such areas could gain increasing conservation significance over time (Ihlow et al., 2012; Agha et al., 2018). On the other hand, some hotspots were revealed as inter-regional areas, representing high β-diversity among

Table 2
The mean and standard deviation from the four conservation metrics by terminal node based on the classification tree analysis (Fig. 3). Acronyms are defined as follows: Red List Index (RLI), economic value of land (EVL), human footprint (HFP), and sea-level rise (SLR).

Conservation node	RLI	EVL	HFP	SLR
Node 2	0.18 ± 0.08	117.43 ± 91.05	30.04 ± 4.25	2.27 ± 3.21
Node 5	0.75 ± 0.17	21.33 ± 28.74	9.56 ± 3.87	3.63 ± 4.89
Node 6	0.62 ± 0.16	38.33 ± 22.35	19.18 ± 3.21	0.74 ± 0.85
Node 7	0.7 ± 0.1	156.77 ± 143.91	35.74 ± 5.89	7.09 ± 12.61



CONSERVATION

BIODIVERSITY

	HIGHLY IMPERILED NODE 2	LOW HUMAN FOOTPRINT NODE 5	MOD HUMAN FOOTPRINT NODE 6	HIGH HUMAN FOOTPRINT NODE 7
HIGH LOGIT ENDEMIC NODE 2	**IN5** Galapagos Islands	**IN8** Pilbara Coastal Drainages **IN7** Northern New Guinea **AU2** East Coastal-Murray-Darling-Bass Straits	**IN2** Australian Southwestern Coast	**IN6** Hispaniola
LOW RESTRICTED ENDEMIC/ HIGH SPECIES RICHNESS NODE 5		**AF12** Upper Zambezi	**AF4** Central Africa-Upper Nile **NE3** Gran Chaco-Rio Negro Patagonia **AF9** Kasai **AF1** African Sahel-Savannah **NE9** Rio Parnaiba **AF5** Congo Basin **AF11** Tropical Wet/Dry Forest **AF8** Kalahari Basin-Rift Valley	**NE1** Caatinga-San Francisco-Mata Atlantica **NE8** Parana-Iguassu-Uruguay-Bonaerensean Drainages
LOW RESTRICTED ENDEMIC/ LOW SPECIES RICHNESS NODE 6	**IM7** Songhua Jiang-Liao He-Amur-Korea		**AF13** Western Red Sea **PA5** Northwestern Asia **AF2** African Mediterranean Coast **AF7** Horn of Africa	**PA2** Europe-Western Asia **PA3** Lower Tigris & Euphrates **PA4** Northwest African Coast-Upper Tigris & Euphrates **PA1** Cyprus-Disjunct Hydrobasins
MOD-HIGH RESTRICTED ENDEMIC/ MODERATE LOGIT ENDEMIC NODE 8	**AF3** Arabian Peninsula Coastal Fog Desert **IM10** Upper Yangtze **IM9** Timor Island **IM5** Ryukyu Islands and Disjunct Hydrobasins **IM11** Yangtze-Huang He-Xi Yiang **IM4** Lower Mekong-Malayasia-Indonesia-Philippines **IM1** Indian Subcontinent	**AU3** Kimberley Region **AU4** South New Guinea	**IN3** Bolsón de Mapimí **AF10** Northern Great Karoo-South Africa **AF6** East African Coast-Madagascar **NE7** Orinoco-Amazon Basin-Tocantinus **NA8** Sonora-Gila-Guzman-Samalayuca	**IN4** Cuba **IM3** Japan **PA6** Sicily **NE4** Lower Rio Catatumbo **IM8** Sri Lanka **NE10** Upper Usumacinta **NE6** Northern Mexican Gulf Coast-Yucatan Peninsula **NA6** Northern Nearctic-Great Plains-Glacial
MOD-HIGH RESTRICTED ENDEMIC/ LOW LOGIT ENDEMIC NODE 9	**IM6** Song Hong **NA9** Southern California-Northern Baja **IM2** Irrawaddy-Salween-Mekong	**NA2** Cuatro Cienegas-Rio Salado **AU5** West Papua **AU1** Coastal Rivers of Timor-Arafura Seas-Gulf of Carpentaria	**NA10** Upper Rio Grande-Rio Conchos-Mayran-Viesca **NA4** Greater California **NA5** Mojave **NA1** Baja	**NE5** Mosquitia-Isthmus-Rio Atrato-Magdalena **NE2** Central American Pacific Slope **NA7** Sinaloa-Mexican Pacific Coast **NA3** Florida Peninsula

