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Global rarity of high-integrity tropical rainforests for threatened and declining terrestrial vertebrates

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Structurally intact native forests free from major human pressures are vitally important habitats for the persistence of forest biodiversity. However, the extent of such high-integrity forest habitats remaining for biodiversity is unknown. Here, we quantify the amount of high-integrity tropical rainforests, as a fraction of total forest cover, within the geographic ranges of 16,396 species of terrestrial vertebrates worldwide. We found up to 90% of the humid tropical ranges of forest-dependent vertebrates was encompassed by forest cover. Concerningly, however, merely 25% of these remaining rainforests are of high integrity. Forest-dependent species that are threatened and declining and species with small geographic ranges have disproportionately low proportions of high-integrity forest habitat left. Our work brings much needed attention to the poor quality of much of the forest estate remaining for biodiversity across the humid tropics. The targeted preservation of the world's remaining high-integrity tropical rainforests that are currently unprotected is a critical conservation priority that may help alleviate the biodiversity crisis in these hyperdiverse and irreplaceable ecosystems. Enhanced efforts worldwide to preserve tropical rainforest integrity are essential to meet the targets of the Convention on Biological Diversity's 2022 Kunming-Montreal Global Biodiversity Framework which aims to achieve near zero loss of high biodiversity importance areas (including ecosystems of high integrity) by 2030.

forest cover | forest integrity | habitat quality | intact forests | terrestrial vertebrates

Significance

It has long been known that intact, undisturbed native forests of high integrity are indispensable for sustaining tropical biodiversity. But what fraction of tropical rainforest cover remains intact and undisturbed for biodiversity? For 16,396 species of terrestrial vertebrates worldwide, we show that less than a quarter of remaining tropical rainforest cover is of high integrity. Concerningly, species threatened with extinction, having declining populations, and with small geographic ranges have disproportionately low amounts of high-integrity forest habitats left. Our findings highlight the urgent need for enhanced conservation efforts globally to preserve areas of high-integrity tropical rainforests that are currently unprotected.

Conservation strategies that treat forests as uniform land-cover and focus primarily on reducing deforestation have been largely inadequate in slowing the loss of biodiversity (1–3). This is because merely maintaining forest cover, without considering its quality, does not limit various large-scale human pressures (*e.g.,* logging, roads, mining) that alter forest structure, function, and species composition (1, 4). Thus, structurally intact native forests under negligible human pressures (hereafter "high-integrity forests") are exceptionally important for biodiversity conservation (3, 5, 6). In tropical rainforests, the most biodiverse of all terrestrial ecosystems on Earth (7), a recent evaluation of the relative importance of forest cover, structural condition, and integrity for vertebrate species extinction risk suggests high-integrity forests can buffer species against extinction, when directly compared with forest cover (3). But how much high-integrity forest, as a fraction of total forest cover, remains within the geographic ranges of tropical rainforest vertebrates? This fundamental question remains unanswered despite longstanding knowledge that intact and undisturbed native forest ecosystems are indispensable for sustaining tropical biodiversity (5, 6, 8). Furthermore, global variation in integrity of remaining extents of tropical rainforests as a function of species conservation concern is yet to be evaluated. Such an assessment of habitat quality for tropical rainforest vertebrates worldwide can help establish current baselines for these hyperdiverse ecosystems, which in turn can facilitate the monitoring of progress toward international conservation targets (9).

In this study, we use a recently developed remotely sensed measure of tropical rainforest integrity—the Forest Structural Integrity Index (FSII) (10, 11)—to quantify the extent (km^2) of high-integrity forests remaining for 16,396 mammal, bird, reptile, and amphibian species whose geographic ranges overlap the tropical and subtropical moist broadleaf (or humid tropical) biome (12). The FSII combines the Structural Condition Index (SCI) (10, 11)—a 30 m resolution measure of tropical rainforest condition—with the global Human Footprint (HFP) (13) to distinguish structurally intact rainforests under minimal human pressures from those of lower integrity. The FSII thus provides a measure of forest quality relevant to biodiversity conservation by quantifying both structural condition and human pressure intensity within tropical forests (3). We first partitioned species as either rainforest-obligate (dependent on tropical rainforests, hereafter "forest-dependent",

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n = 5,258; *SI Appendix*, Table S1) or rainforest-associated (use rainforests and other habitats, hereafter "forest-associated," n = 11,138) to avoid potential confounding effects due to non-forest habitat use by forest-associated species (3, 7). We analyzed forest-dependent and associated species separately throughout this study. Based on key structural attributes of forests and prior research on HFP thresholds and their relationship with extinction risk for terrestrial vertebrates (3, 11, 14), we pooled the forest quality gradient in the SCI and FSII data into high, moderate, and low structural condition and integrity categories (*Materials and Methods*). We then quantified the proportion of rainforests along this gradient of high, moderate, and low integrity out of the total rainforest cover (hereafter "forest cover") within species humid tropical ranges.

We used linear mixed-effects models fit in a Bayesian framework to examine variation in the proportion of forest within species ranges, as a function of two-way interactions between the gradient in forest integrity and species classified as threatened (critically endangered, endangered, vulnerable) and not threatened (near threatened, least concern) as well as species classified as declining and not declining in population by the IUCN Red List of Threatened Species (15). The classification of species into binary threatened and not threatened categories is routine in comparative analyses with IUCN threat status data (3, 16). However, this binary classification may mask important variation in forest integrity along a gradient of decreasing conservation concern specified by the range of IUCN threat categories (critically endangered, endangered, vulnerable, near-threatened, least concern). Therefore, we also tested whether decreasing conservation concern is associated with increasing proportion of high-integrity forest within species ranges. Given forest cover is a key variable in conservation planning and policy (11), we compared patterns in forest integrity with the proportion of forest cover within species ranges. Thereafter, we assessed spatial variation in forest integrity in relation to species threatened status and population trends across the biogeographic realms within the humid tropical biome.

Ecological theory suggests small geographic range size is a key predictor of vulnerability to extinction in terrestrial biodiversity (17), and empirical data confirm small-ranged species can undergo greater population declines in human-modified habitats than large-ranged species (18). Despite these insights, it remains unknown whether and how the integrity of remaining forest habitats within species ranges varies as a function of species geographic range size. We addressed this gap by first exploring variation in the proportion of forest as a function of two-way interactions between the forest integrity gradient and species humid tropical range size. We expected small-ranged species to have lower proportions of high-integrity forest than large-ranged species due to random chance, because small-ranged species are more likely to be completely encompassed by large-scale human disturbances than large-ranged species (19). Finally, we investigated how species threatened status and population trends may influence the relationship between forest integrity and range size. We did so by examining variation in the proportion of forest as a function of three-way interactions between forest integrity, range size, and species threatened status as well as population trends.

