

How many tree species are there in the Amazon and how many of them will go extinct?

Stephen P. Hubbell*^{†‡}, Fangliang He[§], Richard Condit^{†¶}, Luís Borda-de-Água*^{||}, James Kellner^{||}, and Hans ter Steege**

*Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095; [†]Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948; [§]Department of Renewable Resources, University of Alberta, Edmonton, AB, Canada T6G 2H1; [¶]National Center for Ecological Analysis and Synthesis, University of California, Santa Barbara, CA 93101; ^{||}Department of Plant Biology, University of Georgia, Athens, GA 30602; and **Institute of Environmental Biology, Plant Ecology, and Biodiversity Section, National Herbarium of The Netherlands, Utrecht University, 3584 CA Utrecht, The Netherlands

New roads, agricultural projects, logging, and mining are claiming an ever greater area of once-pristine Amazonian forest. The Millennium Ecosystems Assessment (MA) forecasts the extinction of a large fraction of Amazonian tree species based on projected loss of forest cover over the next several decades. How accurate are these estimates of extinction rates? We use neutral theory to estimate the number, relative abundance, and range size of tree species in the Amazon metacommunity and estimate likely tree-species extinctions under published optimistic and nonoptimistic Amazon scenarios. We estimate that the Brazilian portion of the Amazon Basin has (or had) 11,210 tree species that reach sizes >10 cm DBH (stem diameter at breast height). Of these, 3,248 species have population sizes >1 million individuals, and, ignoring possible climate-change effects, almost all of these common species persist under both optimistic and nonoptimistic scenarios. At the rare end of the abundance spectrum, however, neutral theory predicts the existence of ≈5,308 species with <10,000 individuals each that are expected to suffer nearly a 50% extinction rate under the nonoptimistic deforestation scenario and an ≈37% loss rate even under the optimistic scenario. Most of these species have small range sizes and are highly vulnerable to local habitat loss. In ensembles of 100 stochastic simulations, we found mean total extinction rates of 20% and 33% of tree species in the Brazilian Amazon under the optimistic and nonoptimistic scenarios, respectively.

Amazonian tree diversity | neutral theory | tropical tree extinction

“To obtain even a very rough estimate of the total number of species in the [Amazonian] forest community, a hypothesis must be made concerning the relationship between the common and rare species.”

Pires *et al.*, (1)

The watershed of the Amazon River and its tributaries is enormous, covering ≈7,179,100 km², and the longest dimension of the basin is ≈6,815 km. The Amazon Basin contains ≈40% of the world's remaining tropical forest, much of it still botanically intact, or largely so, particularly in Western Amazonia. However, serious concern has been raised about the possibility of large-scale extinctions of tree species in the next several decades, due to the expansion of a network of roads, especially in the Brazilian Amazon (2–5). These roads open undisturbed areas to extractive uses of the Amazon forest in previously inaccessible areas far from rivers and to subsequent clearing of forest for ranching, agricultural crop production, and tree plantations of commercially important species, mostly exotics. Anthropogenic habitat destruction is perhaps the single greatest cause of modern species extinctions (6–8). Climate change may become an even bigger cause of extinction over the next century (9, 10).

This article examines the questions of how many tree species there are in the Amazon and how many of them will go extinct from habitat loss during the next several decades. More than 50 years ago, long before the survival of the Amazon forest became a headline issue, Theodosius Dobzhansky and two experts on the Amazonian tree flora, Pires and Black, made a pioneering

attempt to answer the “how many tree species” question from samples of virgin forest in eastern Amazonia in the state of Pará. In their first paper, which reported counts of tree species in several 1-ha plots, they encountered a large fraction of tree species only once (as a single individual) (11). In their second study (1), they increased their plot size to 3.5 ha in the hope that a larger sample size would reduce the number of singleton species, but the problem only got worse rather than better.

