Tropical forests are home to over half of the world's vertebrate species

Rajeev Pillay[1*], Michelle Venter[1], Jose Aragon-Osejo[1], Pamela González-del-Pliego[2], Andrew J Hansen[3], James EM Watson[4,5], and Oscar Venter[1]

Tropical forests are renowned for their astonishing diversity of life, but the fundamental question of how many species occur in tropical forests remains unanswered. Using geographic range maps and data on species habitat associations, we determined that tropical forests harbor 62% of global terrestrial vertebrate species, more than twice the number found in any other terrestrial biome on Earth. Up to 29% of global vertebrate species are endemic to tropical forests, with more than 20% of these species at risk of extinction. Humid tropical forests (also known as tropical rainforests) and the Neotropics dominate as centers of species diversity, harboring more than 90% and nearly half of all tropical forest vertebrates, respectively. To maintain the biodiversity that underpins the ecosystem functions and services essential for human well-being, we emphasize the critical importance of environmental policies aimed at reducing tropical deforestation and mitigating deleterious anthropogenic pressures on these imperiled ecosystems.

Front Ecol Environ 2022; 20(1): 10–15, doi:10.1002/fee.2420

Tropical forests encompass less than one-fifth of Earth's terrestrial area (Dinerstein *et al.* 2017), yet directly influence the well-being of approximately 1.5 billion people through the provisioning of a multitude of ecosystem services (Lewis *et al.* 2015) and indirectly benefit much of the rest of humanity through their role in climate regulation (Lawrence and Vandecar 2015). The most striking characteristic of tropical forests, however, is the diversity of life they contain. Although the factors that generate and maintain high species diversity in the tropics have attracted considerable scientific focus (Brown 2014), the basic question of how many species actually occur in tropical forests has received surprisingly little attention.

It is widely espoused that tropical forests harbor more than half of Earth's biodiversity. This assertion has persisted in the scientific literature for more than 30 years (Lewis *et al.* 2015; Brancalion *et al.* 2019) despite having a tenuous empirical foundation. The original idea can be traced to Erwin (1982), who extrapolated beetle counts from 19 individuals of one Panamanian tree species to estimate there could be 30 million invertebrate species in tropical forests. Subsequently, EO Wilson's seminal book *Biodiversity* (Wilson 1988) referenced Erwin's research to state that tropical rainforests contain more than half of the world's biota. Over time, Wilson (1988) has in turn become a frequent citation to support the near-mantra that tropical forests house at least half of the world's species. While estimates of species richness across tropical terrestrial and marine biomes indicate that a majority of species within several taxonomic groups are indeed found in the tropics (Barlow *et al.* 2018), there is little empirical evidence to support the claim that tropical forests house a majority of the world's species.

Quantifying how many species occur in tropical forests is a fundamental question in biology (May 1990). Such knowledge can facilitate a deeper understanding of the ecological and evolutionary processes that maintain species diversity and help identify and conserve the species that provision ecosystem services crucial to humanity (May 2011). Furthermore, with species extinctions due to tropical forest loss becoming a defining feature of the Anthropocene, knowing the precise number of species inhabiting these imperiled ecosystems can help improve estimates of extinction rates (Pimm *et al.* 2014). However, the answer to this central question remains enigmatic even for terrestrial vertebrates, which are relatively well studied compared with other taxa.

Here, we address this knowledge gap by combining the latest established geographic range maps and data on habitat associations for all known extant species of terrestrial mammals, birds, reptiles, and amphibians with maps of the tropical forest biome (Dinerstein *et al.* 2017). We focused on terrestrial vertebrates because they comprise the only taxonomic groups for which all known species have a described geographic range. In addition, the habitat associations of most species within these four taxonomic groups are assessed in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. We quantified the number of terrestrial vertebrate species in tropical forests based on two hierarchical criteria: (1) geographic range overlap with the tropical forest biome and (2) reported association with, but not exclusively limited to, tropical forest habitats. We compared the

