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Estimating the global conservation status of over 15,000 Amazonian tree species

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Estimates of extinction risk for Amazonian plant and animal species are rare, and not often incorporated into land-use policy and conservation planning. Here we overlay spatial distribution models with historical and projected deforestation to show that at least 40% and up to 64% of all Amazonian tree species are likely to qualify as globally threatened under IUCN Red List criteria. If confirmed, these results would increase the number of threatened plant species on Earth by 22%. We further show that the trends observed in Amazonia apply to trees throughout the tropics, and predict that most of the world's >40,000 tropical tree species currently qualify as globally threatened. A gap analysis suggests that existing Amazonian protected areas and indigenous territories will protect viable populations of most threatened species if those areas suffer no further degradation, highlighting the key roles that protected areas, indigenous peoples, and improved governance can play in preventing large-scale extinctions in the tropics in this century.

Amazonian forests have lost ~12% of their original extent and are projected to lose another 9-28% by 2050 (1, 2). The consequences of ongoing forest loss in Amazonia (here all rainforests of the Amazon basin and Guiana Shield) are relatively well understood at the ecosystem level, where they include soil erosion (3, 4), diminished ecosystem services (5-8), altered climatic patterns (5, 7, 9-11), and habitat degradation. By contrast, little is known about how historical forest loss has affected the population sizes of plant and animal species in the basin, and how ongoing deforestation will affect those populations in the future.

As a result, the conservation status of the >15,000 species that compose the Amazonian tree flora, one of the most diverse plant communities on Earth, remains unknown. Only a tiny proportion of Amazonian tree species have been formally assessed for the IUCN Red List to date. Two previous studies have attempted to estimate the extinction threat to Amazonian plants using theory, data, and vegetation maps to model reductions in range size, but disagreed on whether the proportion of threatened plant species in the Amazon is low (5-9%) (12) or moderate (20-33%) (13).

Here we build on that work by using a spatially explicit model of tree species abundance (14) based on 1,485 forest inventories (Fig. S1) to quantify how historical deforestation across Amazonia (1, 2, 15) has reduced the population sizes of 4,953 relatively common tree species. We use a separate model to estimate population declines for an additional 10,247 rarer tree species (14). For both models we also estimate the population losses expected under two deforestation scenarios for 2050 (1, 2), and ask to what extent projected losses can be prevented by Amazonia's existing protected area network. In contrast to previous studies, which presented results in the currency of statistical probability of extinction, we interpret our results using the criteria of the IUCN Red List of Threatened Species, the most commonly used yardstick for species conservation status.

Results

Effects of historical forest loss on tree populations

The original lowland forests of Amazonia are estimated to have covered 5.74 million km² (Fig S2), 11.4% of which had been deforested by 2013 (1, 2) (Figs. S3, S4A, Appendix S1). Most of the estimated 3.2×10^{10} individual trees lost to date (Appendix S2, 3) were in southern and eastern Amazonia (Fig. 1A).

Overlaying these deforestation data with the output of our spatial model of the distribution and abundance of 4,953 relatively common tree species allowed us to estimate the impact of forest loss on the Amazonian populations of these species. Forest loss to 2013 (Fig. S3, S4A) caused a mean 11% decline in the number of individuals of tree species across Amazonia (median = 6%, Fig. 1A, Fig. S4D), and mean declines of 2–32% in individual Amazonian regions. A total 342 of the 4,953 common species (7.5%) have lost a large enough proportion of their original populations ($\geq 30\%$) to qualify as globally threatened under IUCN Criterion A2 (Fig. 1A, Appendix S2). A separate analysis to model the distribution and extinction risk of 10,247 rare tree species in the Amazon suggested that 9% of them—a total of 967 species—have lost enough individuals to qualify as globally threatened under the same criterion (Fig. S5A). Together, these analyses suggest that 9% of all Amazonian tree species likely qualify as threatened due to historical forest loss through 2013 (Fig. 1C). Adding the 2,579 rare species that may qualify as threatened because they have an estimated <1,000 individuals (IUCN Criterion D1) increases the proportion of all species threatened to 25% (Table 1).