Fig. 4. A matrix displaying biodiversity and conservation terminal branches from the classification-tree analyses (Fig. 3). Global turtle regions (with ID numbers) are listed within the matrix according to their placement on branches within the biodiversity (rows) and conservation (columns) classification trees. Turtle regions with red highlight are highest conservation priorities because of high biodiversity and threatened species. Turtle regions with yellow highlight are considered intermediate because of high biodiversity with either high human footprint or threatened species. The colored and numbered hexagons correspond with classification-tree branches in Fig. 3. Although excluded from the classification-tree analyses due to missing data, we manually inserted the Galápagos Islands turtle region into this matrix, based on its high logit endemism and low RLI relative to other turtle regions. Empty cells, colored gray, have no turtle regions (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

contiguous regions, a scenario more complex than the concept of a simple hotspot. This distinction is new and has global implications for inter-regional conservation.

Our systematic assessment prioritizes two new turtle hotspots with high α-diversity (i.e., Yangtze-Huang He-Xi Jiang and Kalahari Basin-Rift Valley). The recognition of two new turtle hotspots highlights the value of our objective biogeographical framework to delineate clade-specific regions for conservation. Recently, other clade-specific approaches have identified new hotspots for other animal groups, in particular a new bird-derived hotspot was recently identified in China (Hu et al., 2017) which, notably, overlaps considerably with the Yangtze-Huang He-Xi Jiang turtle region identified here. The Kalahari Basin-Rift Valley turtle hotspot encompasses the Eastern Afromontane biodiversity hotspot (Plumptre et al., 2007; Mittermeier et al., 2011); however, this turtle-derived hotspot was much larger in area than the Eastern Afromontane hotspot. The conservation value of this newly identified African turtle hotspot will likely increase further as new species descriptions continue to be published from this region (TTWG, 2017).

The remaining nine turtle hotspots (*sensu* Mittermeier et al., 2015) are identified here to span multiple turtle regions, indicating the biodiversity of these turtle hotspots actually reflects inter-regional β diversity. Notably, the adjacent Mesoamerican and North American Desert Wilderness Area turtle hotspots described previously include portions of multiple turtle regions. The broad area encompassing these turtle regions includes the Nearctic-Neotropical transition zone where inter-area species turnover is prominent (Buhlmann et al., 2009; Rodrigues and Diniz-Filho, 2017) and represents a major transition zone for North American turtles (Ennen et al., 2017).

Our study revealed that turtle hotspots (*sensu* Mittermeier et al., 2015) with the highest α-diversity (i.e., Indo-Burma and Southeastern USA turtle hotspots) consist of overlapping multiple turtle regions as well. These areas are not prominent transition zones for turtles, but likely represent unique evolutionary histories (i.e., radiation, extinction, and dispersal), creating high species turnover among the regions within the hotspots (Bentley and Knight, 1998). Thus, in multi-regional turtle hotspots, preservation of collective turtle diversity requires conservation efforts in each of multiple contributing regions.

4.2. Regions of concern for global turtle conservation

Another important finding is that turtle regions with high conservation value occur worldwide (Fig. 4; Table 3). Conservation opportunities of highest global importance identified here exist mostly in the Indomalayan turtle realm and on islands and archipelagoes therein, which agrees with other recent conservation assessments of turtles (Rhodin et al., 2018). Conservation concern for many Indomalayan turtle regions is notable as well because of the Asian Turtle Crisis, fueled by unsustainable trade and consumption of turtles (Rhodin et al., 2018). Unfortunately, turtle biodiversity hotspots, such as turtle regions in the Indomalayan, have both high human disturbance and economic value of land (Supplemental Table A), which poses a large hurdle for

Table 3
Prioritization (i.e., high or intermediate) of turtle region based on the classification tree analyses (Fig. 3) including biogeographical turtle realm and turtle region identification (ID). Turtle region identification (turtle region ID) uniquely identifies each turtle-region on Figs. 1 and 2, and these identifiers are defined in Appendix A and Supplemental Tables A and B. All other turtle regions not listed are considered low conservation priorities.