[1]*Natural Resources and Environmental Studies Institute, University of Northern British Columbia, Prince George, Canada* [*]*(rajeev.p20a@gmail.com);* [2]*Rui Nabeiro Biodiversity Chair, MED Institute, Universidade de Évora, Évora, Portugal;* [3]*Department of Ecology, Montana State University, Bozeman, MT;* [4]*Centre for Biodiversity and Conservation Science, The University of Queensland, Brisbane, Australia;* [5]*School of Earth and Environmental Sciences, The University of Queensland, Brisbane, Australia*

© 2021 The Authors. *Frontiers in Ecology and the Environment* published by Wiley Periodicals LLC on behalf of the Ecological Society of America.

number of vertebrate species in the tropical forest biome with the remaining terrestrial biomes on Earth, and then enumerated (a) the percentage of global vertebrate species endemic to tropical forests and the number of these endemics threatened with extinction, and (b) the percentage of bird species dependent on tropical forests in terms of wintering range, given that tropical forests provide critical wintering habitat for migratory birds. Finally, we quantified the relative percentage of species in the (c) humid, dry, mangrove, and coniferous biomes that together constitute the tropical forest biome, and (d) four biogeographic realms within the tropical forest biome. These biogeographic realms closely approximate the continents and represent broad spatial extents within which ecosystems and species share a similar evolutionary history.

Methods

The primary focus of our study was pantropical, and therefore the analyses were conducted across tropical and subtropical moist broadleaf (humid), dry broadleaf, coniferous, and mangrove forest biomes. These tropical forests generally span the latitudes between 23.5°N and 23.5°S but in some areas can extend into the subtropics. To compare the number of vertebrate species in the tropical forest biome with other terrestrial biomes, we pooled various broad habitat types into the remaining five major terrestrial biomes on Earth, following the IUCN Habitat Classification Scheme (IUCN 2012). For all biomes, we used the boundaries defined by Dinerstein *et al.* (2017).

We obtained the most up-to-date geographic range maps for all known species of mammals (IUCN 2020), birds (BirdLife International 2018), reptiles (Roll *et al.* 2017), and amphibians (González-del-Pliego *et al.* 2019; IUCN 2020). The original datasets contained range maps for 5566 mammals, 11,125 birds, 10,064 reptiles, and 6684 amphibians, and include ranges for species known to be extinct as well as polygons based on uncertain data. Because the IUCN range map data for amphibians do not comprise all known species, we included range maps for 659 additional amphibian species presented in González-del-Pliego *et al.* (2019) after cross-verification to avoid overlap (eg synonyms for the same species). We filtered these datasets so that only extant species and spatial range attributes based on certain data were retained; for birds, we also retained attributes to quantify the wintering or nonbreeding grounds of migratory species within tropical forests. Our final list of species included 5529 mammals, 10,935 birds, 10,054 reptiles, and 7264 amphibians, for a total of 33,782 species of extant terrestrial vertebrates worldwide (for details about the processing of geographic range maps, see WebPanel 1).

We projected all geographic range and biome maps to the Mollweide world map projection and performed all subsequent geospatial analyses with Python code implemented with the ArcPy module in ArcGIS Pro 2.5.0. The global range area (in square kilometers) of each species was first calculated to facilitate subsequent estimation of the extent of overlap of the global range with tropical forest and other biomes. We then overlaid the global range map of each species with the map of each terrestrial biome to distinguish parts of species' ranges that overlap the constituent parts of a given biome (should there be such overlap for a given species). Finally, we calculated the range area of a species within each biome and its various constituent parts. We did not set a lower bound for range overlap with tropical forests because, aside from being arbitrary, such a threshold may exclude species marginally occurring in tropical forests but for which tropical forests represent important habitats. For example, the Newell's shearwater (*Puffinus newelli*) has <1% range overlap with the tropical forest biome but tropical moist montane forests are vital breeding grounds for this species; similarly, the Christmas frigatebird (*Fregata andrewsi*) has <1% of its global range within the tropical forest biome but 100% of this tropical forest range represents its wintering habitat. The terrestrial biome maps contain an attribute delineating the various biogeographic realms (Dinerstein *et al.* 2017), which allowed us to calculate the area of species ranges within each realm (for details about the geospatial methods, see WebPanel 2).