The data in Fig. S4A&D suggest an approximately one-to-one relationship between percent historical forest loss and mean percent loss of individuals to date. Consequently, population losses of the common species are highest in regions where deforestation rates are highest, the so-called ‘Arc of Deforestation’ in southern and eastern Amazonia. The same patterns were observed for rare species.

Effects of projected forest loss on tree populations

We repeated the above analyses for two scenarios of projected forest loss (which include historical loss). The business-as-usual (BAU) scenario model (1) estimates that by 2050 ~40% of the original Amazon forest will be destroyed (Figs. S4B, S6; Appendix S1). The improved governance scenario (IGS) model (1) estimates forest loss by 2050 at 21% (Figs. S4C, S7; Appendix S1). Under these two scenarios, just 31–42% of grid cells maintain >95% forest cover. As is the case for historical deforestation, future deforestation is projected to be most severe in southern and eastern Amazonia (34–66% and 42–76% forest cover loss, respectively).

For common species, mean population declines under BAU are estimated to be 35% (median 32%), and absolute declines range from 0% to 83% (Figs. 1D, S4E; Appendix S2,3). Under BAU, 2,567 or 51% of all

common species likely qualify as threatened under IUCN Criterion A4 (Fig. 1D). Under IGS, average losses are lower, with a mean of 20% (median 18%) and a range of 0-82% (Fig. S4F; Appendix S2,3); 774 or 16% of common species likely qualify as threatened (Fig 1G). Again, the severest threat is in southern and eastern Amazonia (Fig 1G, S4D).

Both scenarios also pose severe threats to rare species. Under BAU, 4,466 or 43% of all rare species are predicted to lose $\geq 30\%$ of their populations by 2050 (Fig. S5B). The comparable numbers under IGS are 2,590 or 25% of all rare species (Fig. S5C). Under BAU, rare species are expected to be most severely hit in southern and eastern Amazonia, where the median population loss is 100% and more than 65 and 86% of the species, respectively, have population losses over 80% (Table S1).

Combining the analyses of common and rare species suggests that 3,364 to 7,033 Amazonian tree species likely qualify as globally threatened due to a combination of historical and projected forest loss (Fig. 1F,I). An additional 1,657–2,151 species in the dataset are likely to qualify as globally threatened because they have very small population sizes (IUCN Criteria C1 and D1). When all criteria are included, we find that 36–57% of Amazonian tree species likely qualify as globally threatened (Table 1).

To what degree will protected areas and indigenous territories prevent declines of Amazonian tree populations?

Over the last 50 years Amazonian countries have formalized a large network of protected areas and indigenous territories (Fig. S8, Appendix S1) that currently cover 52.2% of the basin: 9% in strict conservation reserves (SCR, Fig. S9A) and 44.3% in sustainable use and indigenous reserves (SUIR, Fig. S9B). Our models suggest that all of the 4,953 common species are protected to some degree by SCR and SUIR (for convenience we refer to both as PAs; Figs S9C, D). Every common species is estimated to have more than 5,500 adult individuals within PAs, with an average 23% of these individuals occurring in SCRs and 77% in SUIRs. Performance is poor in some Amazonian regions, however. For example, the scarcity of SCRs in central and eastern Amazonia means that on average only 2% of individuals of common species in those regions are in SCRs (Figs. S9C, D).

Our simulation models also suggest that 580 of the 10,247 rare species have more than 70% of their individuals in SCRs (Fig S10A). The comparable number occurring in SUIRs is 4,005.

