Humid tropical vertebrates are at lower risk of extinction and population decline in forests with higher structural integrity

Reducing deforestation underpins global biodiversity conservation efforts. However, this focus on retaining forest cover overlooks the multitude of anthropogenic pressures that can degrade forest quality and imperil biodiversity. We use remotely sensed indices of tropical rainforest structural condition and associated human pressures to quantify the relative importance of forest cover, structural condition and integrity (the cumulative effect of condition and pressures) on vertebrate species extinction risk and population trends across the global humid tropics. We found that tropical rainforests of high integrity (structurally intact and under low pressures) were associated with lower likelihood of species being threatened and having declining populations, compared with forest cover alone (without consideration of condition and pressures). Further, species were more likely to be threatened or have declining populations if their geographic ranges contained high proportions of degraded forest than if their ranges contained lower proportions of forest cover but of high quality. Our work suggests that biodiversity conservation policies to preserve forest integrity are now urgently required alongside ongoing efforts to halt deforestation in the hyperdiverse humid tropics.
not all forest cover is equal. The degree of anthropogenic degradation can diminish forest integrity34, which in turn may have severe adverse effects on biodiversity35. Recognizing this, the Convention on Biological Diversity (CBD) has included in their draft post-2020 Global Biodiversity Framework (GBF) a goal to enhance the integrity of native ecosystems36. The aspiration behind this goal is to achieve greater conservation success than occurred under the Aichi Biodiversity Targets3. Yet, there remains a lack of evidence on whether intact tropical rainforests have the potential to buffer species against extinction, when directly compared with forest cover.

Recent advances in remote sensing have facilitated the development of two fine-scale indices of tropical forest quality37, which now provide the ability to quantify the association between structurally intact forests under low human pressures and measures of biodiversity. The Structural Condition Index (SCI), a consistent 30 m resolution measure of forest condition across the global humid tropics, enables identification of taller, older, more structurally complex, closed-canopy rainforests (hereafter, ‘structurally intact forests’)38. Structurally intact forests may deteriorate with anthropogenic pressures (for example, settlements, roads, fire, selective logging and hunting), and the adverse impacts of such pressures on biodiversity may surpass those of deforestation alone39. To capture such pressures, the Forest Structural Integrity Index (FSII)38,9 combines the SCI with the Human Footprint (HFP)37 to distinguish rainforests of intact structural condition and minimal human modification (hereafter, ‘high-integrity forests’).

Here, we quantify the association between species extinction risk and population trend and the amount of high-integrity forest remaining within the geographic ranges of humid tropical vertebrates, relative to the amount of structurally intact forest and forest cover alone (without consideration of either structural condition or integrity). We used the IUCN Red List category of extinction risk and overall population trend40 for 16,396 mammal, bird, reptile and amphibian species whose ranges overlap the tropical and subtropical moist broadleaf biome (also known as the tropical rainforest or humid tropical biome)40. We classified species as either rainforest-obligate (dependent on rainforests) or rainforest-associated (use rainforests as well as other habitat types) on the basis of the extent of range overlap with the tropical rainforest biome and association with tropical forest habitats40, expecting the potential effects of forest integrity to be stronger for rainforest-obligate species than for associated species. Within species humid tropical ranges (the sampling unit for this study), we used the SCI and FSII datasets to calculate the area (km²) of structurally intact and high-integrity forests, relative to the area of structurally degraded and low-integrity forests. We also pooled all SCI values representing forest to calculate the total area of forest cover within species ranges, relative to non-forest area.

We used a generalized linear modelling framework that accounts for the phylogenetic non-independence of species to test whether greater high-integrity forest area within species ranges is associated with lower odds of species extinction risk and declining population trends across rainforest-obligate and rainforest-associated vertebrate groups, compared with forest cover alone (Fig. 1). A 95% confidence interval (CI) of odds ratios of standardized coefficients did not overlap 1; Supplementary Table 2, false discovery rate (FDR)-adjusted P < 0.05). For example, among rainforest-obligate mammals, greater high-integrity forest area within species ranges was associated with less than half the odds of being threatened (odds ratio: 0.40, 95% CI: 0.33–0.48) relative to greater area of forest cover alone (odds ratio: 1.32, 95% CI: 1.00–1.77). We also found that structurally intact forests tended to be associated with lower odds of species extinction risk and declining populations than forest cover alone. This pattern was stronger in some groups (for example, rainforest-obligate and rainforest-associated birds being threatened and amphibians having declining populations; Fig. 1) than in others (for example, rainforest-associated reptiles having declining populations). However, structurally intact forests tended to be associated with higher odds of species extinction risk and declining populations than were high-integrity forests, with this pattern again stronger in some groups (for example, rainforest-obligate and rainforest-associated mammals, reptiles and amphibians being threatened; Fig. 1) than in others (for example, rainforest-obligate birds having a declining population). The strength of high-integrity forests in being associated with low extinction risk and declining populations was similar for both species extinction risk and declining population trends than either structural condition or human pressures considered individually (Extended Data Fig. 1 and Supplementary Table 3).

Species tended to face higher probabilities of extinction risk and declining populations if their ranges contained high proportions of forest cover but forest of low structural condition and integrity (large extents of degraded forest) than if their ranges contained lower proportions of forest cover of high condition and integrity (Fig. 2). Evidence for this finding is the strong positive statistical interaction (95% CIs did not overlap zero and FDR-adjusted P < 0.05; Supplementary Tables 4 and 5) in 18 out of 32 models testing for two-way interactions between forest cover and condition and between forest cover and integrity on both response variables in each taxonomic group. A further nine such interactions were positive albeit statistically non-significant (95% CIs overlapped zero and FDR-adjusted P > 0.05). These patterns were also consistent for two-way interactions between forest condition and integrity on both response variables (Extended Data Fig. 2 and Supplementary Table 6). However, inconsistent with these general trends, rainforest-obligate birds, reptiles and amphibians had lower probabilities of declining populations when larger proportions of high-integrity forest cover remained within species ranges (Fig. 2 and Extended Data Fig. 2), as indicated by negative two-way interactions between forest cover and condition, forest cover and integrity and forest condition and integrity in 6 out of 48 models (Supplementary Tables 4–6).