To limit some forms of commission or false positive errors that may occur with range maps, we used species-level attributes from the IUCN Red List of Threatened Species to obtain data on the major habitats in which each species is found. Specifically, these errors include species whose ranges may overlap a given biome but which do not actually use the habitats within that biome. For species whose ranges overlap the tropical forest biome, we retained only those reported to inhabit at least one of the six tropical forest habitat types listed in the IUCN Habitats Classification Scheme (IUCN 2012). We merged this list of species that occur in tropical forest habitats with the list of species whose ranges overlap the tropical forest biome to retain species with both range overlap *and* habitat association with tropical forests. We performed similar analyses to assign species to the remaining five terrestrial biomes (for details about criteria on inclusion of species in each biome, see WebTable 1).

We defined endemism to tropical forests based on two criteria: (1) 100% and (2) 80–100% range overlap with the tropical forest biome; the second criterion was considered because in a few areas the tropical forest biome extends beyond the 23.5°N and 23.5°S latitudes and into the subtropics. In both definitions, we imposed an additional filter of association with only tropical forest habitats for a species to be considered endemic. However, we did not exclude wetlands, rocky, and cave habitats from this filter, under the reasonable assumption that for species with >80% range overlap with tropical forests and reported to be nearly exclusively associated with tropical forest habitats, these three other habitat types are likely to be within tropical forests (eg bats that roost in caves within forests). We quantified the dependency of migratory birds on tropical forests in a similar manner, imposing criteria of 100% and 80–100% wintering range overlap with the tropical forest biome for a species to be considered dependent on tropical forests.

Results

Our analyses revealed that tropical forests are home to 62% of global terrestrial vertebrates (n = 21,092 species), despite covering only 18% of Earth's total land area. Specifically, 63% of mammals (n = 3480), 72% of birds (n = 7918), and 76% of amphibians (n = 5503) occur in tropical forests (Figure 1a). Reptiles represent the only taxonomic group for which <50% of global species (n = 4191) occur in tropical forests. However, reptiles remain one of the most understudied terrestrial vertebrate groups (Böhm *et al.* 2013) and the habitat associations of 31% of reptile species (n = 2318) whose ranges overlap tropical forests are currently unknown. Therefore, our criteria likely underestimate the number of tropical forest reptile species. In contrast, the habitat associations of only 1.2% (n = 52) of mammals, 1.5% (n = 92) of amphibians, and zero birds whose ranges overlap with tropical forests are unknown. In terms of absolute numbers, tropical forests were found to harbor more than twice as many vertebrate species as any other terrestrial biome on Earth; no other terrestrial biome approaches 50% of global vertebrate species (Figure 1, b–f; WebTable 2).

With respect to endemism, at least 17% and up to 29% (100% and 80–100% range overlap, respectively) of global terrestrial vertebrates are endemic to tropical forests (associated with only tropical forest habitats), with endemism levels in amphibians being notably high (33–44% of global species; Figure 2, a and b). In comparison, we found endemism to be lower for mammals (14–28%), birds (8–24%), and reptiles (12–21%). In each taxonomic group, ≥20% of endemic species are threatened with extinction (28–34% on average), with the number of endemic amphibians at risk being especially high (39–42%; Figure 2, a and b; WebTable 3). Of the 643 species of migratory birds that winter in tropical forests, we found 14–34% (n = 92–219) to be highly dependent on these dwindling ecosystems (100% and 80–100% wintering range overlap, respectively; Figure 2c; WebTable 4).