Preventing deforestation within PAs between now and 2050 could significantly reduce the number of threatened Amazonian tree species. The reason is that both 2050 deforestation scenarios assume significant deforestation

within PAs (Figs. S11-S13): one third of projected BAU deforestation and 16% of projected IGS deforestation. If deforestation projected to occur within PAs under the BAU and IGS scenarios is not factored in, the number of common species that likely qualify as threatened under Criterion A4 falls by 29–44%. For example, 63% of wild Brazil nut trees (*Bertholletia excelsa*) are expected to be lost by 2050 under BAU. Under a modified IGS scenario that allows for no deforestation within PAs, that percentage drops to 27% and *B. excelsa* no longer qualifies as threatened (Appendix S2).

DISCUSSION

Our analyses suggest that historical and ongoing forest loss may cause population declines of >30% in one quarter to one half of all Amazonian tree species by 2050. These declines affect species in all Amazonian regions, including iconic Amazonian trees such as Brazil nut (*Bertholletia excelsa*), wild populations of major food crops such as cacao (*Theobroma cacao*, 50% population decline with BAU) and açai palm (*Euterpe oleracea*, 72% decline with BAU), and 167 of the 227 hyperdominant taxa that account for half of all Amazonian trees (14). And while these declines comprise both historical population losses and population losses projected to occur in the future, they could be used to currently classify these species as threatened under IUCN Criterion A4b.

Thousands of other Amazonian tree species are likely to qualify as globally threatened because they have very small populations (Table 1). And while our methods and results are preliminary (see online supporting material), the statistical independence we find between the estimated population size of a species and its fractional decline in numbers (Fig. S14) suggests that the primary findings will remain stable as sampling improves.

A 22% increase in the global red list for plants

Our estimates of the threat status of all Amazonian tree species constitute the largest threat assessment ever carried out. In fact, the number of species assessed in our analyses (15,200) is nearly as large as the number of all plant species evaluated by the IUCN over its 50-year history (19,738; table 3 (16)). If the 194 countries that have adopted the Global Strategy for Plant Conservation are to meet Target 2—"a preliminary assessment of the conservation status of all known plant species" by 2020—it will require large scaling-up approaches such as the one described here (see also (17)).

Such approaches are urgently needed for South America's tropical flora. Over the last 10 years just 1,275 plant species from tropical South America were added to the IUCN Red List, despite strong evidence that the number should be at least an order of magnitude higher (18-21). In general, our results provide strong support to predictions that at least one in four plant species in the South American tropics currently deserve listing as globally threatened (20). They also show that most of the species that likely qualify as threatened in the region remain absent from global and national red lists. For example, of the 2,567 common species that qualify as threatened under our BAU analysis, only 351 (14%) had previously been assessed using IUCN criteria and 94% are currently not listed as threatened. Adding all of our threatened Amazonian tree species to the IUCN red list would increase the number of globally threatened plants on Earth by 22% and the number of globally threatened tree species by 36%.

We are aware, however, that our results are too preliminary to constitute a red list for Amazonian trees. Red-listing these species will require case-by-case assessments by the IUCN/SSC Global Tree Specialist Group and country-level teams, taking into account other data sources and threat criteria. What we show here is the size, urgency, and feasibility of that task. A recent Brazilian effort to evaluate the threat status of 4,617 plant species in that country reported a per-species cost of ~US\$50 (19). This suggests that individually assessing the named species we suspect are threatened, and making their threat status visible to the conservation community, would cost <US\$1,000,000.

Most tropical tree species may be globally threatened

Despite strong spatial clustering in both deforestation scenarios and species distributions, our analyses reveal a simple rule of thumb that works at both regional and basin-wide scales: n% forest loss yields an average ~n% population loss (Figs. 1, S4A&D). This implies that tree species in other forest biomes of tropical South America have lost much larger proportions of their populations than in the core closed-canopy Amazonian moist forest: e.g. the Atlantic Forest (84-88% forest loss) (22), the cerrado (53%) (23), the caatinga (37%) (23), and dry forests in general (>60%) (24).

Given that Africa has lost ~55% of its tropical forests and Asia ~35%, mostly since 1900 (25), our analyses suggest that most tree species in the Old World tropics have lost more than 30% of their individuals over the last 150 years and thus qualify as globally threatened under Criterion A4. In turn, because >90% of all tree species on Earth are tropical (26), trees may deserve to join cycads (63%), amphibians (41%), and corals (33%) on the list of the groups with the highest proportions of globally threatened species.