Results

Forest Structural Condition and Integrity for Forest-Dependent Species. When considering only the structural condition of tropical rainforests and not the human pressures within, we found structurally intact forests (SCI values 14 to 18) (3, 11) encompassed more than half of species humid tropical ranges (average 59% across all taxonomic groups; Fig. 1*A*). In contrast, forests in highly degraded structural condition (SCI values 2 to 5) and moderately degraded forests (SCI values 6 to 13) comprised only 7% and 34% of forest cover within species ranges respectively (averaged across all taxonomic groups). The quality of forests that appear structurally intact can nevertheless be diminished by numerous insidious human activities, which in turn can adversely affect biodiversity (3). Thus, when both structural condition and human pressures were considered, high-integrity forests (FSII values 14 to 18) (3, 11) comprised merely 25% of the forest cover within species ranges on average (Fig. 1*B*). Conversely, low-integrity forest (FSII values 1 to 5) encompassed 69% of species ranges on average, which is substantially greater than the proportion of structurally degraded forests.

Forest Integrity and Species Conservation Concern. Threatened and declining species had significantly lower proportions of high-integrity forest within their ranges compared with nonthreatened and nondeclining species across all forest-dependent groups

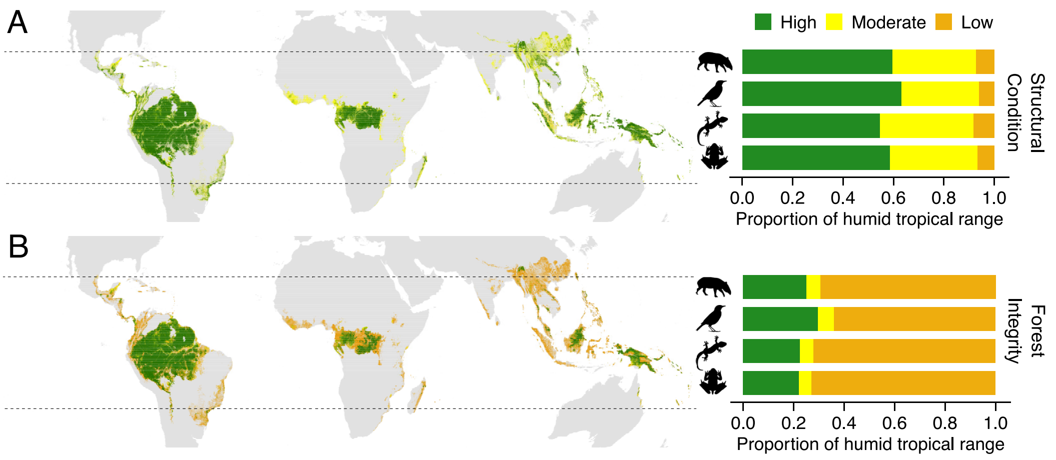

Fig. 1. Structural condition and integrity of tropical rainforests worldwide for forest-dependent terrestrial vertebrates. (*A*) Tropical rainforest structural condition (SCI) and (*B*) integrity (FSII) maps (10, 11). The SCI is a remotely sensed measure combining data on canopy cover, tree height, and time since disturbance to distinguish taller, older, more structurally complex closed-canopy forests from degraded forests. The FSII is a cumulative measure of structural condition and major human pressures as captured by the global human footprint (13). Tropical rainforests largely span the latitudes between 23.5° N and 23.5° S (indicated by the horizontal dashed lines on each map) but extend into subtropical latitudes in some areas. Bar plots in each panel show the proportion of humid tropical range for forest-dependent mammals, birds, reptiles, and amphibians encompassed by rainforest in high, moderate, and low structural condition and integrity. Proportions are averaged across the species in each taxonomic group; *SI Appendix*, Table S1 for sample sizes.

(Fig. 2). This is evident from the strong negative statistical interactions between threatened or declining status of species and the high-integrity forest category (95% credible intervals (CRIs) of estimated posterior means did not overlap zero; *SI Appendix*, Table S2). For example, merely 9% (95% CRI: 8 to 11%) of remaining forests for threatened birds were of high integrity, compared with 26% (CRI: 24 to 27%) for nonthreatened birds (Fig. 2). Similarly, only 6% (CRI: 5 to 7%) of forests for declining amphibians were of high integrity, compared with 36% (CRI: 32 to 39%) for nondeclining amphibians. Threatened and declining species also had significantly lower proportions of moderate-integrity forest than nonthreatened and nondeclining species but these differences were smaller in magnitude compared with those for high-integrity forests (Fig. 2 and *SI Appendix*, Table S2). Conversely, threatened and declining species had significantly greater proportions of low-integrity forest than nonthreatened and nondeclining species (Fig. 2 and *SI Appendix*, Table S2). Notably, the proportion of high-integrity forest tended to be higher along a gradient of decreasing conservation concern such that critically endangered forest-dependent species had the least amount of high-integrity forest habitat remaining whereas least concern species had the most (Fig. 3 and *SI Appendix*, Table S3). We observed the opposite pattern for low-integrity forest (Fig. 3).

High-Integrity Forests Versus Forest Cover. In sharp contrast with the sparse proportions of high-integrity forest, the median proportion of forest cover was considerably greater, comprising 82 to 90% of forest-dependent species ranges (Figs. 2 and 3). The larger proportions of forest cover within species ranges, compared with high-integrity forests, are unsurprising given high-integrity forests constitute a subset of overall forest cover. However, threatened and declining species had significantly lower forest cover than nonthreatened and nondeclining species in only five out of eight comparisons (*SI Appendix*, Table S4). Moreover, even in the five statistically significant comparisons, forest cover was only marginally lower within threatened and declining species ranges (*SI Appendix*, Fig. S1). For example, forest cover encompassed 86% (85 to 88%) of the ranges of threatened forest-dependent birds compared with 89% (88 to 89%) of nonthreatened birds (*SI Appendix*, Fig. S1), which contrasts with the greater differences in high-integrity forest proportions as a function of species threatened status and population trends (Fig. 2).

Comparisons Across Biogeographic Realms. The global patterns in forest integrity in relation to species threatened status and population trends were consistent across biogeographic realms, albeit with some variability. Except for Afrotropical birds, all threatened forest-dependent groups had significantly lower proportions of high-integrity forest than nonthreatened groups in every biogeographic realm (Fig. 4 and *SI Appendix*, Table S5). We found these patterns to be more variable with respect to population trends. For example, inconsistent with overall patterns, declining forest-dependent Afrotropical reptiles and Indomalayan birds had significantly more high-integrity forest than nondeclining species in these groups. We also observed no differences in high-integrity forest proportions between declining and nondeclining Afrotropical birds as well as Indomalayan mammals and reptiles (Fig. 4).