The humid tropics are particularly important for an overwhelming majority of species across all taxonomic groups. Of the 21,092 vertebrate species that occur in tropical forests, more than 90% exhibit varying extents of range overlap with the humid tropics (Figure 3a). Consistent with prior research (Jenkins *et al.* 2013), we found that the Neotropics harbor nearly half (45% on average) of all tropical forest vertebrate

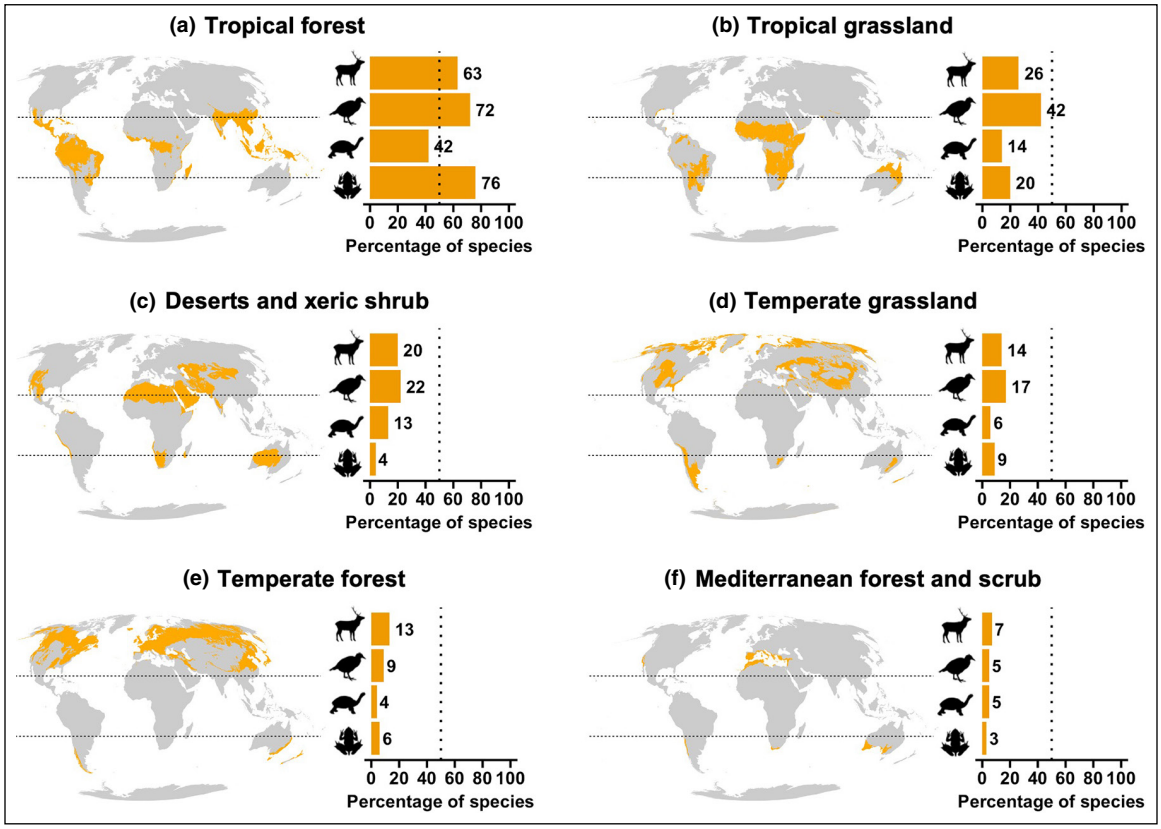

Figure 1. (a) The percentage of global mammal, bird, reptile, and amphibian species that occur in tropical forests based on geographic range overlap with the tropical forest biome *and* association with tropical forest habitats. The tropics lie between the 23.5°N and 23.5°S latitudes (indicated by the horizontal dotted lines on the map). Tropical forest and grassland biomes together represent all mesic ecoregions within the tropics but extend into the subtropics in a few areas. As indicated by the vertical dotted line on the bar graph, tropical forests harbor more than 50% of global terrestrial vertebrates, with the potential exception of reptiles (see Results). (b)–(f) The percentages of terrestrial vertebrates in all other biomes on Earth as compared with tropical forests. Various broad habitat types were pooled into each biome following the International Union for Conservation of Nature (IUCN) Habitat Classification Scheme (IUCN 2012); for instance, the temperate grassland biome includes tundra and the temperate forest biome includes boreal forest/taiga (see WebTable 1 for further details).