Although many tropical tree species have symbiotic relationships with animals and co-occur with thousands of species of non-arboreal plants, high rates of threat cannot be inferred for these organisms in the same way, due to their much shorter lifespans. Bird et al. (27) compared estimated range maps of Amazonian bird species with maps of projected deforestation during three bird generations and found that just 5.5–18.8% species qualified as threatened under Criterion A4. Three bird generations in their model averaged 14.8 years, compared to 150 years in our tree model.

Linking forest loss, species threat status, and protected areas management in the Amazon

Heavy forest clearing in southern and eastern Amazonia has put an especially high proportion of tree species there at risk of extinction (Fig. 1A). In the worst-hit areas of the Arc of Deforestation, a third of tree species have already lost >30% of their populations to deforestation and more than half likely qualify as globally threatened based on projected (and historical) forest loss (Fig. 1B).

By linking spatial trends in forest loss to trends in the population sizes of individual Amazonian plant species in this way, models like ours should soon make it possible to translate remote sensing-based data on Amazonian deforestation into site-specific and species-specific guidance for conservation managers. It will also be possible to model how individual species will be impacted by infrastructure projects (28) such as major hydroelectric dams (29), degazetting of protected areas (30), and other drivers of Amazonian forest loss. This could have serious implications for large-scale development projects, which are increasingly required to protect IUCN-listed taxa and their habitat (e.g., (31)).

These models can also generate predictions about which plant species occur in which protected areas, and thus to what extent those species are protected and where. For example, floristic surveys at Cristalino State Park, in one of Brazil's most severely deforested regions, have recorded at least 551 tree species (32). Appendix S4 lists another 766 species that have a high probability of occurring at Cristalino according to our model, and shows that as many as 1214 of the 1317 species known or expected from Cristalino likely qualify as globally threatened under BAU. Similar analyses could help ensure that Amazonian protected areas with especially high numbers of globally threatened tree species receive the level of protection and funding they merit.

Many practical and scientific obstacles stand in the way of a stable, comprehensive red list for Amazonian tree species (see OSM). What we have shown in this study is that such a list will include several thousand species, many of which are currently considered common, and will include a very large majority of the tree species

occurring in the Amazon's worst-hit regions. As Amazonian forest loss continues, new approaches such as these will be needed to help guide management away from business-as-usual scenarios and ensure a long-term future for the world's richest tree flora. Indeed, sustaining the recent historical trend of reduced Amazonian deforestation through 2050 will keep as many tree species from becoming Critically Endangered as there are Critically Endangered plant species on the IUCN Red List today.

Materials and Methods

Amazonian base map

In order to overlay spatial data on deforestation, protected areas, and tree species distribution and abundance, we first made a base map of Amazonia. The borders of the base map were the same as those in (14). We gridded this landscape into 0.1-degree grid cells (01DGC) (33) and eliminated all 01DGCs that were more than 50% water (33), non-forest vegetation such as open wetlands or savannahs (1), or >500m elevation (34). This reduced the total area by 17%. We then quantified the area of all individual 01DGCs, which varies with latitude due to distance from the equator (~124 km² at the equator, ~106 km² at 14° S, and ~120 km² at 8° N). The final forest map consists of 46,986 01DGCs, or 5.79 million km² (Fig. S1).

Tree density

Our tree inventory data come from the ATDN network (14). The methods we used to estimate tree density, abundance, and distribution are similar to those of (14), but based on >20% more tree plots than in that study. Currently the ATDN network comprises 1,766 1-ha tree inventory plots scattered throughout Amazonia (Fig. S1).