Forest Integrity and Geographic Range Size. Across all forest-dependent groups, species with larger ranges had significantly greater proportions of moderate- and especially high-integrity forest remaining (Fig. 5*A*). Conversely, the proportion of low-integrity forest dropped significantly with increasing range size (Fig. 5*A*). These findings are supported by the strong positive statistical interactions between the forest integrity gradient and range size, the relative magnitude of the estimated posterior means and differences in slopes (Fig. 5*A* and *SI Appendix*, Table S6). Importantly, this effect of larger range size on the amount of high-integrity forest habitat remaining for species was stronger for nonthreatened and nondeclining species. Thus, larger-ranged species that are not threatened and not declining had greater proportions of high-integrity forest as well as lower proportions of low-integrity forest within their ranges than threatened and declining species (Fig. 5*B*). These patterns are evident from the differences in slopes predicted by the models fitted to the data

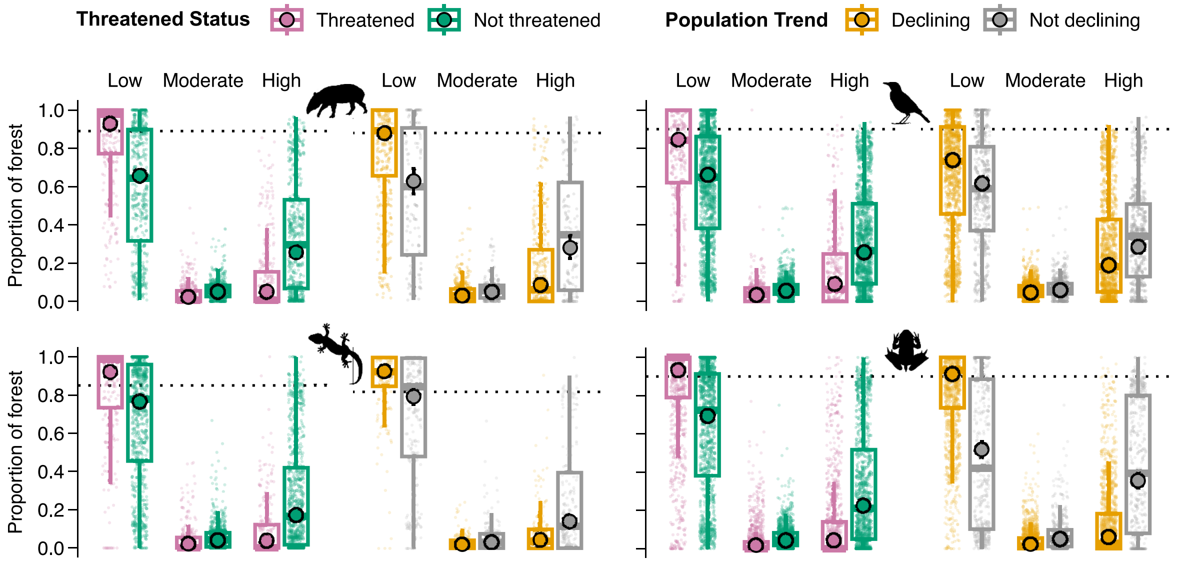

Fig. 2. Variation in the proportion of tropical rainforest with low, moderate, and high integrity in the ranges of forest-dependent terrestrial vertebrate groups in relation to their IUCN threatened status and population trend. Points denote the proportion of forest in each forest integrity and threat or population trend category for individual species and are jittered horizontally to limit overlap. Box plots show the median, 25th, and 75th percentiles. Filled circles represent the mean proportion of forest predicted by the linear mixed models fitted to the data and the associated black error bars are the predicted 95% credible intervals (CRIs). Horizontal dotted lines show the median proportion forest cover (*i.e.*, without considering forest integrity) calculated across all species in each panel. *SI Appendix*, Table S2 for model estimates.

and were consistent across all taxonomic groups (Fig. 5*B* and *SI Appendix*, Table S7).

Forest-Associated Species. Forest-associated species use multiple habitat types, but tropical rainforests may nevertheless provide important refugia or seasonal habitats for many such species (3). Forest-associated species also had low proportions of high-integrity forest within their humid tropical ranges (average 18% across all taxonomic groups; *SI Appendix*, Fig. S2). The differences in high-integrity forest proportions between threatened and nonthreatened and declining and nondeclining forest-associated species were smaller in magnitude than for forest-dependent species, but the overall patterns remained similar and statistically significant in many cases (*SI Appendix*, Fig. S3 and Table S8). Forest-associated species also showed greater high-integrity forest proportions with decreasing conservation concern (*SI Appendix*, Fig. S4 and Table S9) and had low variability in forest cover as a function of threatened status and population trends (*SI Appendix*, Fig. S5 and Table S4). Spatial variation in forest integrity across biogeographic realms observed for forest-dependent species was largely mirrored in forest-associated species (*SI Appendix*, Fig. S6 and Table S10) as were the relationships between forest integrity, range size, and species threatened status and population trends (*SI Appendix*, Fig. S7 and Tables S6 and S11).

Effects of Phylogeny and Other Sensitivity Analyses. We tested whether evolutionary nonindependence influenced our results by including phylogenetic covariance matrices enumerating the proportion of the evolutionary path shared between each pair of species and species identity from the respective phylogenies as random effects in our models (20, 21). We also performed additional tests incorporating taxonomic order and family as random effects. Using phylogenetic covariance matrices, we estimated Pagel's λ phylogenetic correlation measure to be nearly zero (*SI Appendix*, Tables S12 and S13). The low Pagel's λ values are consistent with the variable of interest in this study (*i.e.,* proportion of tropical rainforest of varying integrity) being independent of species phylogenies (21). Consequently, incorporating phylogeny into our analyses yielded nearly identical results (*SI Appendix*, Figs. S8 and S9) as did including random effects for taxonomic order and family in addition to species identity (*SI Appendix*, Figs. S10 and S11). In addition, phylogenetic variance estimated by including species identity from phylogenetic trees as a random effect was consistently low (*SI Appendix*, Tables S2, S3, S12, and S13), and remained low when including taxonomic order, and family as additional random effects in our models (*SI Appendix*, Tables S14 and S15). Together, these analyses suggest our findings are not influenced by potential phylogenetic nonindependence.

The ranges of many species in our dataset overlap, which could lead to potential lack of spatial independence when extracting and analyzing forest structural integrity data from the same regions across many species. Therefore, we used Moran's I statistic and spline correlograms to test for spatial autocorrelation in model residuals as a function of distance between centroids of species humid tropical ranges (3). However, we did not find any evidence for spatial autocorrelation in model residuals (Moran's $I \sim 0$ and $P > 0.05$; *SI Appendix*, Fig. S12). Our results remained consistent after excluding 3,745 species listed as threatened under both IUCN Criteria A (due to decline in habitat extent and/or quality) and B (due to restricted and fragmented geographic ranges) (*SI Appendix*, Figs. S13 and S14 and Table S16). Excluding these species avoids potential circularity in comparative analyses using IUCN threat status data, given habitat extent and/or quality are the variables used to assess their risk of extinction in the first place (3, 16). We did not consider population trends in these analyses of potential circularity because the IUCN Red List criteria are not used for determining overall population trends (3). Further, the relationships between forest integrity, range size, and threatened status also remained robust to the exclusion of species under Criteria A and B (*SI Appendix*, Figs. S15 and S16 and Tables S17 and S18), suggesting our results are not driven by threatened small-ranged species, but reflect broader relationships between geographic range size and forest integrity.