Pires and coworkers did not set themselves the ambitious goal of attempting to estimate the number of tree species in all of the Amazon but just in the particular “association” they sampled. Nevertheless, the quote above indicates that Pires *et al.* (1) were aware of the difficulty of answering the “how many species” question without having a theoretical hypothesis concerning the distribution of relative species abundance. Two primary competing statistical hypotheses were available, then as now: Fisher's logseries (12) and Preston's lognormal (13). The logseries predicts that the most frequent abundance class will be the rarest—singletons, which is what Pires and coworkers observed. Of the 179 species they found, 45 species (25%) occurred just once. Despite this observation, Pires *et al.* (1) argued that the Preston lognormal was the “most reasonable” hypothesis, although they did not fit or mention Fisher's logseries, of which Preston's paper was a critique. When one does this exercise, Fisher's logseries actually fits their data quite well (Fig. 1). But these data were from small plots in forest that was relatively species-poor by Amazonian standards. The question therefore arises: Which of these two distributions is a better fit to the distribution of relative tree species abundance in tropical tree communities in general and, more specifically, to relative tree species abundances in the entirety of the Amazon Basin?

The answer to this question is highly relevant to the questions posed in the title of this article because these two relative-abundance hypotheses yield profoundly different predictions for the total number of tree species in the Amazon as well as for how many of these species are likely to go extinct. The logseries hypothesis predicts a far larger number of species—and that a far larger fraction of these species are rare to very rare—than does the lognormal hypothesis. This is because Preston's (14) canonical lognormal hypothesis postulates a fixed variance or spread in the distribution of log abundance of species irrespective of sample size. The result of this assumption is that the number of octaves of log₂ abundance separating the commonest and rarest species does not increase with increasing sample size. Conse-

This paper results from the Arthur M. Sackler Colloquium of the National Academy of Sciences, “In the Light of Evolution II: Biodiversity and Extinction,” held December 6–8, 2007, at the Arnold and Mabel Beckman Center of the National Academies of Sciences and Engineering in Irvine, CA. The complete program and audio files of most presentations are available on the NAS web site at www.nasonline.org/Sackler.biodiversity.

Author contributions: S.P.H. performed research; F.H., R.C., L.B.-d.-Á., J.K., and H.t.S. contributed new reagents/analytic tools; S.P.H. analyzed data; and S.P.H. wrote the paper.

The authors declare no conflict of interest.

[†]To whom correspondence should be addressed. E-mail: shubbell@eeb.ucla.edu.

© 2008 by The National Academy of Sciences of the USA

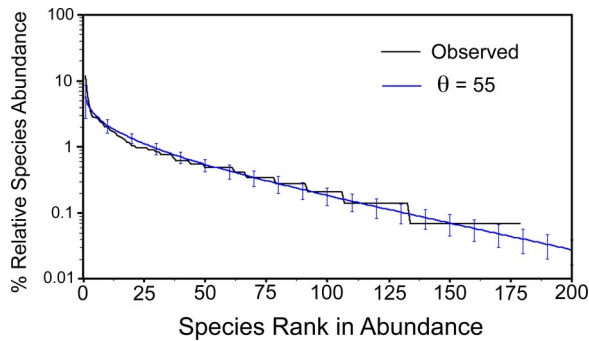


Fig. 1. Fit of Fisher's logseries to the Amazonian relative tree species abundance data of Pires, Dobzhansky, and Black (1).

quently, as the abundance of common species increases in larger samples, so the sample abundance of rare species must also increase in logarithmic proportion. The canonical lognormal hypothesis, in turn, implies that if one takes a large enough sample, as for example, the entire Amazon, the number of absolutely very rare species ought to be extremely small because the total abundance of the most common Amazonian tree species is very large.

In contrast, Fisher's logseries makes no such fixed-variance assumption, and the variance in log species abundance increases steadily with increasing sample size. This is because extremely rare species not previously encountered are continually discovered as sample sizes increase, even as previously discovered species become ever more common in the larger samples. In the logseries, the expected number of species ϕ having abundance n is given by

$$\phi(n) = \alpha \frac{x^n}{n},$$

where α is a fitted diversity parameter, and x is a parameter whose value is close to but less than unity (if $x > 1$, then the series does not converge). Fisher's α , as parameter α is now known, has become one of the most widely used measures of species diversity because its value changes only slowly in the face of increasing sample sizes of individuals drawn from communities and sorted into species. Why Fisher's α should be relatively constant, and the biological significance of both parameters α and x , were not understood until the development of neutral theory.

Applying Neutral Theory: Fisher's Logseries or Preston's Lognormal?