The total number of trees ≥ 10 cm dbh in Amazonia was estimated as in (14) but with a larger subset of plots (1,625) and at the 1-degree grid-cell level (DGC). We constructed a LOESS regression model for tree density (stems ha⁻¹) on the basis of observed tree density in 1,625 plots, with latitude, longitude, and their interaction as independent variables. The span was set at 0.5 to yield a relatively smooth average. The model was used to estimate average tree density in each DGC (D_{DGC} , stems ha⁻¹, Fig S15). This average density per ha was then multiplied by the total forested area of each DGC to obtain the total number of trees in the DGC. The total

number of trees estimated was 3.2×10^{11} . This is 17.9% lower than (14) as this number corrects for the actual lowland forest cover in each DGC.

Modeled population sizes and species distributions (common species)

Analyses of tree species composition were performed with a subset of 1,560 plots in which all 775,532 free-standing trees ≥ 10 cm dbh had been identified with a valid name at the species (86.0%), genus (97.2%), or family (99.0%) level prior to our study. Most plots (1,282) measured exactly 1 ha, 392 were smaller (0.25-0.99), 91 were larger (1.01-4), and four were plotless samples (point centered quarter) for which the number of trees was equivalent to that typically found in 0.5–1 ha. Most issues of species identification and nomenclature were handled as in (14), but there were some exceptions. Species with a “cf.” identification were accepted as belonging to the named species, while those with “aff.” were tabulated at the genus level. All data associated with names that were clearly wrong (e.g. those of small herbs) were disregarded.

While we assume that identification error is within acceptable limits for common species (see discussion in (14)), we retained only plots in which $\geq 60\%$ of individuals were identified to species (1,480 plots, Figure S16). The number of trees belonging to each species in the DGC was estimated as follows. Abundances of all valid species were converted to relative abundances for each plot: $RA_i = n_i/N$, where n_i = the number of individuals of species i and N = the total number of trees in the plot (including unidentified trees) (14). For each of the 4,953 species with a valid name in the 1,485 plots, we constructed an inverse distance weighting (IDW) model for RA_i , with a power of 2, a maximum number of plots used for each local estimation of 150, and a maximum distance parameter of 4 degrees. We did not use a LOESS model (14) as this had the undesirable effect of predicting very small occurrences of species far from localities where the species was actually recorded. For a similar reason we used a cut-off of 4 degrees with the IDW modeling, because otherwise species would have very low densities over the entire Amazon. These adjustments have a significant effect on the ranges of species (i.e., ranges here are smaller than in (14)), but a negligible effect on their total number of individuals. The number of individuals of species i in a given DGC was then simply the total number of trees in the DGC multiplied by the fraction of the species i . While this is a slightly different approach and a slightly larger dataset than those of (14), the results are very similar to that study.

Modeled population sizes and species distributions (rare species)

To estimate the total number of tree species present in Amazonia, we extrapolated the rank-abundance distribution of the 4,953 named species as in (14). This yielded an additional 10,247 species, for a total of 15,200 estimated tree species in Amazonia. For shorthand, in this paper we refer to the 4,953 named species as 'common species,' and to the 10,247 other taxa as 'rare species.'

Because our tree plot data cannot tell us how these very rare species are distributed, we carried out a separate modeling exercise to estimate the degree to which their ranges overlap with deforestation or PAs. In doing this we relied on two simplifying assumptions. The first is that these rare species have small, circular geographic ranges whose sizes are correlated to their population sizes (13). The second assumption is that these species are not randomly distributed across the Amazon but instead more likely to occur in DGCs with higher overall tree diversity. This stratification is consistent with the theoretical notion that there is a one-to-one relationship between Fisher's α at large sample sizes and rare species (in large samples the number of singletons actually equals Fisher's α ; the doubletons equal $\sim\alpha/2$, tripletons $\sim\alpha/3\dots$)(35). To estimate how many rare species occur in each DGC, we made an updated map of tree diversity (Fisher's α) in Amazonia (36) at 0.1 degree resolution and used this map to stratify the position of rare species. For each rare species a DGC was chosen randomly, with a probability proportional to the DGC's Fisher's α . Range size was calculated for all 10,247 species as in ref (13). Each circular range was overlain on deforestation and protected area maps (pixels at 0.1 degree resolution). The fraction of the population intersecting those maps was then calculated as the number of pixels of deforestation (or protected area) divided by the total number of pixels of forest within that circular section. This was repeated 500 times to provide the mean expectation and confidence limits.