Our conclusions were robust to alternative classifications of the FSII gradient (*SI Appendix*, Figs. S17–S20 and Tables S19–S22) (*Materials and Methods*), based on underlying FSII data distributions rather than the biological rationale (*i.e.,* structural attributes and HFP thresholds—species extinction risk) underpinning our main classification (*e.g.,* Fig. 2 and *SI Appendix*, Fig. S3) (3, 11). Finally, an analysis with the entire forest integrity gradient (FSII values 1 through 18) revealed findings consistent with our main results (*SI Appendix*, Figs. S21 and S22 and Tables S23 and S24). Thus, threatened and declining species tended to have greater proportions of low-integrity forest at FSII values 1 to 3 (than nonthreatened and nondeclining species), with the pattern reversing (change in sign of estimated posterior means; *SI Appendix*, Tables S23 and S24) from FSII 3 or 4 and having greater magnitude (steeper slopes) from FSII 14 onward (*i.e.,* high-integrity forests).

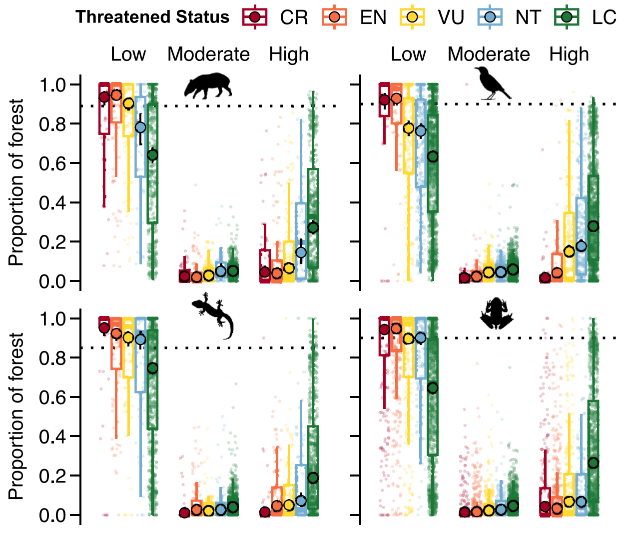

Fig. 3. Variation in the proportion of tropical rainforest with low, moderate, and high integrity in the ranges of forest-dependent terrestrial vertebrate groups in relation to the various IUCN Red List categories (in order of decreasing species conservation concern): Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), and Least Concern (LC). Points denote the proportion of forest in each forest integrity and threat category for individual species and are jittered horizontally to limit overlap. Box plots show the median, 25th, and 75th percentiles. Filled circles represent the mean proportion of forest predicted by the linear mixed models fitted to the data and the associated black error bars are the predicted 95% CRIs. Horizontal dotted lines show the median proportion forest cover calculated across all species in each panel. *SI Appendix*, Table S3 for model estimates.

Discussion

The Importance of High-Integrity Forests for Biodiversity. Habitat loss is considered the leading driver of global declines in biodiversity (22) and the quality of the habitat remaining within species ranges is a key element in determining species extinction risk and population declines (3, 19). In this context, high-integrity tropical rainforests represent critically important biodiversity habitats that, if preserved, may prevent more forest