Priority	Biogeographical realm	Turtle region	Turtle region ID
High			
	Independent	Galapagos Islands	IN5
	Indomalayan	Indian Subcontinent	ID1
	Indomalayan	Irrawaddy-Salween-Mekong	ID2
	Indomalayan	Lower Mekong-Malayasia-Indonesia-Philippines	ID4
	Indomalayan	Ruykyu Islands-Disjunct Hydrobasins	ID5
	Indomalayan	Song Hong	ID6
	Indomalayan	Timor Island	ID9
	Indomalayan	Upper Yangtze	ID10
	Indomalayan	Yangtze-Huang He-Xi Yiang	ID11
	Nearctic	Southern California-Northern Baja	NA9
	Afrotropical	Arabian Peninsula Coastal Fog Desert	AF3
Intermediate			
	Independent	Cuba	IN4
	Independent	Hispaniola	IN6
	Indomalayan	Japan	ID3
	Indomalayan	Songhua Jiang-Liao He-Amur-Korea	ID7
	Indomalayan	Sri Lanka	ID8
	Nearctic	Florida Peninsula	NA3
	Nearctic	Northern Nearctic-Great Plains-Glacial	NA6
	Nearctic	Sinaloa-Mexican Pacific Coast	NA7
	Neotropical	Central American Pacific Slope	ME2
	Neotropical	Lower Rio Catatumbo	NE4
	Neotropical	Mosquitia-Isthmus-Rio Atrato-Magdalena	NE5
	Neotropical	Northern Mexican Gulf Coast-Yucatan Peninsula	NE6
	Neotropical	Upper Usumacinta	NE10
	Neotropical	Sicily	PA6

conservation initiatives. Highest conservation concern for many island and insular turtle regions is further emphasized by the fact that 9 of 10 modern turtle species listed as extinct (excluded from this study) were endemic to islands (TEWG, 2015; Butler et al., 2016; Rhodin et al., 2018). An 11th species became functionally extinct in April of 2019 with the death of the last known female Yangtze River giant soft-shelled turtle (*Rafetus swinhoei*).

A goal of no future turtle extinctions implies that conservation efforts in all turtle-regions are needed (Buhlmann et al., 2009; Mittermeier et al., 2015). Continental turtle regions include several main centers of turtle biodiversity. Although many of these have relatively moderate or low imperilment, many are impacted by high human footprint, which increases their conservation concern and suggest imperilment may soon emerge (Supplemental Table A). Examples of this are turtle regions in the Central American transition zone between the Nearctic and Neotropical Realms. Collectively, these turtle regions are inhabited by numerous species, including endemic species, many of which are data deficient (Macip-Ríos et al., 2015). In general, endemic reptiles (i.e., restricted-range habitat specialists) inhabiting areas in close proximity to humans are more threatened with extinction (Böhm et al., 2016). In these areas, conservation opportunities may be geographically widespread and many different habitats may need conservation attention. Furthermore, the spatial scale and geographic complexity of conservation may increase for turtles with greater tendencies for dispersal (Fachín-Terán et al., 2006) or higher sensitivity to habitat fragmentation (Rizkalla and Swihart, 2006). This is especially true for sea turtles (not included in our analyses) because of their global migration (Mazaris et al., 2017). Adjacent areas, especially turtle regions to the north, could become important for turtle diversity as the climate responds to anthropogenic forcing (Ihlow et al., 2012; Rödder et al., 2013; Agha et al., 2018).