The buffering effect of forest integrity against species extinction risk was observed in every biogeographic realm (Fig. 3 and Supplementary Table 7). After statistically controlling for the effects of forest cover (among species with average area of forest cover within their ranges), the probability of rainforest-obligate vertebrates being threatened decreased significantly with increasing forest integrity, compared with baseline estimates for each realm (without consideration of either forest cover or integrity; Fig. 3). Similarly, the probability
of rainforest-obligate vertebrates having declining populations also decreased significantly with increasing forest integrity in some realms, compared with baseline estimates. However, there was considerable variation in this trend among mammals and birds in the Indomalayan and Neotropical realms and reptiles in the Afrotopics, such that the probability of population decline with increasing forest integrity was not significantly different from baseline estimates (95% CIs overlapped; Fig. 3). Indomalayan vertebrates faced the highest overall risk (with the exception of amphibians in Australasia and reptiles in the Afrotopics, congruent with prior findings for non-vertebrates in this region23. These findings for rainforest-obligate vertebrates were mirrored in species associated with tropical rainforests (Extended Data Fig. 3).

Our conclusions were robust to a range of plausible error in mapping canopy cover and height with the SCI and FSII datasets, performed by adjusting the SCI classification boundaries for canopy cover and height up and down by 20% to simulate potential errors (Methods; Supplementary Table 8 and Extended Data Fig. 4) and thereafter propagating such errors to statistical models (Extended Data Fig. 5 and Supplementary Tables 9 and 10). Our findings also remained consistent when we pooled the area of moderate structural condition and integrity forests with high structural condition and integrity forests (Methods; Extended Data Fig. 6 and Supplementary Table 11), suggesting that forests of moderate structural condition and integrity can support biodiversity conservation. We conducted an alternative statistical analysis based on model selection with Akaike’s Information Criterion (AIC) to further test the robustness of our conclusions. Here, we fit a candidate set of four univariate models (forest integrity, structural condition, human pressure and forest cover parameterized individually) to each response variable. This analytical approach also showed substantial support for forest integrity as the most important variable in predicting low likelihood of species extinction risk and declining population trends (lowest AIC score and highest model weight; Supplementary Table 12).

Our results were consistent across degrees of threat; critically endangered, endangered and vulnerable species showed positive effects of forest integrity (Extended Data Fig. 7 and Supplementary Tables 13 and 14). We also performed sensitivity analyses to exclude species designated as threatened because of decline in habitat extent and/or quality (criterion A of the IUCN Red List22) and because of restricted and fragmented geographic ranges (criterion B24). The exclusion of species under criteria A and B avoids potential circularity between comparative analyses of extinction risk and the IUCN criteria used to assess extinction risk22. However, the association of high-integrity tropical rainforests with lower odds of species extinction risk (relative to forest cover alone) remained evident even after excluding species threatened under criteria A and B (Extended Data Fig. 8 and Supplementary Tables 15–17). We note that we did not consider declining population trends in this analysis of potential circularity because the IUCN Red List criteria are not used for determining overall population trends. The humid tropical ranges of many species in our dataset overlap, leading to a potential lack of spatial independence when extracting and analysing forest structural condition and integrity data from the same regions across multiple species. Therefore, we tested model residuals for spatial autocorrelation as a function of distance between centroids of species humid tropical ranges (Moran’s I25). We found no evidence for spatial autocorrelation (Moran’s I < 0.1 and P > 0.05; Supplementary Figs. 1–6).

Discussion

Reducing deforestation is a central pillar of global biodiversity conservation efforts and indeed represents a critical first step in averting species losses26. However, we demonstrate that high-integrity forests are associated with considerably lower risk of humid tropical vertebrate species extinctions and population declines, when directly compared with forest cover. We show that high-integrity forests are important not only for rainforest-obligate species but also for rainforest-associated species that may use these ecosystems as refugia or on a seasonal basis. Moreover, high-integrity forests were associated with lower odds of species extinction risk and declining population trends than either structural condition or human pressures considered individually, suggesting that intact structure alone may be insufficient to conserve rainforest biodiversity without also limiting human pressures within forests. Consequently, preserving the last-remaining structurally intact tropical rainforests and limiting human pressures within these ecosystems may prevent more species from becoming threatened and undergoing population declines over time. Furthermore, high-integrity forests may be more resilient to large-scale environmental perturbations (for example, climate change) than are degraded forests27. Thus, the buffering effect of high-integrity forests on biodiversity may potentially increase over time because forests that are already degraded will probably experience intensifying pressures exacerbated by climate change28. Overall, our work suggests that biodiversity conservation policies aimed at preserving forest structure and maintaining low human pressures
The higher odds of species extinction risk and declining populations associated with forest cover may be surprising given existing knowledge on the benefits of forest cover on biodiversity, typically when forest cover is considered in standalone analyses or compared with land-uses often inimical to biodiversity such as agriculture and development. However, our work is an assessment of the importance of forest cover relative to remotely sensed measures of forest structural condition and integrity (variables that represent the quality of forest cover) on species extinction risk and population trends across the global humid tropics. We report odds ratios of standardized partial regression coefficients, which represent unbiased estimates of the effects of forest cover alone on each response variable, relative to structurally intact and high-integrity forests (controlling statistically for the effects of forest condition and integrity). Thus, our results probably reflect how various forms of structural degradation (for example, selective logging) and human pressures (for example, hunting) within forest cover may adversely affect biodiversity, compared with structurally intact forests with low levels of such pressures. We note that when forest cover was considered in univariate models for each response variable (not analysed relative to forest condition and integrity), it tended to be associated with low odds of species extinction risk and declining populations, as would be expected (Supplementary Table 18). Similarly, when human pressure was considered in univariate models, it was always associated with high odds of species extinction risk and declining populations as expected (Supplementary Table 18).