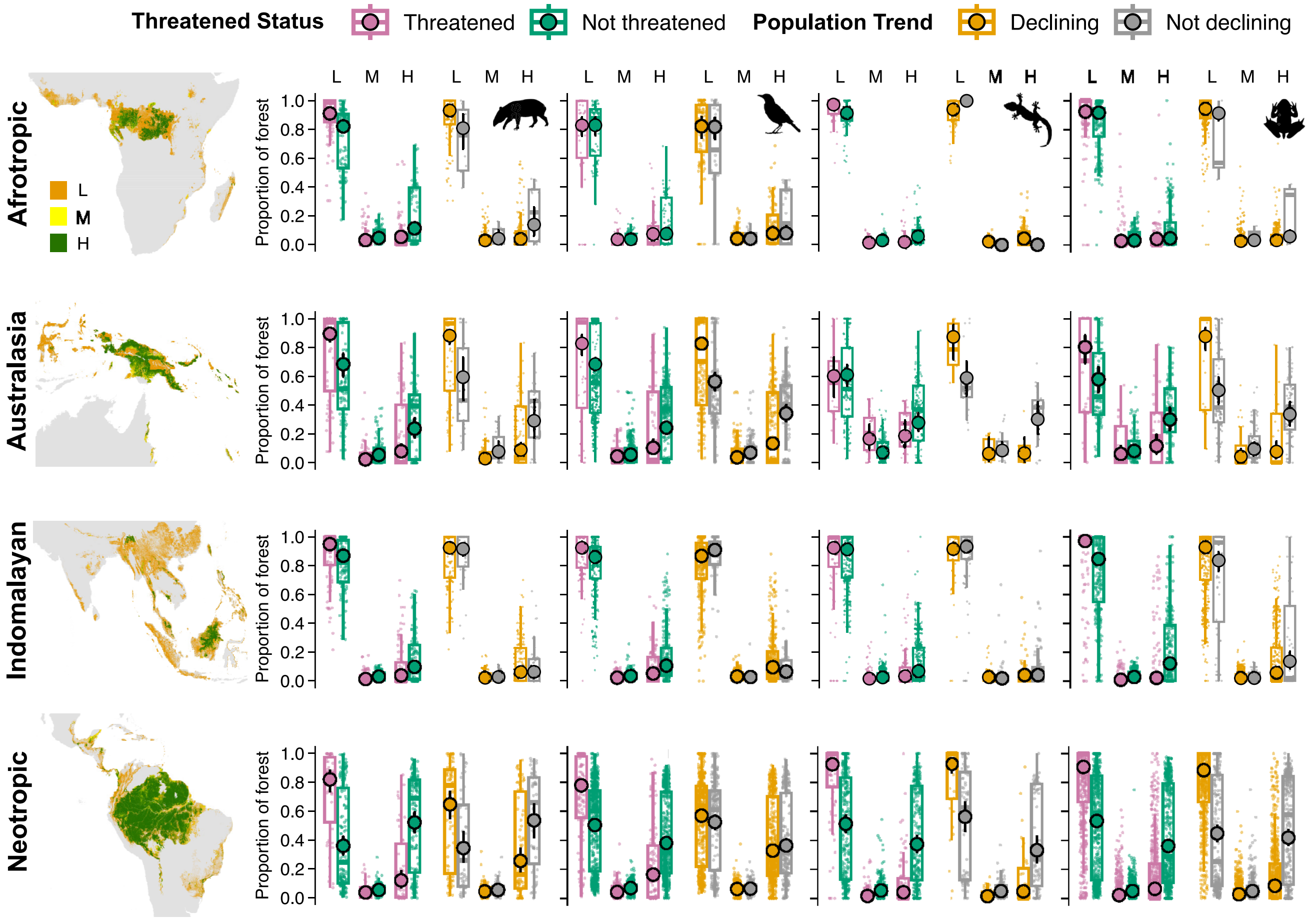

Fig. 4. Comparisons across biogeographic realms: variation in the proportion of tropical rainforest with low (L), moderate (M), and high (H) integrity in the ranges of forest-dependent terrestrial vertebrate groups in relation to their IUCN threatened status and population trend. Orange, yellow, and green areas on the maps of each realm show the distribution of low-, moderate-, and high-integrity rainforest respectively. Points denote the proportion of forest in each integrity and threat or population trend category for individual species and are jittered horizontally to limit overlap. Box plots show the median, 25th, and 75th percentiles. Filled circles represent the mean proportion of forest predicted by the linear mixed models fitted to the data and the associated black error bars are the predicted 95% CRIs. *SI Appendix*, Table S5 *A–D* for model estimates.

species from becoming threatened and undergoing population declines over time (3). We show high-integrity forests currently encompass only a quarter of the humid tropical ranges of forest-dependent vertebrates. Of this sparse amount of high-integrity forest, disproportionately lower extents are left within the ranges of threatened and declining vertebrates compared with nonthreatened and nondeclining species. Crucially, species at greatest risk of extinction have the least high-integrity forest habitat remaining, such that further deforestation and forest degradation could trigger a cascade of extinctions (3, 16). Threatened species are exposed to intense human pressure, even across range sizes (19), which explains why threatened and declining species had lower extents of high-integrity forest than nonthreatened and nondeclining species along a range size gradient. Although up to 90% of forest-dependent species ranges was encompassed by forest cover, much of this forest cover is structurally degraded and under high pressures, as evident when juxtaposed against our findings on the large extents of low-integrity forest within species ranges.

Our work represents a comprehensive assessment quantifying the proportion of high-integrity tropical rainforests left within the ranges of all four taxonomic groups of terrestrial vertebrates worldwide. These findings are an advance over prior research that has mostly focused on how forest cover loss impacts biodiversity (23, 24) and on intact forest landscapes and species extinction risk (25). Our inferences are not based on a random sample from the evolutionary tree of life but limited to terrestrial vertebrates. We focused on terrestrial vertebrates because they represent the only taxonomic groups for which all known species have a described geographic range and the habitat associations of most of these vertebrates are also assessed in the IUCN Red List of Threatened Species (7). Although the ranges of species in other understudied taxonomic groups such as trees and ants have recently been described (26, 27), comparable data on range maps and habitat associations remain unavailable for the majority of invertebrates and vascular plants that dominate tropical species diversity and biomass (28, 29). Obtaining such data on species in these highly biodiverse groups is an imposing challenge, but one that must be surmounted to understand the distribution of biodiversity on Earth and the extent and consequences of human modification of their native habitats.

Prior work has shown intense human pressure is pervasive within vertebrate species ranges (19). Further, it is now known that intact forest structure and low human pressure are cumulatively associated with lower species extinction risk than either structure or pressure considered individually (3). In this context, our work draws attention to the degraded structural condition and high human pressures within much of tropical rainforest habitats remaining for biodiversity. Degraded forests are increasingly dominating tropical landscapes and selective logging is the main driver of this trend (30, 31). Although no amount of degradation

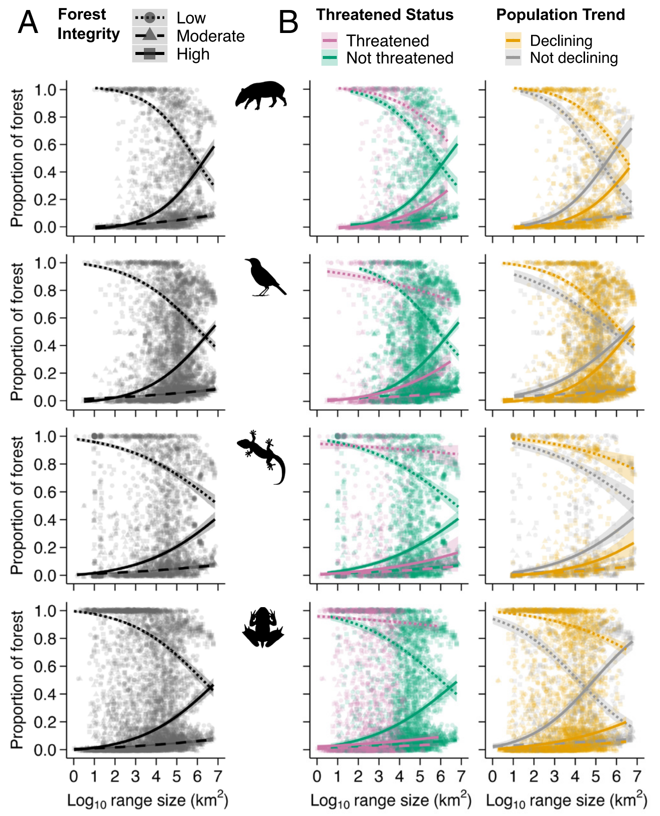

Fig. 5. Relationships between forest integrity, geographic range size of forest-dependent terrestrial vertebrate groups, and their threatened status or population trend. (*A*) Species with larger ranges had a greater proportion of moderate- (dashed lines) and especially high-integrity forest (solid lines), and a lower proportion of low-integrity forest (dotted lines) than species with smaller ranges. (*B*) Larger-ranged species that are not threatened and not declining had greater proportions of high-integrity forest and lower proportions of low-integrity forest within their ranges than threatened or declining species. Points represent the proportion of forest for species as a function of range size and threat status or population trend and are jittered vertically and horizontally to reduce overlap. Circle, triangle, and square point types denote low-, moderate-, and high-integrity forest respectively. The lines show the mean relationships between the forest integrity gradient, range size, and threat or population trend predicted by the linear mixed models fitted to the data and the shaded areas of the lines are the predicted 95% CRIs. Dotted, dashed, and solid line types denote predicted relationships for low-, moderate-, and high-integrity forest respectively. *SI Appendix*, Tables S6 and S7 for model estimates.

from logging is too low to have zero impact on biodiversity, recent work in Southeast Asia suggests low intensity logging (<29% biomass removal) is associated with largely intact functional composition (32). Given logged structurally degraded forests under high human pressures can still harbor considerable biodiversity and maintain ecosystem functioning (33–35), it would be worth restoring logged forests of lower integrity wherever feasible as opposed to converting them into agricultural lands or monoculture plantations. Yet, halting the expansion of logging, roads, and other major pressures within remaining high-integrity tropical rainforests is crucial to arrest any further degradation of these irreplaceable ecosystems (30, 31, 36). Additionally, mandating reduced impact logging practices, sustainable harvest yields, and alleviating major human pressures within forests will allow natural regeneration and recovery of rainforests that are already disturbed (32, 36).