Protected areas and deforestation

Spatial data and categories of Amazonian PAs were gathered from the World Database of Protected Areas (37), and updated with individual country park service sources (e.g., <http://geo.sernanp.gob.pe/geoserver>), and, for indigenous territories of Guyana, Peru, and Bolivia, with data from Red Amazónica de Información Socioambiental Georeferenciada (<http://raisg.socioambiental.org/>). We did not include indigenous territories from Suriname, Venezuela and Ecuador, as these areas are not yet officially designated. PAs were classified as strict conservation reserves (SCR; IUCN categories 1a - IV) or sustainable use and indigenous reserves (SUIR; IUCN V - VII and all other types, Table S1). Where the data indicated overlap between SCR and SUIR, the overlap was designated as SCR.

Historical deforestation up to 2013 was based on data from (1, 2, 15). To estimate projected deforestation in 2050 (including historical deforestation), we used both a business-as-usual (BAU) and an improved governance scenario (IGS), based on (1, 2). Every 01DGC of the Amazonian based map was classified as protected or unprotected, and as forested or deforested, depending on whether >50% of the 01DGC was occupied by a PA or deforestation.

For common species, we estimated the number of individuals of a given species that fell within areas of deforestation or protection by first multiplying the population size in each DGC by the proportion of its 01DGCs that were classified as deforested or protected. This analysis assumes that the individuals of a species are distributed homogeneously within each DGC. We then summed results for all DGCs to yield the total number of individuals of each species that were lost to deforestation or occurred within a PA.

For rare species, the proportion of the number of individuals of a given rare species lost in a given DGC was quantified as the proportion of that DGC classified as deforested. Rare species in heavily deforested DGCs thus show a much higher loss than those in less-disturbed DGCs, and those in intact DGCs had zero losses. The degree to which rare species' distributions overlap with PAs was estimated in the same fashion.

All analyses were carried out with the R software platform (38).

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HtS conceived the study; HtS and NP designed the analyses; HtS carried out most analyses; HtS, NP, TK, WL, CP and JG wrote the manuscript; all others contributed data, discussed further analyses, and commented on various versions of the manuscript.

A summary of the data is given in Appendix 1. Plot metadata is given in Appendix 4.

Supplementary Materials

Supplementary text

Figs. S1 to S17

Table S1 to S3

Appendices S1 to S4

Table 1. Number of Amazonian tree species estimated to qualify as globally threatened under four IUCN threat status criteria. Numbers of threatened species are non-overlapping, i.e., species listed for C1 did not qualify for A4. BAU = projected (including historical) deforestation through 2050 based on a business-as-usual deforestation scenario (1, 2); IGS = projected (including historical) deforestation through 2050 based on an improved governance scenario (1, 2).

	Forest loss 1900–2013	Forest loss 1900–2050 (BAU)	Forest loss 1900–2050 (IGS)
Total no. spp.	15200	15200	15200
No. spp. with >30% observed pop. decline to date (IUCN A2)	1309	–	–
No. spp. with >30% projected pop. decline over 3 generations (IUCN A4)	–	7033	3364
No. spp. with >10% projected pop. decline over 3 generations and <10,000 individuals (IUCN C1)	–	38	44
No. spp. with <1,000 individuals (IUCN D1)	2505	1619	2107
Total no. threatened species	3814	8690	5515
% of all species threatened	25%	57%	36%