Large, well-connected forest landscapes are essential for biodiversity conservation, especially in an era of climate change. We show a higher likelihood of extinction risk and declining populations when large extents of forest cover within species ranges were degraded, emphasizing the importance of minimizing human disturbances in remaining intact tropical rainforest landscapes. In contrast, we found a lower likelihood of extinction and declining populations when species ranges contained lower proportions of forest cover but forest of high integrity, adding to the growing evidence that remnant high-integrity forests can play an important supporting role for biodiversity by providing refugia or habitat for numerous species. Remnant high-integrity forests face a higher likelihood of loss compared with larger forested extents because of the severe land-use pressures around them and improved access for resource extraction. Moreover, sensitivity to isolation in remnant forests may be a likely explanation for the higher probability of declining populations even in high-integrity remnant forests for rainforest-obligate birds, reptiles and amphibians, potentially signalling the presence of an extinction debt for these vertebrate groups in fragmented landscapes. Thus, proactively prioritizing the protection of remnant high-integrity forests from loss while simultaneously setting targets for restoring degraded forests are both important to limit the loss of already threatened and declining species.

Human influence is not limited to tropical rainforests but extends over much of Earth’s land surface. Future research should leverage global forest integrity and ecosystem intactness datasets to quantify the importance of ecosystem integrity for terrestrial biodiversity in all regions.
forest as well as non-forest biomes. In addition, datasets on potential forest structural complexity (the theoretical potential native vegetation in a region in the absence of human disturbance)\textsuperscript{37}, when related to actual structural complexity (for example, the SCI data used here), can help to monitor the effectiveness of forest management and restoration efforts.

The SCI and FSII datasets are static in time (centred on 2013)\textsuperscript{8}, while our biodiversity datasets are from 2019–20 (Methods), allowing for a time lag between forest degradation and species responses to potentially be reflected in IUCN assessments. Nevertheless, our analyses represent a space-for-time substitution. Albeit widely used in ecological studies given the paucity of long-term datasets, predicted probabilities from 100 phylogenetic logistic regressions. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Error bars and the shaded areas of the lines represent median 95% CIs generated with 2,000 parametric bootstraps in each regression. These results were mirrored in rainforest-associated vertebrates (Extended Data Fig. 3). See Supplementary Table 1b and Table 7 for sample sizes and model estimates, respectively. AF, Afrotropic; AU, Australasia; IN, Indomalayan; NE, Neotropic. Illustration credits: S. Traver, F. Sayol, B. Szabo and J. C. Arenas-Monroy.

Fig. 3 | Predicted probabilities of rainforest-obligate mammals, birds, reptiles and amphibians being threatened and having declining population trends across the four biogeographic realms within the tropical rainforest biome. The bar plots show the baseline probabilities in each realm estimated without consideration of either forest cover or integrity. The adjacent line plots show the probability of being threatened and having a declining population with increasing forest integrity after statistically controlling for the effects of forest cover (among species with average area of forest cover within their ranges). Data points (1, threatened/declining; 0, not threatened/not declining) are vertically and horizontally jittered to reduce overlap. The bars and lines represent median predicted probabilities from 100 phylogenetic logistic regressions. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Error bars and the shaded areas of the lines represent median 95% CIs generated with 2,000 parametric bootstraps in each regression. These results were mirrored in rainforest-associated vertebrates (Extended Data Fig. 3). See Supplementary Table 1b and Table 7 for sample sizes and model estimates, respectively. AF, Afrotropic; AU, Australasia; IN, Indomalayan; NE, Neotropic. Illustration credits: S. Traver, F. Sayol, B. Szabo and J. C. Arenas-Monroy.
space-for-time substitution may underestimate the effects of tropical forest disturbances such as selective logging on biodiversity. Indeed, preliminary analysis of the effect of change in SCI from 2012 to 2018 on species extinction risk and population trends suggests that degradation of tropical rainforest structural condition may pose a similar, and sometimes greater, threat to biodiversity than the outright loss of forest cover (Methods; Extended Data Fig. 9 and Supplementary Table 19). Therefore, investigating the effects of change in forest structural condition and integrity on shifts in species extinction risk and population trends over longer timeframes is an important future research direction.

Invertebrates and vascular plants comprise the greatest share of tropical biodiversity in terms of species diversity and biomass. Comparable range map and habitat preference data for non-vertebrate groups remain unavailable, but future work with alternative datasets and statistical approaches can help to quantify the importance of forest integrity for such diverse yet understudied taxonomic groups. Further, investigating links between remotely sensed indices of forest structural condition and integrity and species traits may offer insights into the potential role of intact forests as a buffer for functional species groups particularly susceptible to environmental change.

Our findings demonstrate a clear need for the targeted preservation of the last remaining high-integrity forests across the global humid tropics. A unique opportunity to advance biodiversity conservation is at hand, given that 86% of high-integrity tropical rainforests remain unprotected. Focusing environmental policies and management actions on preserving their integrity alongside ongoing efforts to halt deforestation will probably improve conservation outcomes by preventing more tropical rainforest species from becoming threatened or undergoing population declines over time. On the basis of our findings, we argue that the single most important policy action nations can take to prevent catastrophic biodiversity loss in tropical rainforests is to commit to a target of ‘net gain in area, connectivity and integrity’ of these hyperdiverse ecosystems. Proactive targets to preserve and restore forest integrity are an urgent priority to ‘bend the curve’ on species loss and ensure that nations stand a chance to put biodiversity on a path to recovery for benefit of planet and people by 2030.