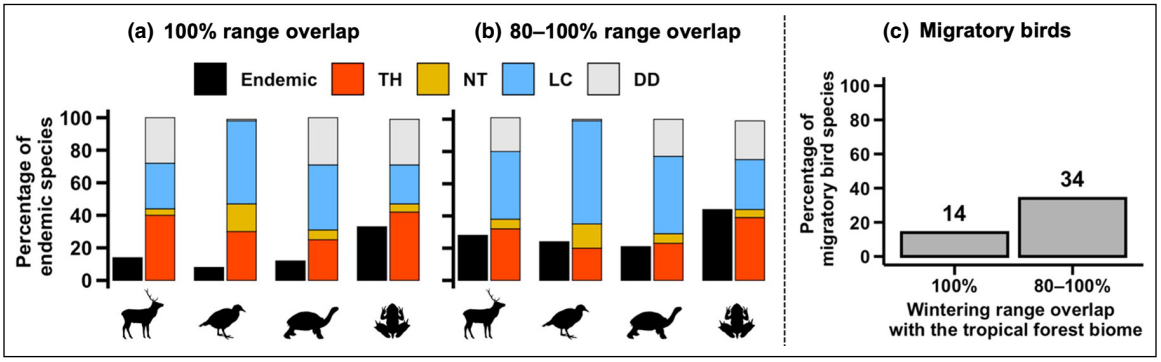

Figure 2. The percentage of global mammals, birds, reptiles, and amphibians endemic to tropical forests and the threatened status of these endemic species based on (a) 100% and (b) 80–100% range overlap with the tropical forest biome. In both cases, for a species to be classified as endemic, we imposed an additional criterion of exclusive association with tropical forest habitats (see Methods for details). Species in IUCN Critically Endangered, Endangered, and Vulnerable threat categories were collectively classified as Threatened (TH). Other categories include Near Threatened (NT), Least Concern (LC), and Data Deficient (DD). (c) The percentage of migratory bird species dependent on tropical forests in terms of wintering range overlap.

species among the biogeographic realms, and are exceptionally diverse with respect to amphibians; more than half of all tropical forest amphibian species were found to occur in the Neotropics (Figure 3b; WebTable 5).

Discussion

The primary message emanating from our analysis is that tropical forests contain more than half of global terrestrial vertebrate species, with the potential exception of reptiles. Furthermore, tropical forests are the most biodiverse of all terrestrial biomes on Earth in terms of vertebrate diversity. Tropical forests are extraordinarily important habitats for amphibians, as evidenced from the degree of endemism, and provide critical wintering habitats for over 200 species of migratory birds. The pronounced diversity of amphibians in tropical forests assumes particular importance for conservation, given that recent worldwide amphibian declines and subsequent trophic cascades in the form of decreased reptile diversity have occurred mainly in the tropics (Scheele *et al.* 2019; Zipkin *et al.* 2020). Humid tropical forests and the Neotropics dominate as centers of terrestrial vertebrate diversity. The continued clearing and degradation of humid tropical forests for agro-industrial and forestry operations worldwide and escalating forest loss in the Amazon region (Hansen *et al.* 2008, 2020) portend imminent vertebrate extinctions in these most hyperdiverse of all tropical forest biomes and biogeographic realms, respectively.