How do we estimate Amazonian tree-species richness and extinction risk due to habitat loss? We can begin by using the framework of neutral theory to estimate the total tree diversity in the Amazonian metacommunity and the expected distribution of relative species abundance and species range sizes. The "metacommunity" refers to the evolutionary-biogeographic unit in which most member species spend their entire evolutionary lifetimes, from origination to extinction, a concept *apropos* to the entire Amazon Basin. Neutral theory generates a biodiversity number θ that uniquely specifies not only how many species are expected to be present at steady-state between speciation and extinction in the metacommunity but also the expected abundances of each species. The number θ is a fundamental quantity in neutral theory that is proportional to the product of the average per capita speciation rate in the metacommunity and the size of the metacommunity. Metacommunity size is simply the sum of the population sizes of all species in the metacommunity. An important discovery from neutral

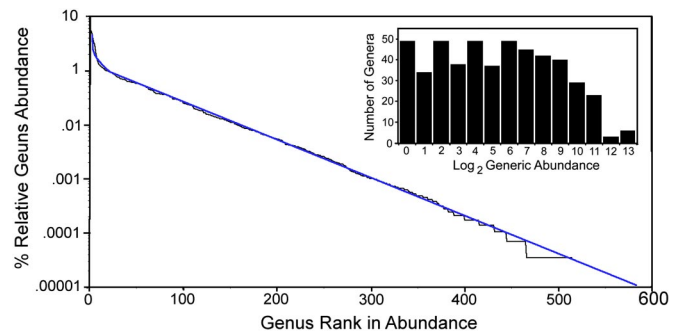


Fig. 2. Fit of Fisher's logseries to the relative abundance data of Amazonian tree genera (data from ref. 18). Fisher's α (θ) is ≈ 71 .

theory is that the expected distribution of metacommunity relative species abundance is Fisher's logseries (15, 16).

The logseries distribution applies in cases when the metacommunity is continuous, as in continental tropical forests, but not necessarily if an island model is more appropriate for the metacommunity, as in the case of isolated coral reefs scattered across the Pacific Ocean (17). Remarkably, it also turns out that the fundamental biodiversity number θ of neutral theory is identical to Fisher's α , the celebrated diversity index of Fisher's logseries, and parameter x of the logseries is the ratio of the average per capita birth rate to per capita death rate in the metacommunity. The reason Fisher's α is so stable, according to neutral theory, is that it is proportional to the average speciation rate in the metacommunity and to the size of the metacommunity, both very stable numbers.

How do we fit Fisher's logseries when the total number of tree species in the Amazon and their relative abundances are unknown? Extensive areas of the Amazon have not yet been adequately collected. Moreover, a large amount of material already collected remains to be described and classified for the first time, and many groups need revision to eliminate synonyms for species described multiple times from collections made by different museums at different times from different parts of Amazonia. Despite current problems with species-level identifications, however, generic-level determinations of Amazonian trees are much more reliable. Most undescribed tree species can at least be placed with reasonable confidence into a known genus. This is fortunate because we can test the fit of the logseries and the lognormal to the abundances of Amazonian genera.

Neutral theory asserts that generic- and familial-level clades should also obey the same metacommunity dynamics as species, the only difference being that they should have lower rates of origination and extinction than species do. Over the last two decades, a dataset comprising over a quarter million individual tree records has been assembled by many people from a large number of small plots over the Amazon Basin (18). The plots extend throughout the Brazilian Amazon into Amazonian Colombia, Ecuador, Peru, and Bolivia to the west and into the Guianan Shield to the northeast. The 288,973 trees have been classified into 514 genera.

The abundances of these genera are fit very well by Fisher's logseries and not by Preston's lognormal (Fig. 2). The data are well fit with a value of Fisher's α (θ) of 71. The Preston-style histogram of species binned into doubling classes of abundance (Fig. 2 *Inset* graph) has no mode at intermediate abundances and exhibits a flat top as predicted by the logseries in species-rich assemblages but not by the lognormal. Given this result—although we do not yet know the species abundance distribution for the tree flora of the Amazon—it is highly unlikely that the species distribution will be a Preston canonical lognormal. This is different from the prevailing view, which is that tropical

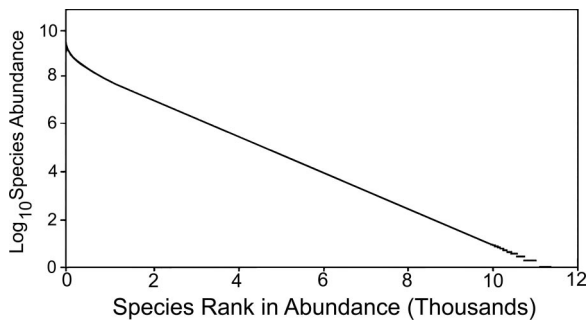


Fig. 3. The predicted logseries rank abundance curve for tree species in the Brazilian Amazon. The size of the metacommunity for this calculation was taken as 4,648,400 km² times 60,000 stems >10 cm DBH km⁻². The value of Fisher's α (or θ) for this calculation was 500.

lowland forests have low β -diversity and are comprised of relatively widespread common species (19) although some dispute this view (20).