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. These forests largely span the latitudes between 23.5° N and 23.5° S but extend into the subtropics in some areas (Extended Data Fig. 4). Despite covering a mere 14% of Earth’s terrestrial area, these forests are home to over a mere 14% of Earth’s terrestrial area; they are home to over 659 additional amphibian species from ref. 4, after cross-verification to omit synonyms and extinct species. Because we obtained the reptile database from a source other than the IUCN Red List, we were unable to perform the same suite of filters on reptiles. However, our analyses showed that ten species from this list are now regarded as extinct. Therefore, we discarded these ten species. 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.

We projected all geographic range maps to the World Mollweide projection before 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 and also exclude species that marginally occur in tropical rainforests but for which these ecosystems nevertheless represent important habitats (for example, some species of wintering migratory birds). Therefore, 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. 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. 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. We discarded additional species from this dataset on the basis of matching species names with those in the respective phylogenetic trees (for the final list of species in this study, see section on Statistical analyses). We note that the habitat associations of ~30% of reptile species whose ranges overlap tropical forests remain unknown because reptiles are one of the most understudied terrestrial vertebrate groups. We took several steps to limit potential geographic bias from this issue. Specifically, we matched reptile species in geographic range maps with the best-available reptile phylogenetic trees as with the other taxonomic groups, analysed each taxonomic group independently and explicitly estimated variation in species extinction risk across biogeographic realms (see section on Statistical analyses).

Definition of tropical rainforest-obligate species
We defined dependency on tropical rainforests following the criteria established by ref. 1. We considered a species to be rainforest-obligate if (1) ~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. 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 (for example, 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\(^8,9\). The SCI is a fine-scale (30 m resolution) raster derived from three datasets: global tree canopy cover in 2010\(^5\), time since forest loss (between 2000 and 2017)\(^7\) and canopy height in 2012\(^8,9\). 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\(^8,9\). The lowest SCI value delineates stands <5 m tall, disturbed since 2012 or with canopy cover <25%. The highest SCI value represents tall, closed-canopy stands undisturbed since 2000.

To ensure that 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 non-forest and completely removed these values from analyses of structural condition and integrity (see section on Predictor variables). The FSII is derived by overlaying the HFP, a 1 km resolution measure of the cumulative, in-situ pressures humans exert on natural areas across terrestrial Earth\(^8\), on the SCI. The HFP ranges from 0 to 50, representing a gradient of increasing human pressure\(^9\). The original 1993 HFP\(^8\) was updated to 2009\(^9\) and more recently to 2013\(^9\). 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 refs. \(^8,9\).

As with the range maps, we projected the SCI, FSII and HFP raster datasets to the World Mollweide projection before analyses. Given the differing resolutions of the SCI and FSII rasters (30 m and 1 km, respectively), we first made them comparable by resampling both to 1 km resolution (identical to the HFP) 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\(^8,9\).

We then 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, 19 values of the FSII and 51 values of the HFP rasters within the humid tropical range of each species. Following the criteria established by ref. \(^8\), we categorized and summed the area of 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 of FSII pixel values ranging from 0 to 3 as low human footprint or pressure, 4 to 15 as moderate pressure and 16 to 50 as high pressure regions within species ranges.

**Simulating plausible error in structural condition and integrity indices**

We expected errors of 10–30% as plausible in maps of canopy cover and height derived from multispectral satellite imagery\(^8,9\). Therefore, we adjusted SCI classification boundaries for canopy cover and height up and down by 20% to simulate a plausible range of scenarios and enable testing of the sensitivity of statistical models to these potential errors (Extended Data Fig. 4). Adjusting the canopy cover and height classification boundaries downward had the effect of increasing the number of pixels classified as high SCI (values 14–18), effectively simulating overestimates of canopy cover and height (Supplementary Table 8). Adjusting the cover and height classification boundaries upward had the opposite effect. As with the original SCI, we overlaid the HFP on both reclassified SCI rasters to generate FSII rasters incorporating the assumed ±20% error in mapping canopy cover and height. We then performed our statistical analyses with these reclassified SCI and FSII datasets, as detailed with the original datasets, to examine whether our model estimates remained robust to the simulated range of potential error.

**Forest cover loss and change in structural condition**

We created a raster for forest cover loss by identifying pixels lost between 2012 and 2018, which were initially classified as forest in 2012 on the basis of canopy cover and height thresholds >25% and >5 m, respectively. We also created a change in structural condition dataset for the same timeframe by subtracting the baseline 2012 SCI pixel values from the 2018 values. Given this short window over which we have temporal data, little change in structural condition was observed (<1% of pixels show change in SCI), which may affect statistical power. Efforts are ongoing to update the SCI and FSII datasets to allow change analyses over a longer timeframe (2000–2017), which would allow a stronger analysis of the association between change in forest quality and recent genuine changes in extinction risk, for example, ref. \(^9\). We note that we did not use a change in forest integrity dataset because HFP layers matching the 2012–2018 timeframe are unavailable.