Finally, levels of conservation concern may differ between global, regional, and local spatial scales (Macip-Ríos et al., 2015), indicating a need for concerted and coordinated multi-scale assessments. That is, a designation of lowest conservation value for a given turtle region in the global analysis presented here does not preclude the presence of important conservation concerns within each region for two reasons. First, turtles exhibit strong regionalization at the global scale (Rodrigues and Diniz-Filho, 2017), meaning that distinct species-poor turtle regions have unique evolutionary and ecological properties that should be worth conserving (De Klerk et al., 2002). At smaller spatial scales, for instance, widespread species commonly exhibit phylogeographical structure that can only be conserved with population-level conservation (e.g., Spinks and Shaffer, 2005; Rödder et al., 2013; Sethuraman et al., 2014; Stuckas et al., 2014). Peripheral populations also may rely on refugial habitats that are themselves significant to regional biodiversity (Sommer et al., 2009, 2011; Jensen et al., 2014).

5. Conclusions

In this assessment of turtle biogeography, we identified a set of turtle-regions that reflected high to moderate conservation concern as they harbored faunas characterized by high endemism and range restriction coupled with either high imperilment among species (proposed highest priority) or with high human footprint (proposed intermediate priority). Overall, our clade-specific approach spatially delineated global regions unique to turtles. Our results revealed that prevailing, somewhat subjective, systems used to identify priority turtle-regions areas can result in conservation gaps, as we not only identified known hotspots but also documented two additional hotspots using a more objective method. Moreover, by developing a regional framework that scales down the global fauna of non-marine turtles and compliments traditional conservation prioritization methods, we hope these findings and our preliminary prioritization provide a spatially informed template for conservationists worldwide. Specifically, we propose the findings can point conservation planners with taxonomically limited but geographically flexible conservation funding to regions most in need of help. Further, we hope the findings are useful for conservationists living and/or working within high or intermediate priority regions, for helping demonstrate the global significance of their turtle faunas. Finally, while our systematic conservation prioritization approach provides novel insights that are intended to directly benefit turtles, this framework is flexible and can also be used as an objective approach for identifying global and regional conservation gaps for other imperiled taxonomic groups.

Declaration of Competing Interest

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

Acknowledgements

We thank the Tennessee Aquarium for financial support and providing other resources for this project. We are grateful to B. Riddle and two anonymous reviewers for providing helpful comments on an earlier draft of this manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.biocon.2019.108323.

References

Abell, R., Thieme, M.L., Revenga, C., Bryer, M., Kottelat, M., Bogutskaya, N., Coad, B., Mandrak, N., Balderas, S.C., Bussing, W., Stiassny, M.L.J., Skelton, P., Allen, G.R., Unmack, P., Naseka, A., Ng, R., Sindorf, N., Robertson, J., Armijo, E., Higgins, J.V., Heibel, T.J., Wikramanayake, E., Olson, D., López, H.L., Reis, R.E., Lundberg, J.G., Sabaj Pérez, M.H., Petry, P., 2008. Freshwater ecoregions of the world: a new map of biogeographic units for freshwater biodiversity conservation. BioScience 58, 403–414.

Agha, M., Ennen, J.R., Bowever, D.S., Nowakowski, A.J., Sweat, S.C., Todd, B.D., 2018. Salinity tolerance and use of saline environments by freshwater turtles: implications of sea level rise. Biol. Rev. 93, 1634–1648.

Angielczyk, K.D., Burroughs, R.W., Feldman, C.R., 2015. Do turtles follow the rules? Latitudinal gradients in species richness, body size, and geographic range area of the world's turtles. J. Exp. Zool. B Mol. Dev. Evol. 324 1–1-25.

Arrhenius, O., 1921. Species and area. J. Ecol. 9, 95–99.

Barnosky, A.D., Matzke, N., Tomiya, S., Wagan, G.O., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57.

Barth, D., Bernhard, D., Fritzsch, G., Fritz, U., 2004. The freshwater turtle genus *Mauremys* (Testudines, Geoemydidae) - a textbook example of an east-west disjunction or a taxonomic misconcept. Zool. Scr. 33, 213–221.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143.

Baselga, A., 2012. The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Glob. Ecol. Biogeogr. 21, 1223–1232.

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., 2018. Betapart-package: Partitioning Beta Diversity Into Turnover and Nestedness Components. R. Package Version 1.5.0. https://cran.r-project.org/web/packages/betapart/betapart.pdf.