High-Integrity Forests in Conservation Policy and Research. Halting deforestation represents a vital first step in mitigating the loss of tropical forest biodiversity (3). However, as the rates of degradation and conversion of tropical forests intensify worldwide (37, 38), a growing number of calls have advocated for preserving the highest quality remaining forests (4, 6, 39). Such calls are based on strong evidence that the world's high-integrity forests sustain a remarkable convergence of biodiversity, carbon stocks, and indigenous cultures and influence planetary health through their role in climate regulation (6, 40–42). The recent shift in conservation policy is exemplified by the direct inclusion of ecological integrity, for the first time, in the goals and targets of the Convention on Biological Diversity's 2022 Kunming-Montreal Global Biodiversity Framework (GBF) (9). Indeed, Target 1 of the GBF aims to achieve near zero loss of high biodiversity importance areas—including ecosystems of high integrity—by 2030, while Target 2 additionally calls for global action to restore ecological integrity. Together, these targets can support longstanding goals of protecting ecosystems and species as called for in Targets 3 and 4 (9).

To support governments in quantifying their contributions toward meeting native ecosystem integrity targets, the global forest integrity data in this study can be adapted to reflect unique ecoregional characteristics of forests in individual countries and generate national forest quality indicators feasible to implement under specific national contexts (43). Understanding the effects of forest degradation on species populations has long been reliant on field studies to estimate differences in species occurrence and abundance in degraded versus reference primary forests (44). With advances in remote sensing (45), a key future research direction is the development of statistical methods to integrate fine-scale field data on species abundance with high-resolution remotely sensed ecosystem integrity for inferences on local species populations at global and national scales (46, 47). Future maps of forest structural condition can also be informed and refined by considering the climatic, environmental, evolutionary, and biogeographic drivers underlying variation in canopy cover and height across different regions (48). Moving forward, the Global Ecosystem Dynamics Investigation (GEDI) instrument onboard the International Space Station, expected to operate through 2030, will ensure the continuity of Earth observations on three-dimensional forest structure and facilitate future efforts at monitoring forest integrity (49–51).

Conclusions

Our research suggests the targeted preservation of remaining high-integrity tropical rainforests that are currently unprotected would represent a key step toward limiting the scale and magnitude of the biodiversity crisis across the hyperdiverse humid tropics. Preserving high-integrity forests may also prevent native humid tropical ecosystems from crossing critical ecological tipping points (32, 52, 53) and catalyze action toward the ambitious vision of a world living in harmony with nature by 2050 (9). Time is rapidly running out for many tropical rainforest species such that targeted action to secure their imperiled habitat is of paramount importance before extinction becomes a foregone conclusion.

Materials and Methods

Geographic Range Maps. We conducted our analyses across the full extent of the tropical and subtropical moist broadleaf forest biome, which encompasses the present-day distribution of tropical rainforests around the Equator and primarily between the Tropics of Cancer and Capricorn (12). These forests largely span the latitudes between 23.5°N and 23.5°S but extend into the subtropics in some areas (3, 11). We obtained established geographic range maps for terrestrial mammals (15), birds (54), reptiles (55), and amphibians (15, 56). The original datasets contained range maps for 5,566 mammals, 11,125 birds, 10,064 reptiles, and 6,684 amphibians and include ranges for species that are extinct as well as range extents based on uncertain data. We processed range maps following the protocols in Pillay et al. (7), performing a series of filters to discard extinct species and records based on uncertain data. After performing these filters, our list of species for subsequent analyses included 5,529 mammals, 10,935 birds, 10,054 reptiles, and 7,264 amphibians, for a total of 33,782 species of extant terrestrial vertebrates worldwide (*SI Appendix*, *Supporting Text*).

We projected all geographic range maps to the World Mollweide projection prior to analyses and used Python code implemented with the ArcPy module in ArcGIS Pro 2.5.0 to perform a union of the range map of each species with the map of the tropical rainforest biome. This procedure allowed us to distinguish parts of the global range of species that overlap the tropical rainforest biome, should there be such overlap for a given species. We did not set a lower bound for range overlap with tropical rainforests because such a threshold would be arbitrary. Moreover, it would also exclude species that marginally occur in tropical rainforests but for which these ecosystems nevertheless represent important habitats (*e.g.,* some species of wintering migratory birds) (7). Thereafter, we used species-level attributes from the IUCN Red List of Threatened Species to obtain data on the major habitats in which each species occurs to limit some forms of commission or false positive errors that may occur with range maps. Specifically, these errors include species whose ranges may overlap with the tropical rainforest biome but do not actually use the forests within that biome (7). For species having range overlap with the tropical rainforest biome, we retained only species reported to occur in tropical forest habitat types listed in the IUCN Habitats Classification Scheme (57). We merged this list of species reported to occur in tropical forest habitats with the list of species whose ranges overlap the tropical rainforest biome to retain 3,327 mammals, 7,704 birds, 3,828 reptiles, and 5,298 amphibians, for a total of 20,157 species (7). To ensure the names of vertebrate species being analyzed matched those considered by Pillay et al. (3), we discarded additional species from the above dataset by matching species names with those in the respective phylogenetic trees for each taxonomic group (for the final list of species in this study, see Statistical Analyses). We note the habitat associations of approximately 30% of reptile species whose ranges overlap tropical forests remain unknown because reptiles are one of the most understudied terrestrial vertebrate groups (7, 58). We tried to limit potential geographic bias from this issue by analyzing each taxonomic group independently and by estimating spatial variation in the extent of high-integrity forests across biogeographic realms (3).

Definition of Tropical Rainforest Obligate Species. We defined dependency on tropical rainforests following the criteria established by Pillay et al. (7). We considered a species to be rainforest obligate if 1) 80 to 100% of its global range overlapped with the tropical rainforest biome, and 2) it was near-exclusively reported from the tropical rainforest habitat types listed in the IUCN Habitats Classification Scheme (57). We did not exclude wetlands, rocky, and cave habitats from this second criterion, making the reasonable assumption that for species with >80% range overlap with the tropical rainforest biome and nearly exclusively associated with rainforest habitats, these three other habitat types are likely to be within tropical rainforests (*e.g.,* bats that roost in caves within rainforest habitats).