**Predictor variables**

We calculated the relative difference between the area of high and low SCI forest within the humid tropical range of species \(j\) as

\[
d_{sci}^j = \frac{(\sum_{C_j}^{H} M_{sci}) - (\sum_{C_j}^{L} M_{sci})}{\sum_{C_j} M_{sci}},
\]

where \(M_{sci}^h\) and \(L_{sci}^j\) are the areas of high and low SCI forest, respectively, and \(C_j\) is the area of humid tropical forest cover within the range of species \(j\). Likewise, we calculated the relative difference between the area of high and low FSII forest as

\[
d_{fsii}^j = \frac{(\sum_{C_j}^{H} M_{fsii}) - (\sum_{C_j}^{L} M_{fsii})}{\sum_{C_j} M_{fsii}}.
\]

The calculated values range between −1 and +1 and represent the relative percentage difference between the areas under high and low SCI or FSII forests within the humid tropical range of a species. Thus, a value of −1 indicates that -100% of the humid tropical range of a species is encompassed by low SCI or low FSII forest, whereas a value of +1 means 100% of the humid tropical range of a species is encompassed by high SCI or high FSII forest (a gradient of increasing SCI/FSII). For the analysis of HFP, we similarly calculated the relative difference between the areas of high and low HFP within the humid tropical range of species \(j\) as

\[
d_{hfp}^j = \frac{(\sum_{C_j}^{H} M_{hfp}) - (\sum_{C_j}^{L} M_{hfp})}{\sum_{C_j} M_{hfp}},
\]

Here, a value of −1 means -100% of the humid tropical range of a species is encompassed by low HFP areas, whereas a value of +1 signifies that -100% of the humid tropical range of a species is encompassed by high HFP areas (a gradient of increasing HFP). For the analyses including forests of moderate structural condition and integrity with those of high structural condition and integrity, we recalculated these relative difference values as

\[
d_{sci}^{m} = \frac{(\sum_{C_j}^{M} M_{sci}) - (\sum_{C_j}^{L} M_{sci})}{\sum_{C_j} M_{sci}}\quad \text{and}\quad d_{fsii}^{m} = \frac{(\sum_{C_j}^{M} M_{fsii}) - (\sum_{C_j}^{L} M_{fsii})}{\sum_{C_j} M_{fsii}},
\]

where \(M_{sci}^m\) is the area of moderate SCI forest within the range of species \(j\) that was summed with \(H_{sci}^{m}\) and similarly for \(M_{fsii}^{m}\).

We used the lowest SCI value of 1 to identify stands <5 m tall, disturbed since 2012 or with canopy cover <25%, which are considered highly disturbed, and categorized the area of this pixel value
as non-forest. We categorized and summed the remaining SCI values from 2 to 18 as forest. We then calculated the relative difference between the area of forest cover and non-forest within the humid tropical range of species \( j \) as \( d^2_j = \sum_{i=1}^{18} \frac{c_i^j - NC_i^j}{NC_i^j} \), where \( c_i^j \) and \( NC_i^j \) are the area of forest cover and non-forest within the range of species \( j \) and the denominator sums the humid tropical range area of species \( j \). Similar to the SCI and FSI relative difference values, these calculated values of forest cover also range between \(-1\) (signifying 100% of the humid tropical range of a species consists of non-forest) and \(1\) (signifying that 100% of the humid tropical range of a species is forested). We thereby brought all predictor variables in this study (forest cover, condition, integrity and human footprint) to a consistent scale for further analyses. However, for the analysis of change, we used proportion loss in forest cover and proportion change in structural condition as predictor variables because of the sparse data on change.

### Statistical analyses

The response variables in this study are binary—threatened/non-threatened and declining population/not declining in population. To achieve this binary classification, we defined species in the IUCN critically endangered, ‘endangered’ and ‘vulnerable’ categories as threatened and species in the ‘near threatened’ and ‘least concern’ categories as non-threatened while discarding species in the ‘data deficient’ category (see Extended Data Fig. 7 for analyses of alternative threatened definitions). For the IUCN population trend data, we defined species in the ‘decreasing’ category as declining in population and species in the ‘increasing’ and ‘stable’ categories as not declining in population while discarding species in the ‘unknown’ category.

We used a generalized linear modelling framework, specifically logistic regression, for statistical inference. Our primary units of analyses—species—cannot be considered as independent because of the variable degree of evolutionary relatedness between the species in each taxonomic group. To account for the potential effect of evolutionary dependence, we first obtained phylogenetic trees for mammals, birds, reptiles and amphibians and 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 total of 16,396 species in the analyses of threatened status. We also discarded 5,842 species of unknown population trend for a final total of 12,533 species in the analyses of declining population (Supplementary Table 1). For each taxonomic group, we partitioned species into forest-obligate and rainforest-associated categories. Next, we randomly sampled 100 trees out of 10,000 available full phylogenetic trees for each taxonomic group, as recommended by ref. 20, to construct covariance matrices enumerating the proportion of the evolutionary path shared between each pair of species. We used these covariance matrices in phylogenetic logistic regression models to generate inferences corrected for phylogenetic signal.

We parameterized identical models for rainforest-obligates and rainforest-associated species in each taxonomic group to estimate the relative importance of high-integrity forests within species ranges in being associated with reduced odds of species: (1) being threatened and (2) having a declining population, compared with structurally intact forests and forest cover alone. Before analyses, we standardized each predictor variable (forest cover, condition and integrity) to have a mean of 0 and a standard deviation of 1 (z-transformation). We examined the effects of the three predictor variables on the respective response variable (threatened status or declining population) by parameterizing them as additive effects in multiple phylogenetic logistic regression models and used the standardized partial coefficient of each predictor variable as a measure of its effect on the response variable. In this form of multiple logistic regression, the exponentiated standardized partial coefficient of a given predictor variable represents the odds of a 1-unit increase in that variable on the response, controlling for the effects of the other predictor variables by statistically holding them at their average values. Given the correlated nature of the predictor variables (Supplementary Table 20), standardized partial regression coefficients can provide unbiased estimates of the relative importance of forest cover, condition and integrity on the odds of species being threatened or having a declining population. We estimated 95% CIs for the estimated standardized coefficients in each regression with 2,000 parametric bootstraps as recommended by ref. 20 and made inferences based on the median of 100 regressions, each regression being performed with one phylogenetic tree randomly drawn from 10,000 available trees.