Basile, E.R., Avery, H.W., Bien, W.F., Keller, J.M., 2011. Diamondback terrapins as indicator species of persistent organic pollutants: using Barnegat Bay, New Jersey as a case study. Chemosphere 82, 137–144.

Battisti, C., Luiselli, L., 2011. Selecting focal species in ecological network planning following an expert-based approach: Italian reptiles as a case study. J. Nat. Conserv. 19, 126–130.

Bentley, C.C., Knight, J.L., 1998. Turtles (Reptilia: Testudines) of the Ardis Local Fauna Late Pleistocene (Rancholabrean) of South Carolina. Brimleyana 25, 3–33.

Böhm, M., Williams, R., Bramhall, H.R., McMillian, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Bour, R., 2008. Global diversity of turtles (Chelonii; Reptilia) in freshwater. Hydrobiologia 595, 593–598.

Bubb, P.J., Butchart, S.H.K., Collen, B., Dublin, H., Kapos, V., Pollock, C., Stuart, S.N., Vie, J.-C., 2009. IUCN Red List Index - Guidance for National and Regional Use. IUCN.

Buhlmann, K.A., Akre, T.S.B., Iverson, J.B., Karapatakis, D., Mittermeier, R.A., Georges, A., Rhodin, A.G.J., van Dijk, P.P., Gibbons, J.W., 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. Chelonian Conserv. Biol. 8, 116–149.

Butler, C.J., Stanila, B.D., Iverson, J.B., Stone, P.A., 2016. Projected changes in climatic suitability for *Kinosternon* turtles by 2050 and 2070. Ecol. Evol. 6, 7690–7705.

Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., Purvis, A., 2008. The predictability of extinction: biological and external correlations of decline in mammals. Proc. R. Soc. B: Biol. Sci. 275, 1441–1448.

Catano, C.P., Stout, I.J., 2015. Functional relationships reveal keystone effects of the gopher tortoise on vertebrate diversity in longleaf pine savanna. Biodivers. Conserv. 24, 1957–1974.

De'ath, G., Fabricius, K.A., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178–3192.

De Klerk, H.M., Crowe, T.M., Fjeldså, J., Burgess, N.D., 2002. Biogeographical patterns of endemic terrestrial Afrotropical birds. Divers. Distrib. 8, 147–162.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J., Collen, B., 2014. Defaunation in the anthropocene. Science 345, 401–406.

Ennen, J.R., Agha, M., Matamoros, W.A., Hazzard, S.C., Lovich, J.E., 2016. Using climate, energy, and spatial-based hypotheses to interpret macroecological patterns of North American chelonians. Can. J. Zool. 94, 453–461.

Ennen, J.R., Matamoros, W.A., Agha, M., Lovich, J.E., Sweat, S.C., Hoagstrom, C.W., 2017. Hierarchical, quantitative biogeographic provinces for all North American Turtles and their contribution to the biogeography of turtles and the continent. Herpetol. Monogr. 31, 114–140.

Fa, J.E., Funk, S.M., 2007. Global endemicity centres for terrestrial vertebrates: an ecoregion approach. Endanger. Species Res. 3, 31–42.

Fachín-Terán, A., Vogt, R.C., Thorbjarnarson, J.B., 2006. Seasonal movements of *Podocnemis sextuberculata* (Testudines: Podocnemididae) in the Mamirauá Sustainable Development Reserve, Amazonas, Brazil. Chelonian Conserv. Biol. 5, 18–24.

Farris, J.S., 1969. On the cophenetic correlation coefficient. Syst. Biol. 18, 279–285.

Funk, S.M., Fa, J.E., 2010. Ecoregion prioritization suggests an armoury not silver bullet for conservation planning. PLoS One 5, eB923.

Hattab, T., Albouy, C., Lasram, F.B.R., Le Loc'h, F., Guilhaumon, F., Leprieur, F., 2015. A biogeographical regionalization of Mediterranean fishes. J. Biogeogr. 42, 1336–1348.

Heppell, S.S., 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998, 367–375.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., et al., 2010. The impact of conservation on the status of the world's vertebrates. Science 330, 1503–1509.

Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, Rahbek, C., 2013. An update of Wallace's zoogeographic regions of the world. Science 339, 74–78.