There is increasing evidence to suggest human well-being is dependent upon the diversity of life (Cardinale *et al.* 2012; Isbell *et al.* 2017). Our findings underscore the critical importance of conserving the last remaining tropical forests to maintain their

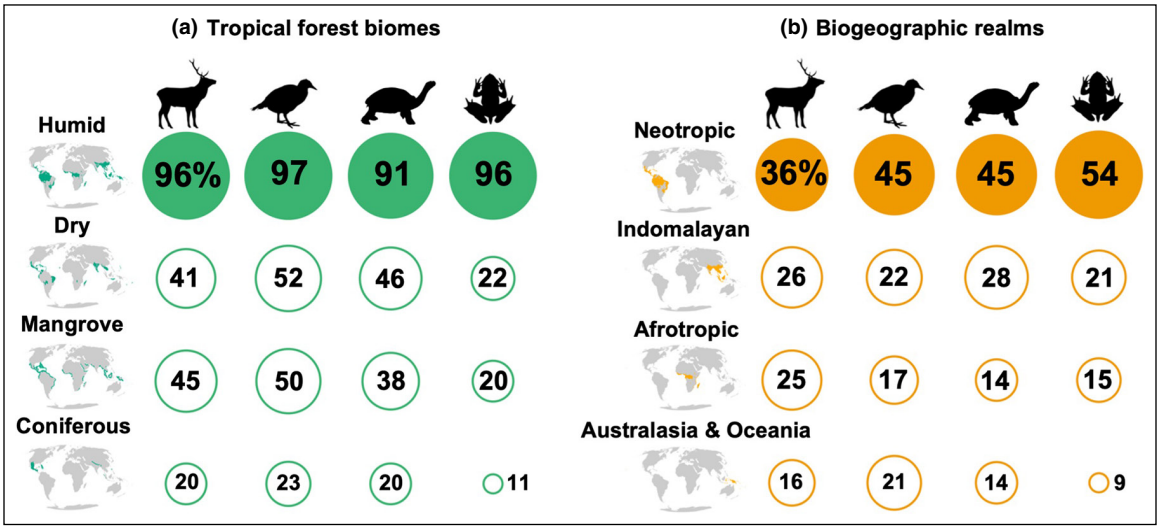

Figure 3. The percentage of tropical forest mammal, bird, reptile, and amphibian species occurring in (a) the humid, dry, mangrove, and coniferous biomes, which together constitute the tropical forest biome, and (b) the four biogeographic realms within the tropical forest biome. Percentages across biomes and realms for each taxonomic group do not sum to 100 because a species can occur in more than one biome or realm. Two Palearctic and four Nearctic ecoregions fall within the tropical forest biome, and were pooled with the Indomalayan and Neotropic realms, respectively.

exceptional biodiversity (Betts *et al.* 2017; Watson *et al.* 2018; Hansen *et al.* 2020). However, we caution against attributing lower conservation value to other biomes in favor of tropical forests. Indeed, prior work has demonstrated that regions where tropical forest and grassland biomes co-occur along environmental gradients may be comparable in vertebrate species richness (Murphy *et al.* 2016). Moreover, emerging evidence suggests all intact wilderness areas, regardless of their location, are essential to limit biodiversity loss, and all biomes are home to irreplaceable native habitats and assemblages of species with intrinsic conservation values worthy of preserving in their natural states (Betts *et al.* 2017; Di Marco *et al.* 2019).

We acknowledge our inferences are not based on a random sample from the evolutionary tree of life but limited to terrestrial vertebrates, among the most thoroughly studied taxonomic groups. Of the Earth's estimated 8.7 million species (Mora *et al.* 2011), a mere 1.3% (n = 116,000) have been assessed comprehensively (IUCN 2020), and for terrestrial species within this minuscule group, only the ranges of mammals, birds, amphibians, and reptiles have been described. Other major taxonomic groups (eg vascular plants, invertebrates) were therefore excluded from our estimates due to limited data availability. Recent analysis of the number of arthropods in the tropics led to a revised estimate of 6.1 million species (Hamilton *et al.* 2010), most of which are assumed to occur in humid tropical forests (Basset *et al.* 2012) potentially as a function of the latitudinal gradient in plant diversity (Novotny *et al.* 2006). Such assumptions demand rigorous testing, however, as comparable data for non-vertebrates become available.