We then considered two-way interactions between forest cover × condition and forest cover × integrity with phylogenetic logistic regression models to test whether the effects of forest integrity and condition depend on the amount of forest cover within species ranges. We also tested whether the effect of forest integrity depends on the amount of high structural condition forest within species ranges by considering interactions between forest condition × integrity. A positive coefficient for the interaction term (for example, forest cover × condition) would suggest that the effect of forest condition on the probability of being threatened or having declining populations was stronger when species ranges contained low proportions of forest cover in intact structural condition, as opposed to when species ranges contained high proportions of forest cover in degraded structural condition. In contrast, a negative coefficient for the interaction term would indicate that the effect of forest condition was stronger when species ranges contained high proportions of forest cover in intact condition, as opposed to low proportions of forest cover, irrespective of its structural condition. Interaction models were otherwise parameterized in an identical manner to the additive models described above.

To examine variation in extinction risk across biogeographic realms for each taxonomic group, we first fit a model with realm as a categorical predictor variable. We included rainforest dependency as an additive effect in this model to estimate variation in extinction risk between rainforest-obligate and rainforest-associated species. This model enabled estimation of baseline probabilities of species being threatened or having a declining population in each realm. Next, we parameterized a model testing for an interaction between forest integrity and realm, with a positive interaction coefficient suggesting lower extinction probability with increasing forest integrity and the relative strength of the interaction indicating variability in this probability between realms. Given that the amount of forest cover within the humid tropical range of a species can also influence and have a confounding effect on the integrity × realm interaction, we included a second interaction between forest cover and realm in this model, thereby statistically controlling for the effects of forest cover. We did not consider forest structural condition in this analysis because forest integrity was mostly of greater importance in predicting extinction risk than was forest condition (Fig. 1).

We implemented all phylogenetic logistic regression analyses via the package ‘phylolm’ in the R (v.4.0.3) statistical programming language. To limit bias in maximum likelihood estimates of logistic regression coefficients, we used the maximum penalized likelihood method with Firth’s correction implemented in the phylolm function via the parameter logistic_MPLE. We conducted our analyses across thousands of species with three predictor variables in the case of additive models and two predictor variables for interaction models, which risks inflating type 1 error rate. Therefore, we used a procedure adjusted for FDR which corrects for multiple comparisons in comparative extinction risk modelling. We calculated FDR-adjusted \( P \)-values with the p.adjust function in R. We obtained centroids of species humid tropical ranges in ArcGIS Pro 2.5.0 and thereafter used the packages ‘spdep’ and ‘ncf’ in R to calculate geographic distance between species humid tropical range centroids and perform spatial autocorrelation analyses of model residuals.
Influence of phylogenetic correlation
In phylogenetic logistic regression, the parameter $\alpha$ measures the strength of the phylogenetic correlation. When $\alpha = 1$, evolution is approximately by Brownian motion on a given phylogeny, with $\alpha = 0$ indicating lower phylogenetic correlations among species. In most cases across all taxonomic groups and models, the estimated phylogenetic signal $\alpha$ was close to zero (Supplementary Table 21), suggesting that the predictor variables included in the models induced phylogenetic signal in the residuals.

Reporting summary
Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability
All datasets used in this paper are openly available via the citations identified in the Methods. Processed spreadsheets can be accessed at Zenodo [https://doi.org/10.5281/zenodo.7036360](https://doi.org/10.5281/zenodo.7036360). Additional Python code to process species range maps before raster overlay and tabulation of area can also be accessed through the same Zenodo repository [https://doi.org/10.5281/zenodo.7036360](https://doi.org/10.5281/zenodo.7036360).

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Acknowledgements
This work was funded by the NASA Biodiversity and Ecological Forecasting Program under the 2016 ECO4CAST solicitation through grant NNX17AG51G to A.J.H., J.E., S.J.G., P.A.J., J.E.M.W. and O.V., the NASA Global Ecosystem Dynamics Investigation (NNL16AA03 to S.J.G.) and the NASA GEO solicitation (80NSSC18K0338 to P.A.J.).

Author contributions
R.P. conceived this study with O.V., J.E.M.W. and A.J.H. providing major inputs. J.A.O. and R.P. developed the Python code for geospatial analyses. P.A.J. simulated potential error in mapping canopy cover and height for SCI and FSII data. N.P.R. processed change in SCI and forest cover loss data. P.G.D.P. provided amphibian range maps not available in the IUCN Red List. R.P. performed all geospatial and statistical analyses and wrote the manuscript. O.V., J.E.M.W., A.J.H., S.J.G., P.A.J., P.B., C.S., D.A., B.A.W., P.G.D.P., J.A.O., N.P.R., S.C.A., J.E. and A.L.S.V. reviewed and edited manuscript drafts.

Competing interests
The authors declare no competing interests.

Additional information
Extended data is available for this paper at https://doi.org/10.1038/s41559-022-01915-8.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-022-01915-8.

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Peer review information Nature Ecology & Evolution thanks Daniele Baisero, Matthew Betts and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