Hu, R., Wen, C., Gu, Y., Wang, H., Gu, L., Shi, X., Zhong, J., Wei, M., He, F., Lu, Z., 2017. A bird's view of new conservation hotspots in China. Biol. Conserv. 211, 47–55.

Hüber, M., 2019. How trade in ecotourism services can save nature: a policy scenario analysis. Dev. South. Afr. 36, 127–143.

Ihlow, F., Dambach, J., Engler, J.O., Flecks, M., Hartmann, T., Nekum, S., Rajaei, H., Rödder, D., 2012. On the brink of extinction? How climate change may affect global chelonian species richness and distribution. Glob. Chang. Biol. 18, 1520–1530.

Jensen, E.L., Govindarajulu, P., Russello, M.A., 2014. When the shoe doesn't fit: applying conservation unit concepts to Western Painted Turtles at their northern periphery. Conserv. Genet. 15, 261–274.

Joyce, W.G., Parham, J.F., Lyson, T.R., Warnock, R.C.M., Donoghue, P.C.J., 2013. A divergence dating analysis of turtles using fossil calibrations: an example of best practices. J. Paleontol. 87, 612–634.

Kier, G., Barthlott, W., 2001. Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. Biodivers. Conserv. 10, 1513–1529.

Kreft, H., Jetz, W., 2010. A framework for delineating biogeographical regions based on species distributions. J. Biogeogr. 37, 2029–2053.

Ladle, R.J., Whittaker, R.J., 2011. Conservation Biogeography. Wiley-Blackwell, Oxford, UK.

Lehner, B., Grill, G., 2013. Global river hydrography and network routing: baseline data and new approaches to study the world's large river systems. Hydrol. Process. 27, 2171–2186.

Leroy, B., Dias, M.S., Giraud, E., Hugueny, B., Jezequel, C., Leprieur, F., Oberdorff, T., Tedesco, P.A., 2018. Global biogeographical regions of freshwater fishes. bioRxiv, 319566.

Lovich, J.E., Ennen, J.R., Agha, M., Gibbons, J.W., 2018. Where have all the turtles gone, and why does it matter? BioScience 68, 771–781.

Macip-Ríos, R., Ontiveros, R., López-Alcaide, S., Casas-Andreu, G., 2015. The conservation status of the freshwater and terrestrial turtles of Mexico: a critical review of biodiversity conservation strategies. Rev. Mex. Biodivers. 86, 1048–1057.

Matamoros, W.A., Kreiser, B.R., Schaefer, J.F., 2012. A delineation of nuclear middle America biogeographical provinces based on river basin faunistic similarities. Rev. Fish Biol. Fish. 22, 351–365.

Mazaris, A.D., Schofield, G., Gkazinou, C., Almpanidou, V., Hays, G.C., 2017. Global sea turtle conservation success. Sci. Adv. 3, e1600730.

McCune, B., Grace, J.B., 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach, Oregon, USA.

McNeely, J.A., 1998. Economics and Biological Diversity: Developing and Using Economic Incentives to Conserve Biological Resources. IUCN.

Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots. In: Zachos, F.E., Habel, J.C. (Eds.), Biodiversity Hotspots. Springer-Verlag, Berlin, Germany, pp. 3–22.

Mittermeier, R.A., van Dijk, P.P., Rhodin, A.G.J., Nash, S.D., 2015. Turtle hotspots: an analysis of the occurrence of tortoise and freshwater turtles in biodiversity hotspots, high-biodiversity wilderness areas, and turtle priority areas. Chelonian Conserv. Biol. 14, 2–11.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Naidoo, R., Iwamura, T., 2007. Global-scale mapping of economic benefits from agricultural lands: implications for conservation priorities. Biol. Conserv. 140, 40–49.

Olson, D.M., Dinerstein, E., 2002. The global 200: priority ecoregions for global conservation. Ann. Mo. Bot. Gard. 89, 199–224.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Yumiko, Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51, 933–938.

Plumptre, A.J., Davenport, T.R.B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J.K., Pilgrim, J.D., Wilson, M., Languy, M., Moyer, D., 2007. The biodiversity of the albertine rift. Biol. Conserv. 134, 178–194.