Tropical Rainforest Structural Condition and Integrity Indices. We used two indices of tropical rainforest quality in our analyses—the SCI and the FSII (10, 11). The SCI is a fine-scale (30 m resolution) raster derived from three datasets: global tree canopy cover in 2010 (59), time since forest loss (between 2000–2017) (59), and canopy height in 2012 (60). It identifies locations of taller, older, more structurally complex, closed-canopy rainforests across the global humid tropics. The reference year is 2013, with canopy cover from 2010, forest loss expressed as year of loss before 2018 and canopy height for 2012. The SCI ranges from 1 to 18, encompassing short, open-canopy recently disturbed forests to tall closed-canopy stands (10, 11). The lowest SCI value of 1 delineates stands <5 m tall, disturbed since 2012 or with canopy cover <25%. The highest SCI value represents tall, closed canopy stands (>15 m in canopy height and >75% canopy cover) undisturbed since 2000, which represent forests of intact structure typical of native forests in the humid tropical biome (11). An accuracy assessment found that the SCI was able to distinguish forest structure up to this threshold, beyond which the relationship saturated (10). We note approximately 20% of older secondary and logged forests can have structural characteristics that place them in the high SCI category. However, airborne lidar data used for validation of the SCI showed that these older secondary forests had approximately 75 to 80% of the foliage height diversity of primary forests (10). To ensure our analysis deals with the structure of stands that meet the criteria of being forest and is not confounded with recent forest loss, we categorized the lowest SCI values of 1 as nonforest and completely removed these values from analyses of structural condition and integrity. We also pooled all SCI values 2 to 18 that represent forest to calculate the total area of forest cover within species ranges (3).

The FSII is derived by overlaying the Human Footprint (HFP), a 1 km resolution measure of the cumulative in situ pressures humans exert on natural areas across terrestrial Earth (13), on the SCI. The HFP ranges from 0 to 50, representing a gradient of increasing human pressure (13). The original 1993 HFP (61) was updated to 2009 (62), and more recently to 2013 (13). The FSII ranges from 0.1 to 18 with the higher values representing rainforests high in structural complexity and low in human pressure. For comprehensive details on the SCI and FSII datasets, see Hansen et al. 2019 (10), 2020 (11). As with the range maps, we projected the SCI and FSII raster datasets to the World Mollweide projection prior to analyses. Given the differing resolutions of the SCI and FSII rasters, (30 m and 1 km, respectively), we first made them comparable by resampling to 1 km resolution (identical to the HFP) using bilinear interpolation in ArcGIS 10.7. After resampling, the SCI raster comprised 1 km resolution pixels of values ranging from 1 to 18. We also converted the continuous pixel values of the FSII dataset to the nearest integer, such that the resampled FSII raster comprised 1 km resolution pixels of values ranging from 0 to 18. A relatively fine resolution such as used here facilitates efficient identification of forest cover and structurally intact and high integrity forests within species ranges and is recommended when the objective is to distinguish the effects of broad habitat categories on biodiversity (63, 64).

Classifying the SCI and FSII Gradient into High, Moderate, and Low Forest Quality Categories. We used Python code implemented with the ArcPy module in ArcGIS Pro 2.5.0 to calculate the area (km^2) of each of the 18 values of the SCI and 19 values of the FSII rasters within the humid tropical range of each species. Following the criteria established by Hansen et al. (11) and Pillay et al. (3), we categorized and summed the area under SCI pixel values ranging from 2 to 5 (>25% canopy cover and >5 m canopy height) as low SCI or structurally degraded forest, values from 6 to 13 as moderate SCI forest, and values from 14 to 18 (>75% canopy cover and >15 m canopy height) as high SCI or structurally intact forest. We followed a similar procedure to categorize and sum the area under FSII values from 1 to 5, 6 to 13, and 14 to 18 as low, moderate, and high integrity forest respectively. As with the SCI dataset where we removed the lowest values of 1, we also removed the lowest FSII values of 0 to ensure our analysis deals with the structure of stands that meet the criteria of being forest and is not confounded with recent forest loss (3).

The biological rationale underlying our pooling of the SCI and FSII forest quality gradient as noted above is based on key structural attributes of forests as well as prior knowledge of HFP thresholds and their relationship with extinction risk for terrestrial vertebrates (14). Thus, high-integrity forests have >75% canopy cover, >15 m tree height, are undisturbed since 2000, and have low human pressures (HFP ≤ 4) typical of undisturbed native forests in the humid tropical biome (3, 11). Low-integrity forests are not only highly degraded in structure with at least 25% canopy cover and 5 m tree height but also have high human pressures (HFP > 15). Moderate-integrity forests encompass a range of structural complexity with canopy cover from 25 to 95% and canopy height at least 15 m but have intermediate human pressures (HFP > 4 and ≤15) compared with high- and low-integrity forests (10, 11). Prior research suggests these values of HFP represent potential thresholds that can influence vertebrate species extinction risk (3, 11, 14). We note the relatively low frequency of moderate-integrity forests in our data (*e.g.,* Fig. 2) is likely due to the fact that i) forests undisturbed since 2000 but with tree height <15 m, and ii) forests with >15 m tree height but <75% canopy cover both tend to be uncommon.

Alternative Approaches to Classifying the FSII Gradient. The FSII data are distributed toward the low integrity end of the gradient (*i.e.,* most species have considerably greater proportions of low-integrity forest in their ranges than high-integrity forest). Therefore, we also examined two alternative classifications of the FSII gradient to test whether the underlying FSII data distributions would influence our conclusions. In the first classification, we categorized and summed the area under FSII values from 1 to 2, 3 to 13, and 14 to 18 as low, moderate, and high integrity forest respectively. In the second binary classification, we categorized and summed the area of FSII values from 1 to 13 and 14 to 18 as low and high integrity forest respectively.

Species Phylogenies. The vertebrate species in each taxonomic group are the primary units of analysis in this study but may be considered nonindependent due to the variable degree of evolutionary relatedness between the species in each group. To account for the potential effect of evolutionary nonindependence in our statistical analyses, we obtained 10,000 available global or full phylogenetic trees based on Hackett pseudoposterior distributions for mammals (65), birds (66), reptiles (67), and amphibians (68). We matched the species lists from the previous steps to discard species not in the respective phylogenetic trees. Our list of species after this step comprised 3,217 mammals, 6,674 birds, 3,735 reptiles, and 5,069 amphibians, for a total of 18,695 species of vertebrates. We further discarded 2,299 Data Deficient species for a final total of 16,396 species in all analyses where IUCN threatened status served as a predictor variable (*SI Appendix*, Table S1). We also discarded 5,842 species with Unknown population trends for a final total of 12,853 species in all analyses where IUCN population trends were a predictor variable. We performed a series of steps to ensure the phylogenetic trees were ultrametric and rooted and then used these trees to account for potential evolutionary nonindependence as detailed below.

Statistical Analyses. We used linear mixed-effects models fit in a Bayesian framework via the package "MCMCglmm" (69) in R (v.4.3.1) (70) for the statistical analyses in this study. These models not only allow continuous nonbinomial proportions to be used as response variables (see below) but also enable the inclusion of species phylogenies as random effects to test for potential evolutionary nonindependence.