Our use of range maps published by the IUCN and other sources (Roll *et al.* 2017; González-del-Pliego *et al.* 2019) imposes some restraints in understanding biodiversity patterns. Range maps describe broad distributions, and some can have commission errors, as species typically do not occur throughout their mapped range because of various factors such as spatial heterogeneity in habitat availability, topography, and anthropogenic pressures and seasonal movements such as migrations (Jetz *et al.* 2008). We attempted to minimize these commission errors by using data on species habitat associations to exclude species whose ranges overlap a particular biome but do not actually use habitats within that biome (WebTable 1). Given the inherent scarcity of species distribution data (Jetz *et al.* 2019), range maps that account for species habitat associations remain the best available source of data for broad geographic-scale analyses in ecology and conservation science.

That species richness tends to increase with decreasing latitude toward the tropics has long been recognized (Wallace 1878; Novotny *et al.* 2006). Numerous hypotheses have been proposed to explain this latitudinal diversity gradient (Brown 2014). However, the simple but profound question of how many species actually occur in tropical forests has remained unanswered, mainly because the sheer number of species and poor knowledge of their biology and distributions make estimation of their precise numbers a daunting challenge without resorting to extrapolation from local-scale samples (Erwin 1982; Basset *et al.* 2012). We addressed this question for terrestrial vertebrates using established range maps and demonstrate that at least 62% of all such species occur in tropical forests, more than in any other biome on Earth. While we echo the importance of discovering and describing the ecology of every living species (Wilson 2017), conservation efforts must first focus on the core priorities of reducing tropical forest loss and degradation (Betts *et al.* 2017; Hansen *et al.* 2020) and limiting other anthropogenic pressures on natural areas (Barlow *et al.* 2016) to safeguard much of the diversity of life that humanity depends upon.

Acknowledgements

This research was funded by the US National Aeronautics and Space Administration Biodiversity and Ecological Forecasting Program under the 2016 ECO4CAST solicitation through grant NNX17AG51G.

Data Availability Statement

All datasets used in this paper are openly available via the citations identified in the Methods. Data used to create Figures 1–3 are presented in WebTables 2–5. Custom Python code to replicate analyses and processed spreadsheets are available on Zenodo (doi.org/10.5281/zenodo.5525586).

References

Barlow J, Franca F, Gardner TA, *et al.* 2018. The future of hyperdiverse tropical ecosystems. *Nature* **559**: 517–26.

Barlow J, Lennox GD, Ferreira J, *et al.* 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* **535**: 144–47.

Basset Y, Cizek L, Cuénoud P, *et al.* 2012. Arthropod diversity in a tropical forest. *Science* **338**: 1481–84.

Betts MG, Wolf C, Ripple WJ, *et al.* 2017. Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* **547**: 441–44.

BirdLife International. 2018. Bird species distribution maps of the world (v2018.1). Cambridge, UK: BirdLife International. http://datazone.birdlife.org/species/requestdis. Viewed 23 Oct 2020.

Böhm M, Collen B, Baillie JEM, *et al.* 2013. The conservation status of the world's reptiles. *Biol Conserv* **157**: 372–85.

Brancalion PHS, Niamir A, Broadbent E, *et al.* 2019. Global restoration opportunities in tropical rainforest landscapes. *Science Advances* **5**: eaav3223.

Brown JH. 2014. Why are there so many species in the tropics? *J Biogeogr* **41**: 8–22.

Cardinale BJ, Duffy JE, Gonzalez A, *et al.* 2012. Biodiversity loss and its impact on humanity. *Nature* **486**: 59–67.

Di Marco M, Ferrier S, Harwood TD, *et al.* 2019. Wilderness areas halve the extinction risk of terrestrial biodiversity. *Nature* **573**: 582–85.