Price, A.R.G., 2002. Simultaneous 'hotspot' and 'coldspots' of marine biodiversity and implications for global conservation. Mar. Ecol. Prog. Ser. 241, 23–27.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000. Predicting extinction risk in declining species. Proc. R. Soc. B: Biol. Sci. 267, 1947–1952.

R Core Team, 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org/.

Rhodin, A.G.J., Stanford, C.B., van Dijk, P.P., Eisemberg, C., Luiselli, L., Mittermeier, R.A., Hudson, R., Horne, B.D., Goode, E.V., Kuchling, G., Walde, A., Baard, E.H.W., Berry, K.H., Bertolero, A., Blanck, T.E.G., Bour, R., Buhlmann, K.A., Cayot, L.J., Collett, S., Currylow, A., Das, I., Diagne, T., Ennen, J.R., Forero-Medina, G., Frankel, M.G., Fritz, U., García, G., Gibbons, J.W., Gibbons, P.M., Shiping, G., Guntoro, J., Hofmeyr, M.D., Iverson, J.B., Kiester, A.R., Lau, M., Lawson, D.P., Lovich, J.E., Moll, E.O., Páez, V.P., Palomo-Ramos, R., Platt, K., Platt, S.G., Pritchard, P.C.H., Quinn, H.R., Rahman, S.C., Randrianjafizanaka, S.T., Schaffer, J., Selman, W., Shaffer, H.B., Sharma, D.S.K., Haitao, S., Singh, S., Spencer, R., Stannard, K., Sutcliffe, S., Thomson, S., Vogt, R.C., 2018. Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conserv. Biol. 17, 135–161.

Richardson, D.M., Whittaker, R.J., 2010. Conservation biogeography – foundations, concepts and challenges. Divers. Distrib. 16, 31–320.

Rizkalla, C.E., Swihart, R.K., 2006. Community structure and differential responses of aquatic turtles to agriculturally induced habitat fragmentation. Landsc. Ecol. 21, 1361–1375.

Rödder, D., Lawning, A.M., Flecks, M., Ahmadzadeh, F., Dambach, J., Engler, J.O., Habel, J.C., Hartmann, T., Hornes, D., Ihlow, F., Schidelko, K., Stiels, D., Polly, P.D., 2013. Evaluating the significance of paleophylogeographic species distribution models in reconstructing Quaternary range-shifts of Nearctic chelonians. PLoS One 8, e72855.

Rodrigues, J.F.M., Diniz-Filho, J.A.F., 2017. Dispersal is more important than climate in structuring turtle communities across different biogeographical realms. J. Biogeogr. 44, 2109–2120.

Rodrigues, J.F.M., Olalla-Tárraga, M.Á., Iverson, J.B., Akre, T.S.B., Diniz-Filho, J.A.F., 2017. Time and environment explain the current richness distribution of non-marine turtles worldwide. Ecography 40, 1402–1411.

Roll, U., Feldman, A., Novosolov, M., Allison, A., Bauer, A.M., Bernard, R., Böhm, M., Castro-Herrera, F., Chirio, L., Collen, B., Colli, G.R., Dabool, L., Das, I., Doan, T.M., Grimer, L.L., Hoogmoed, M., Itescu, Y., Kraus, F., LeBreton, M., Lewin, A., Martins, M., Maza, E., Meirte, D., Nagy, Z.T., Nogueira, C.C., Pauwels, O.S.G., Pincheira-Donoso, D., Powney, G.D., Sindaco, R., Tallowin, O.J.S., Torres-Carvajal, O., Trape, J.-F., Vidan, E., Uetz, P., Wagner, P., Wang, Y., Orme, C.D.L., Grenyer, R., Meiri, S., 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. Nat. Ecol. Evol. 1, 1677–1682.

Sethuraman, A., McGaugh, S.E., Becker, M.L., Chandler, C.H., Christiansen, J.L., Hayden, S., LeClere, A., Monson-Miller, J., Myers, E.M., Paitz, R.T., Refsnider, J.M., VanDeWalle, T.J., Janzen, F.J., 2014. Population genetics of Blanding's turtle (*Emys blandingii*) in the midwestern United States. Conserv. Genet. 15, 61–73.