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Extended Data Fig. 1 | The relative importance of forest integrity, structural condition, the human footprint or pressure, and forest cover on the odds of mammals, birds, reptiles, and amphibians being threatened and having declining population trends (for sample sizes, see Supplementary Table 1a). Structural condition and human pressures considered together (that is, FSII) tended to be associated with lower odds of species extinction risk and declining population trends than either structural condition or human pressures individually. Point estimates represent median standardized odds ratios of species being threatened (circles) or having a declining population (squares), generated by exponentiating standardized coefficients (log odds) of 100 phylogenetic logistic regressions (Supplementary Table 3). The vertical dotted line represents an odds ratio of 1, denoting statistical non-significance. Error bars represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Separate models were parameterized for rainforest-obligate and rainforest-associated species for each response variable. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 2 | Predicted probabilities of tropical rainforest-obligate and associated mammal, bird, reptile, and amphibian species being threatened and having declining population trends as a function of two-way interactions between forest structural condition and integrity. Species tended to be at higher risk of being threatened and having declining populations when high proportions of forest cover within their ranges were structurally intact but of low integrity (that is, under high human pressure) than when their ranges contained low proportions of forest cover in high structural condition and low human pressure. Median predicted probabilities were generated from 100 phylogenetic logistic regressions. See Supplementary Tables 1a and 6 for sample sizes and model estimates, respectively. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 3 | Predicted probabilities of rainforest-associated mammals, birds, reptiles, and amphibians being threatened and having declining population trends across the four biogeographic realms within the tropical rainforest biome. The bar plots show the baseline probabilities in each realm estimated without consideration of either forest cover or integrity. The adjacent line plots show the probability of being threatened and having a declining population with increasing forest integrity after statistically controlling for the effects of forest cover (that is, among species with average area of forest cover within their ranges). Data points (1, threatened/declining; 0, not threatened/not declining) are vertically and horizontally jittered to reduce overlap. The bars and lines represent median predicted probabilities from 100 phylogenetic logistic regressions. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Error bars and the shaded areas of the lines represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. These results were mirrored in rainforest-obligate vertebrates (Fig. 3). See Supplementary Table 1b and Table 7 for sample sizes and model estimates, respectively. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 4 | Original and reclassified SCI and FSII datasets. (a) The original SCI and FSII raster datasets from Hansen et al. 2019, 2020 and used in the main analyses presented here. The tropics lie between 23.5° N and 23.5° S latitudes (indicated by the dotted lines) but the tropical rainforest or humid tropical biome extends into the subtropics in some areas. (b) A reclassified SCI raster generated by simulating a +20% error in canopy cover and height derived from multispectral satellite imagery (left). This +20% error reduced the number of pixels classified as high SCI (values 14–18), effectively simulating underestimates of canopy cover and height. (c) A reclassified SCI raster simulating a -20% error in canopy cover and height measurements (left). This -20% error increased the number of high SCI pixels, effectively simulating overestimates of canopy cover and height. See Supplementary Table 7 for original and reclassified thresholds of canopy cover and height. As with the original SCI, the Human Footprint was overlaid on both simulated SCI rasters to generate corresponding FSII rasters incorporating the assumed ±20% errors (b, c: right). All raster data were resampled from the original 30 m pixel resolution to 1 km (Methods). See Fig. 1 for model results estimated with the original datasets in Extended Data Fig. 4a, and Extended Data Figs. 5a, b for results estimated with the simulated datasets in Extended Data Figs. 4b, c.
Extended Data Fig. 5 | Propagating simulated errors in mapping canopy cover and height with the SCI and FSII datasets to statistical models. The relative importance of forest integrity, structural condition, and forest cover on the odds of mammals, birds, reptiles, and amphibians being threatened and having declining population trends. The underlying structural condition and integrity data for these analyses are a reclassified SCI raster generated by (a) simulating a +20% error in canopy cover and height derived from multispectral satellite imagery. This +20% error reduced the number of pixels classified as high SCI (values 14–18), effectively simulating underestimates of canopy cover and height (Extended Data Fig. 4b) and (b) simulating a -20% error in canopy cover and height measurements. This -20% error increased the number of high SCI pixels, effectively simulating overestimates of canopy cover and height (Extended Data Fig. 4c). As with the original SCI, the Human Footprint was overlaid on both simulated SCI rasters to generate FSII rasters incorporating the assumed ±20% errors. Our overall conclusions remained robust to this simulated range of potential error in mapping canopy cover and height in the SCI and FSII datasets. Point estimates represent median standardized odds ratios of species being threatened (circles) or having a declining population (squares) generated by exponentiating standardized coefficients (log odds) of 100 phylogenetic logistic regressions. The vertical dotted line represents an odds ratio of 1, denoting statistical non-significance. Error bars represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Separate models were parameterized for rainforest-obligate and associated species for each response variable. See Supplementary Table 1a for sample sizes, Supplementary Table 8 for original and reclassified thresholds of canopy cover and height, and Supplementary Tables 9–10 for model estimates. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 6 | Pooling moderate structural condition and integrity forests with structurally intact and high-integrity forests. The relative importance of forest integrity, structural condition, and forest cover on the odds of mammals, birds, reptiles, and amphibians being threatened and having declining population trends. In the main text, we calculated the area (km²) of structurally intact and high-integrity forests (SCI and FSII values 14–18), relative to the area of structurally degraded and low-integrity forests (SCI values 2–5 and FSII values 1–5) within species humid tropical ranges (Methods). Here, we conducted an additional analysis pooling the area of moderate structural condition and integrity forests (SCI and FSII values 6–13) with structurally intact and high-integrity forests and thereafter parameterizing an identical set of models as the main analyses. We were thus able to consider the entire gradient of forest quality when examining its effects on species extinction risk and declining populations. Our overall conclusions remained consistent, suggesting forests of moderate structural condition and integrity can have value for biodiversity conservation. Point estimates represent median standardized odds ratios of species being threatened (circles) or having a declining population (squares) generated by exponentiating standardized coefficients (log odds) of 100 phylogenetic logistic regressions. The vertical dotted line represents an odds ratio of 1, denoting statistical non-significance. Error bars represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Separate models were parameterized for rainforest-obligate and associated species for each response variable. See Supplementary Tables 1a and 11 for sample sizes and model estimates, respectively. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 7 | Alternative definitions of IUCN Threatened Status. The relative importance of forest integrity, structural condition, and forest cover on the odds of mammals, birds, reptiles, and amphibians being threatened. In the main analyses, we considered a species to be threatened if it was classified in any one of the IUCN Red List categories Critically Endangered (CR), Endangered (EN) or Vulnerable (VU). Here, we performed additional analyses considering a species as threatened only if it was classified as (a) CR and (b) either CR or EN. For all analyses, we classified species in the Near Threatened and Least Concern categories as non-threatened. This allowed us to maintain the binary classification (threatened/non-threatened) of the response variable, which was necessary for the logistic regression analyses used in this paper. Our overall conclusions remained consistent across these different degrees of threat.