Dinerstein E, Olson D, Joshi A, *et al.* 2017. An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* **67**: 534–45.

Erwin TL. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopts Bull* **36**: 74–75.

González-del-Pliego P, Freckleton RP, Edwards DP, *et al*. 2019. Phylogenetic and trait-based prediction of extinction risk for data-deficient amphibians. *Curr Biol* **29**: 1557–63.

Hamilton AJ, Basset Y, Benke KK, *et al*. 2010. Quantifying uncertainty in estimation of tropical arthropod species richness. *Am Nat* **176**: 90–95.

Hansen AJ, Burns P, Ervin J, *et al*. 2020. A policy-driven framework for conserving the best of Earth's remaining moist tropical forests. *Nat Ecol Evol* **4**: 1377–84.

Hansen MC, Stehman SV, Potapov PV, *et al*. 2008. Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *P Natl Acad Sci USA* **105**: 9439–44.

Isbell F, Gonzalez A, Loreau M, *et al*. 2017. Linking the influence and dependence of people on biodiversity across scales. *Nature* **546**: 65–72.

IUCN (International Union for Conservation of Nature). 2012. IUCN Habitats Classification Scheme (v3.1). Gland, Switzerland: IUCN.

IUCN (International Union for Conservation of Nature). 2020. The IUCN Red List of Threatened Species (v2020-1). Gland, Switzerland: IUCN. www.iucnredlist.org. Viewed 23 Oct 2020.

Jenkins CN, Pimm SL, and Joppa LN. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *P Natl Acad Sci USA* **110**: E2603–10.

Jetz W, McGeoch MA, Guralnick R, *et al*. 2019. Essential biodiversity variables for mapping and monitoring species populations. *Nat Ecol Evol* **3**: 539–51.

Jetz W, Sekercioglu CH, and Watson JEM. 2008. Ecological correlates and conservation implications of overestimating species geographic ranges. *Conserv Biol* **22**: 110–19.

Lawrence D and Vandecar K. 2015. Effects of tropical deforestation on climate and agriculture. *Nat Clim Change* **5**: 27–36.

Lewis SL, Edwards DP, and Galbraith D. 2015. Increasing human dominance of tropical forests. *Science* **349**: 827–32.

May RM. 1990. How many species? *Philos T Roy Soc B* **330**: 293–304.

May RM. 2011. Why worry about how many species and their loss? *PLoS Biol* **9**: e1001130.

Mora C, Tittensor DP, Adl S, *et al*. 2011. How many species are there on Earth and in the ocean? *PLoS Biol* **9**: e1001127.

Murphy BP, Andersen AN, and Parr CL. 2016. The underestimated biodiversity of tropical grassy biomes. *Philos T Roy Soc B* **371**: 20150319.

Novotny V, Drozd P, Miller SE, *et al*. 2006. Why are there so many species of herbivorous insects in tropical rainforests? *Science* **313**: 1115–18.

Pimm SL, Jenkins CN, Abell R, *et al*. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**: 1246752.

Roll U, Feldman A, Novosolov M, *et al*. 2017. The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nat Ecol Evol* **1**: 1677–82.

Scheele BC, Pasmans F, Skerratt LF, *et al*. 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* **363**: 1459–63.

Wallace AR. 1878. Tropical nature and other essays. London, UK: Macmillan.

Watson JEM, Evans T, Venter O, *et al*. 2018. The exceptional value of intact forest ecosystems. *Nat Ecol Evol* **2**: 599–610.

Wilson EO. 1988. Biodiversity. Washington, DC: National Academy Press.

Wilson EO. 2017. Biodiversity research requires more boots on the ground. *Nat Ecol Evol* **1**: 1590–91.

Zipkin EF, DiRenzo GV, Ray JM, *et al*. 2020. Tropical snake diversity collapses after widespread amphibian loss. *Science* **367**: 814–16.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2420/suppinfo