The response variable in the main and all supporting analyses in this study is the proportion of tropical rainforest within species humid tropical ranges. We note the proportions of tropical rainforest in our analyses are nonbinomial (*i.e.,* not precisely 0 or 1) but instead range continuously between 0 and 1 (*i.e.,* 0 to 100%). Therefore, we used a linear regression framework for all our analyses. Continuous proportions of this nature are nevertheless bound between 0 and 1, which raises the possibility of model predictions outside these bounds when used as the response variable in regression analyses (71). Yet, proportions are scale-independent and more biologically meaningful than absolute quantities when comparing relative amounts of two or more categories of variables of interest (*e.g.,* high-integrity forest proportions within the ranges of threatened vs. nonthreatened species). To solve the issue of the bounded nature of continuous proportions in our study, we performed a logit transformation of proportion data: $\log y/[1 - y]$, as recommended by Warton and Hui (71). Proportions at exact lower or upper bounds of 0 or 1 can result in undefined values when a logit transformation is applied. To avoid undefined values, we performed the logit transformation via the R package "car" (72), which remaps 0 and 1 values to 0.025 and 0.975 respectively by adding a small constant prior to transformation. The approach transforms continuous proportions to real line values ranging from −*infinity* to +*infinity*, thereby overcoming the bounded nature of proportion data (71).

Fixed Effects. There were two predictor variables (fixed effects) in our main analysis. The first was a categorical variable representing species IUCN threatened status or population trends. Threatened status was represented by two levels: threatened or nonthreatened. To achieve this binary classification, we defined IUCN Critically Endangered, Endangered and Vulnerable species as threatened and Near Threatened and Least Concern species as nonthreatened, while discarding Data Deficient species (3, 16). Similarly, population trends were represented by two levels: declining and not declining. To achieve this binary classification, we defined IUCN Decreasing species as declining in population and Increasing and Stable species not declining in population, while discarding species with Unknown population trends (3, 16). The second predictor variable in our analysis was a categorical variable representing the pooled forest integrity gradient and comprised three levels: low, moderate, and high integrity. We then examined variation in the proportion of forest within species ranges as a function of two-way interactions between species threatened status and the gradient in forest integrity as well as between species population trends and the gradient in forest integrity.

Random Effects and Testing for Phylogenetic Nonindependence. We examined the potential for evolutionary nonindependence to influence our results using two approaches with the phylogenetic trees obtained for each taxonomic group. In the first approach, we explicitly tested for phylogenetic correlation by including not only species identity from the respective phylogenetic trees as a random effect in each analysis, but also phylogenetic covariance matrices enumerating the proportion of the evolutionary path shared between each pair of species. We derived Pagel's lambda (λ) phylogenetic correlation measure from the posterior distributions of estimated phylogenetic and residual variance, which we calculated as

$\lambda = \mathrm{Var}_{[\mathrm{phylogenetic}]} / [\mathrm{Var}_{[\mathrm{phylogenetic}]} + \mathrm{Var}_{[\mathrm{residual}]}]$ (20). Pagel's λ is a phylogenetic correlation measure typically bound between 0 and 1 (21). If $\lambda = 0$, the traits under consideration (or the variable of interest) likely evolved independent of phylogeny. If $\lambda = 1$, traits likely evolved under Brownian motion *i.e.,* variation between species accrued along the branches at a rate proportional to the length of the branches. Intermediate λ values can suggest traits evolved by a process where the effect of phylogeny is weaker than the Brownian model (21).

We found Pagel's λ values were nearly zero across all forest-dependent and forest-associated taxonomic groups in our analyses with the full phylogenetic models (*SI Appendix*, Tables S12 and S13), consistent with the variable of interest in this study (*i.e.,* proportion of tropical rainforest along the gradient of high, moderate, and low integrity) being independent of species phylogenies. Given this negligible phylogenetic signal, we used an alternative model that only included species identity derived from the respective phylogenetic trees as a random effect in all analyses in this study (16). We were thus able to account for any remaining potential statistical nonindependence due to the fact that species are the replicates in this study. Further evidence that phylogenetic nonindependence did not influence our conclusions is the near-identical set of results from these alternative models with species identity as a random effect (Fig. 2 and *SI Appendix*, Fig. S3 and Tables S2 and S8) compared with full phylogenetic models (*SI Appendix*, Figs. S8 and S9 and Tables S12 and S13). Phylogenetic variance, estimated by including species identity from phylogenetic trees as a random effect, remained consistently low across all the various analyses in this study (*SI Appendix*, Tables S2 and S3 and S5–S24). Moreover, additional tests with random intercepts for taxonomic order and family in addition to species identity also showed low phylogenetic signal (*SI Appendix*, Tables S14 and S15) and near-identical results (*SI Appendix*, Figs. S10 and S11). Together, these analyses suggest potential phylogenetic nonindependence did not influence any of our results (*SI Appendix*, Supporting Text for details).

Model Priors and Iterations. Following the recommendations of Hadfield et al. (73), we specified an uninformative inverse-Wishart distribution prior for the fixed effects (threatened status or population trends and FSII category) with variance $V = 1$ and the belief parameter nu = 0.002 for the R-structure (*i.e.,* residuals). We used parameter-expanded priors for G-structure (*i.e.,* random effect of species identity), described by the parameters $V = 1$, nu = 0.02, prior mean (alpha.mu) = 0, and SD (alpha.*V*) = 1,000 to improve mixing and limit autocorrelation among iterations for the random effect. We used a Gaussian distribution for all models and ran simulations for 10,000 iterations, burning in 3,000 iterations and thinning our chains by an interval of 5 for a total of 2,000 posterior samples.

Model Diagnostics. We tested for convergence across the three model runs for each analysis using the Gelman–Rubin convergence diagnostic via the gelman.diag function in the R package "coda" (74), where the upper limits of the potential scale reduction factor (PSR) are required to be <1.1 (75). We also visually examined trace plots to ensure convergence across runs, density plots to ensure approximate normality of the posterior distributions of model parameters, and effective sample sizes to confirm all values exceeded 200.

Across all analyses, our model runs showed strong evidence of good convergence, approximate normality of posterior distributions of fixed effects and residuals, and greater than recommended effective sample sizes (*SI Appendix*, Figs. S23–S30). We note the random effects for species identity showed low variance (*SI Appendix*, Figs. S23–S30) and this low variance was also observed in random effects for taxonomic order and family (*SI Appendix*, Tables S14 and S15), consistent with negligible phylogenetic signal in the response variable in this study (*i.e.,* proportion of tropical rainforest of varying integrity).

Data, Materials, and Software Availability. Data spreadsheets, code, and range maps for 659 amphibian species from González-del-Pliego et al 2019 (56) have been deposited in Zenodo (76).

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