Point estimates represent median standardized odds ratios of species being threatened, generated by exponentiating standardized coefficients (log odds) of 100 phylogenetic logistic regressions. The vertical dotted line represents an odds ratio of 1, denoting statistical non-significance. Error bars represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Separate models were parameterized for rainforest-obligate and associated species. See Supplementary Tables 13–14 for sample sizes and model estimates, respectively. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 8 | Excluding species designated as threatened under IUCN criteria A and B. The relative importance of forest integrity, structural condition, and forest cover on the odds of mammals, birds, reptiles, and amphibians being threatened. These analyses were performed after excluding (a) 2,751 species listed as threatened in criterion B of the IUCN Red List of Threatened Species, and (b) 3,745 species listed as threatened in both criteria A and B of the IUCN Red List. We did not include declining population data in this analysis of potential circularity because the IUCN Red List criteria are not used for determining overall population trends. Point estimates represent median standardized odds ratios of species being threatened, generated by exponentiating standardized coefficients (log odds) of 100 phylogenetic logistic regressions. The vertical dotted line represents an odds ratio of 1, denoting statistical non-significance. Error bars represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Separate models were parameterized for rainforest-obligate and associated species. See Supplementary Tables 15–17 for sample sizes and model estimates. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
Extended Data Fig. 9 | Change in forest structural condition and forest cover loss. The relative importance of change (degradation) in tropical rainforest structural condition and forest cover loss between 2012 and 2018 on the odds of mammal, bird, reptile, and amphibian species being threatened and having declining population trends. Point estimates represent median standardized odds ratios of species being threatened (circles) or having a declining population (squares) generated by exponentiating standardized coefficients (log odds) of 100 phylogenetic logistic regressions. The vertical dotted line represents an odds ratio of 1, denoting statistical non-significance. Error bars represent median 95% confidence intervals generated with 2,000 parametric bootstraps in each regression. Each regression was performed with one phylogenetic tree randomly drawn from 10,000 available trees for each taxonomic group. Separate models were parameterized for rainforest-obligate and associated species for each response variable. See Supplementary Tables 1a and 19 for sample sizes and model estimates, respectively. Illustration credits: Steven Traver, Ferran Sayol, Birgit Szabo, and Jose Carlos Arenas-Monroy.
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- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) and variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted. Give P values as exact values whenever possible.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen’s d, Pearson’s r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection: Custom Python code was used to extract geographic ranges of terrestrial vertebrates from the IUCN Red List of Threatened Species database and peer-reviewed articles, overlay them with tropical forest biome maps, and calculate range area under tropical rainforests. Other data such as forest quality rasters and phylogenetic trees were obtained from publicly available databases that are based on peer-reviewed journal articles cited in the list of References. Further custom Python code was used to calculate the area under structurally intact and high integrity forest within species humid tropical ranges. All code are available at Zenodo.

Data analysis: All geospatial analyses were performed with Python via ArcPy module in ArcGIS Pro 2.5.0. All statistical analyses were performed in R (v. 4.0.3).

For manuscripts utilizing custom algorithms or software that are not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy.

All datasets used in this paper are openly available via the citations identified in the Methods

For manuscripts utilizing custom algorithms or software that are not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data
Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

- Life sciences
- Behavioural & social sciences
- Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description  
This study quantifies the global importance of tropical rainforests of intact structural condition and low human pressures on the risk of extinction and population decline for terrestrial vertebrates, relative to forest cover alone (i.e. without consideration of either structural condition or human pressure). We use two IUCN Red List of Threatened Species variables (1) threatened status and (2) declining population for all mammals, birds, reptiles and amphibians whose ranges overlap the tropical rainforest biome. We use the recently developed remotely sensed data on tropical rainforest structural condition and human pressures in combination with phylogenetic comparative methods for our analyses.

Research sample  
We sampled the tropical rainforest biome and all terrestrial vertebrate species among mammals, birds, reptiles and amphibians that occur in this biome.

Sampling strategy  
From global geographic range maps of all extant terrestrial vertebrates, we sub-sampled to include species that only occur in the tropical rainforest biome given that the forest integrity raster maps we used are relevant to this particular biome. We discarded species that did not match the taxonomic nomenclature in the respective phylogenetic trees for each vertebrate group, as well as species in the Data Deficient and Unknown Population Trend categories. See Methods.

Data collection  
All data in this study, including geographic range maps of terrestrial vertebrate species, forest integrity rasters and phylogenetic trees were downloaded from existing public databases that are based on peer-reviewed journal articles. See Methods.

Timing and spatial scale  
The geographic range maps are from 2019-2020 and the forest quality raster datasets are from a comparable period. The spatial scale is pantropical.

Data exclusions  
Data on extinct species as well as records based on uncertain data were excluded. See Methods.

Reproducibility  
The openly available data and custom code will facilitate the reproduction of the results in this study.

Randomization  
This study is not experimental, therefore randomization of study design was not necessary.

Blinding  
This study is not experimental, therefore blinding of experimental groups was not necessary.

Did the study involve field work?  
Yes  
No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

| n/a | Involved in the study |
|-----|-----------------------|
| ☑️  | Antibodies            |
| ☑️  | Eukaryotic cell lines |
| ☑️  | Palaeontology and archaeology |
| ☑️  | Animals and other organisms |
| ☑️  | Human research participants |
| ☑️  | Clinical data         |
| ☑️  | Dual use research of concern |

Methods

| n/a | Involved in the study |
|-----|-----------------------|
| ☑️  | ChiP-seq              |
| ☑️  | Flow cytometry        |
| ☑️  | MRI-based neuroimaging |