Estimating the Biodiversity Number and Abundance of Amazonian Tree Species

Having established that Fisher's logseries and neutral theory give a good fit to the diversity of genera of trees throughout Amazonia, we now need to estimate tree diversity and relative abundance at the species level. The Amazon Basin has $\approx 50,000$ described vascular plant species, in round numbers, of which approximately half are woody. Of these, approximately half are trees, reaching reproductive maturity >10 cm DBH. This yields an estimate of $\approx 12,500$ tree species in the entire Amazon Basin. This is undoubtedly conservative because the number of synonymous species is probably much less than the number of undescribed species. The Brazilian Amazon, which constitutes two thirds (64.7%) of the entire basin, is expected to have $\approx 11,210$ tree species. This number is what would be expected with an Arrhenius species–area relationship with a z value of 0.25. We can estimate the biodiversity number θ or Fisher's α for all Amazon tree species when we know the number of individual trees in the Amazon. The mean number of trees >10 cm DBH in the 752 plots across the Amazon is 600 ha⁻¹, which translates to 60,000 km⁻². The area of the Amazon Basin is 7,179,100 km², which yields $4.3075 \cdot 10^{11}$ trees >10 cm DBH. The area of the Brazilian Amazon is 4,468,400 km², which gives $2.6810 \cdot 10^{11}$ trees. From the logseries, we have the relationship $S = \alpha \ln(1 + N/\alpha)$, which yields $\alpha = 743$ for the entire Amazon and $\alpha = 500$ for the Brazilian Amazon. These numbers are quite reasonable in light of the estimate of θ for the 50-ha plot in Yasuni National Park in Amazonian Ecuador ($\theta = 212$).

Now that we have estimated the fundamental biodiversity number θ for the Amazon Basin and for that portion of the basin that lies inside Brazil, we can compute the corresponding logseries relative species-abundance distributions. The logseries rank abundance curve for the Brazilian Amazon is shown in Fig. 3. The most abundant species has an estimated total abundance of 3.89 billion individuals >10 cm DBH, but despite its abundance, it comprises only 1.393% of all trees. Large numbers of tree species are very abundant; 3,248 species (29.0%) have >10⁶ individuals in the Brazilian Amazon, and 4,575 species (40.8%) have >10⁵ individuals >10 cm DBH. At the other end of the relative-abundance spectrum, we estimate that more than a third of all species (3,981, or 35.5%) in the Brazilian Amazon each have (or had) total population sizes <10³ individuals. The remaining quarter of tree species in the Brazilian Amazon have estimated abundances between 10³ and 10⁵ individuals >10 cm DBH.

Estimating the Range Sizes of Amazonian Tree Species

Many common Amazonian tree species must have extremely large range sizes. In the fertile-soil, aseasonal-climate, high-diversity forests of western Amazonia, many of the same species are found in tree communities separated by thousands of kilometers north and south along the eastern side of the Andes (18, 19). One can calculate the probability that two trees randomly sampled from geographically separated tree communities are the same species from existing plot data in western Amazonia. After decreasing rapidly over short distances (<100m), this probability decays very slowly over large distances (19). However, there is much higher turnover of species and genera when one traverses the Amazon Basin over the seasonality gradient from the northwest (aseasonal) to southeast (highly seasonal) and on the soil-fertility gradient from the southwest (high fertility) to the northeast (low fertility) (18).

Extremely common, widespread species with >10⁶ adults constitute between a quarter and a third of the total number of Amazonian tree species, and these species are expected to have broad ranges over the Amazon. But what are the range sizes for the many rare to very rare species in the Amazon Basin? By rare in the present context, we mean that the global population size of a given species is small irrespective of the spatial distribution and density of the individual plants of the species. To estimate range size, we need to know the relationship between population size and the area it occupies. If we assume that local population densities of common and rare species are approximately of the same order of magnitude (e.g., because of similar order-of-magnitude seed-dispersal distances), then it follows that rare species will generally have smaller range sizes than common species. This generalization could be violated if rare species are systematically more likely to have a fragmented metapopulation structure than common species.