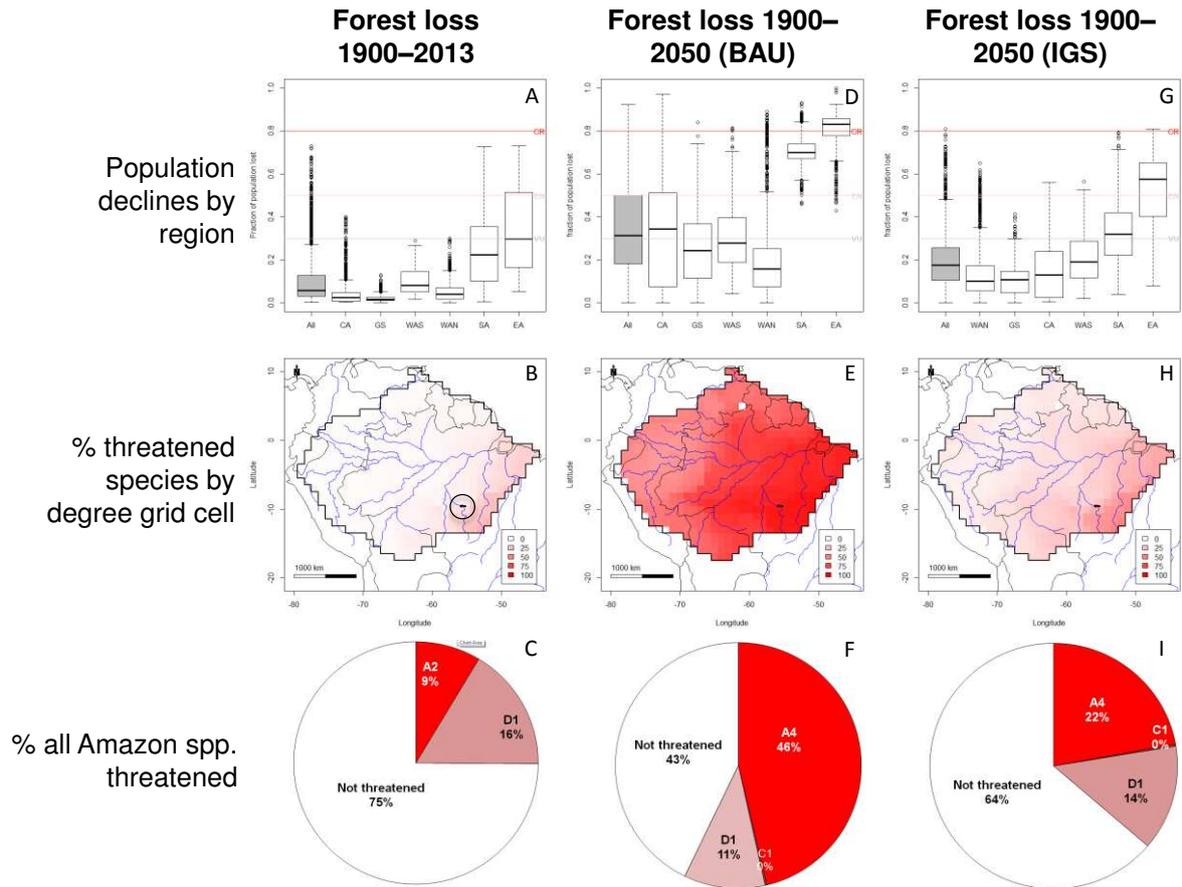


Fig 1. Estimated population declines and threat status of Amazonian tree species under historical deforestation (A-C) and two projected deforestation scenarios (D-I). Top row: Percent population loss of 4,953 tree species in the entire Amazon and in six Amazonian regions. Middle row: Percent species in a one-degree grid cell estimated as globally threatened based on projected (including historical) forest loss (IUCN A2, A4; $n = 4,953$). Bottom row: Proportion of all 15,200 Amazonian tree species estimated to be globally threatened based on four different IUCN threat criteria. BAU: projected (including historical) deforestation through 2050 based on a business-as-usual deforestation scenario (1, 2); IGS = projected (including historical) deforestation through 2050 based on an improved governance scenario (1, 2). Cristalino State Park is the small black polygon in SE Amazonia, circled in B.