Sommer, R.S., Lindqvist, C., Persson, A., Bringsøe, H., Rhodin, A.G.J., Schneeweiss, N., Široký, P., Bachmann, L., Fritz, U., 2009. Unexpected early extinction of the European pond turtle (*Emys orbicularis*) in Sweden and climatic impact on its Holocene range. Mol. Ecol. 18, 1252–1262.

Sommer, R.S., Fritz, U., Seppä, H., Ekström, J., Persson, A., Liljegren, R., 2011. When the pond turtle followed the reindeer: effect of the last extreme global warming event on the timing of faunal change in northern Europe. Glob. Chang. Biol. 17, 2049–2053.

Spinks, P.Q., Shaffer, B., 2005. Range-wide molecular analysis of the western pond turtle (*Emys marmorata*): cryptic variation, isolation by distance, and their conservation implications. Mol. Ecol. 14, 2047–2064.

Stuckas, H., Velo-Antón, G., Fahd, S., Kalboussi, M., Rouag, R., Arculeo, M., Marrone, F., Sacco, F., Vamberger, M., Fritz, U., 2014. Where are you from stranger? The enigmatic biogeography of North African pond turtles (*Emys orbicularis*). Organ. Divers. Evol. 14, 295–306.

Taylor, J.E., Hardner, J., Stewart, M., 2009. Ecotourism and economic growth in the Galapagos: an island economy-wide analysis. Environ. Dev. Econ. 14, 139–162.

Therneau, T., Atkinson, B., Ripley, B., 2018. Rpart: Recursive Partitioning and Regression Trees. R Package Version 4.1-13. https://cran.r-project.org/web/packages/rpart/index.html.

Turtle Extinctions Working Group (TEWG), 2015. Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. In: Rhodin, A.G.J., Pritchard, P.C.G., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B., Mittermeier, R.A. (Eds.), Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5, 000e.1–66.

Turtle Taxonomy Working Group (TTWG), 2017. Turtles of the world, 8th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. In: Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B., van Dijk, P.P. (Eds.), Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SCC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 7, pp. 1–292.

Vilela, B., Villalobos, F., 2015. letsR: a new R package for data handling and analysis in macroecology. Methods Ecol. Evol. 6, 1229–1234.

Wallace, B.P., DiMatteo, A.D., Bolten, A.B., Chaloupka, M.Y., Hutchinson, B.J., Abreu-Grobois, F.A., Mortimer, J.A., Amorocho, D., Bjorndal, K.A., Bourjea, J., Bowen, B.W., Briseno Duenas, R., Casale, P., Choudhury, B.C., Costa, A., Dutton, P.H., Fallabrino, A., Finkbeiner, E.M., Girard, A., Girondot, M., Hamann, M., Hurley, B.J., Lopez-Mendilaharsu, M., Marcovaldi, M.A., Musick, M.A., Nel, R., Pilcher, N.J., Troeng, S., Witherington, B., Mast, R.B., 2011. Global conservation priorities for marine turtles. PLoS One 6, e24510.

WCS and CIESIN, 2005. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). https://doi.org/10.7927/H4M61H5F.

White, D., Gramacy, R.B., 2015. Mapping, Pruning, and Graphing Tree Models. R Package Version 1.4-7. https://cran.r-project.org/web/packages/maptree/index.html.

Whittaker, R.J., Araujo, M.B., Jepson, P., Ladle, R.J., Watson, J.E.M., Willis, K.J., 2005. Conservation biogeography: assessment and prospect. Divers. Distrib. 11, 3–23.

Zalasiewicz, J., Williams, M., Smith, A., Barry, T.L., Coe, A.L., Bown, P.R., Brenchley, P., Cantrill, D., Gale, A., Gibbard, P., Gregory, F.J., Hounslow, M.W., Kerr, A.C., Pearson, P., Knox, R., Powell, J., Waters, C., Marshall, J., Oates, M., Rawson, P., Stone, P., 2008. Are we now living in the Anthropocene? GSA Today 18, 4–8. https://doi.org/10.1130/GSAT01802A.1.