Whatever the spatial structure of tropical tree populations, however, we can take an empirical approach to this question using the mapped 50-ha plots. We can ask: How does the average distance from a focal tree to a conspecific neighbor change with increasing rank of neighbor, i.e., the distance to the first nearest neighbor, the second nearest neighbor, and so on, to the n th nearest neighbor? For a species with a total population size of n individuals, then the average radius of its range will be given by the mean distance to the n th nearest neighbor. In taking this approach, one makes no assumptions about the dispersion or degree of species aggregation of tropical tree species, but we know that most tropical tree species are clumped in distribution (21, 22).

In a population with random (Poisson) dispersion, Thompson (23) proved that the mean distance to the n th nearest neighbor r_n is given by

$$E[r_n] = \frac{1}{\sqrt{\delta}} \frac{n \cdot (2n)!}{(2^n \cdot n!)^2} \approx \frac{1}{\sqrt{\pi \delta}} n^{1/2},$$

where δ is the mean density of trees per unit area. The distance $E[r_n]$ as a function of n is asymptotically a power law for large n . The above approximation is derived from Sterling's formula, which holds very well even for small n . Therefore, the slope of the log–log relationship between distance and rank of nearest neighbor approaches 0.5 as $n \rightarrow \infty$ in a Poisson-distributed population. Power laws are convenient because of their scale independence, which means that we can compute $E[r_n]$ for any arbitrarily large population size. But this result was obtained for a randomly distributed population. What about nonrandomly distributed tropical tree populations?

To a very good approximation, the relationship between $\log E[r_n]$ and $\log n$ is also a power law for nonrandomly distributed tropical tree populations. We computed the relationship be-

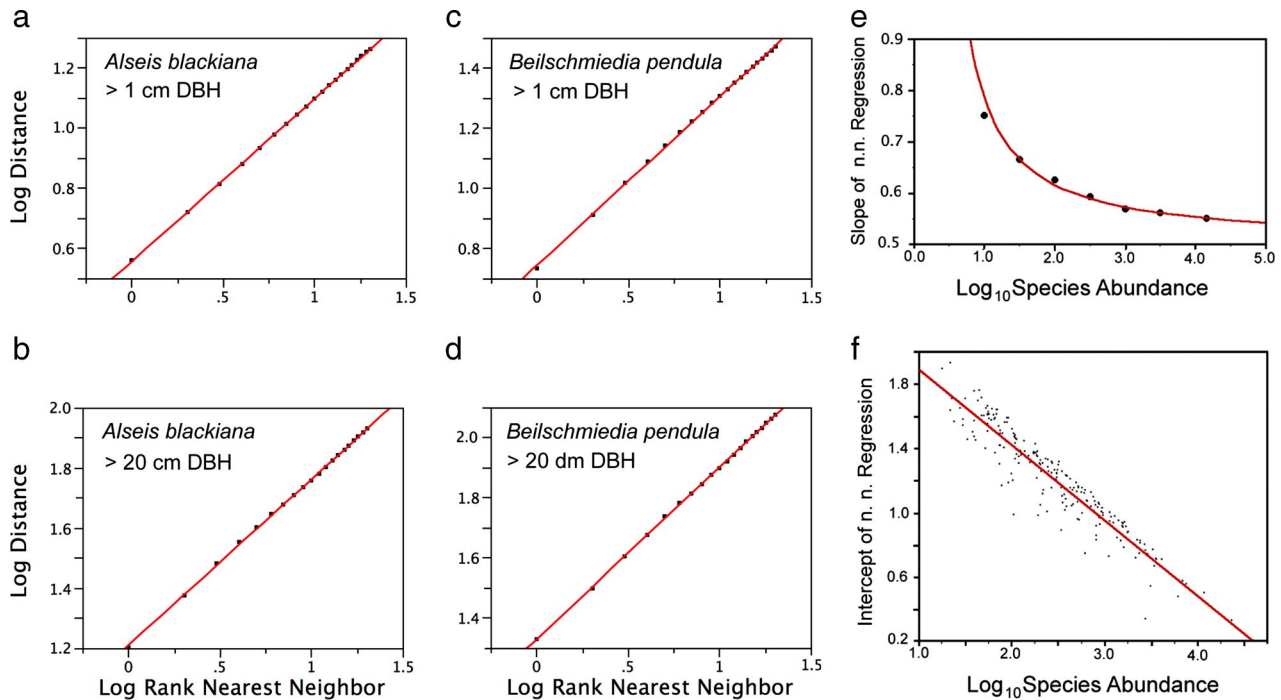


Fig. 4. Log–log relationships between the mean distance to the *n*th nearest conspecific neighbor of a focal plant and the rank of nearest neighbor, for two arbitrarily chosen BCI tree species. (a) *Alseis blackiana* (Rubiaceae), stems >1 cm DBH; $Y = 0.5589 + 0.5419X$, $R^2 = 0.999944$. (b) *A. blackiana* (Rubiaceae), stems >20 cm DBH; $Y = 1.2137 + 0.5514X$, $R^2 = 0.999376$. (c) *Beilschmiedia pendula* (Lauraceae), stems >1 cm DBH; $Y = 0.7472 + 0.5608X$, $R^2 = 0.99951$. (d) *B. pendula* (Lauraceae), stems >20 cm DBH; $Y = 1.3328 + 0.5706X$, $R^2 = 0.999638$. (e) Distribution of slopes of the log–log relationship between the mean distance to the *n*th nearest conspecific neighbor of a focal plant and the rank of nearest neighbor for the 155 tree species on BCI with abundances >10². (f) Distribution of intercepts for the same relationship.

tween log distance to the *n*th nearest neighbor and log rank of nearest neighbor for all tree species with total abundances $\geq 10^2$ individuals (155 species) in the 50-ha plot on Barro Colorado Island (BCI), Panama. Virtually all of these are very good power laws, illustrated for two arbitrarily chosen species in Fig. 4, for all stems >1 cm DBH (Fig. 4a and c) and for canopy adult trees >20 cm DBH (Fig. 4b and d). Based on available data, these power law relationships also appear to hold on spatial scales $\gg 50$ ha. For example, *Tabebuia guayacan* (Bignoniaceae), a canopy-emergent species whose individual adults can be accurately censused by using hyperspectral data from the Quickbird satellite, exhibits a very precise log–log relationship over the entire 15.2 km² area of BCI (Fig. 5) (J.K. and S.P.H., unpublished data). Therefore, we assume that this relationship also holds on larger scales. John Harte has indicated that this result can now be proven (J. Harte, unpublished work). To calculate range sizes of the 11,200 tree species in the Brazilian Amazon, we adjusted the intercept of the log–log regression to reflect the effect of rarity on the first nearest-neighbor distance (Fig. 4f), and we adjusted the slope based on the inverse relationship between log abundance and the slope (Fig. 4e).

The predicted mean range sizes in km² for species differing in abundance by seven orders of magnitude are listed in Table 1. Extremely rare tree species with population sizes <10³ individuals have range sizes <14 km² in area. Conversely, at the other end of the abundance spectrum, species with >10⁶ individuals have range sizes <261,000 km². Species with >10⁸ individuals occupy the entire Amazon Basin. These population and range size calculations are based on the power law formulae for all individuals with a stem diameter of >1 cm DBH, with slope and intercept adjusted for species abundance *n* (Fig. 4e and f).

Estimating Tree Species Extinction Risk in the Brazilian Amazon

The area covered by tropical forest in the Brazilian Amazon is still very large, but, partly because it is so large, Brazil is also

suffering the highest absolute rate of deforestation of any tropical country in the world. Between 1990 and 1994, the mean annual deforestation rate in the Brazilian Amazon was 1.37 million ha·yr⁻¹, which increased 61% to 2.20 million ha·yr⁻¹ a decade later in 2000–2004 (24). This rate of forest loss is equivalent to clearing an area the combined size of the states of Connecticut and Delaware every year. This clearing represents $\approx 0.43\%$ of the total surface area on the Amazon, not correcting for nonforest area in rivers, lakes, and already deforested portions of Amazonia. When such corrections are applied, conservative estimates of the current rate of deforestation in the Brazilian Amazon are $\approx 0.7\% \cdot \text{yr}^{-1}$.

What is the actual risk of extinction of Amazonian tree species posed by this deforestation in the near term, i.e., over the next

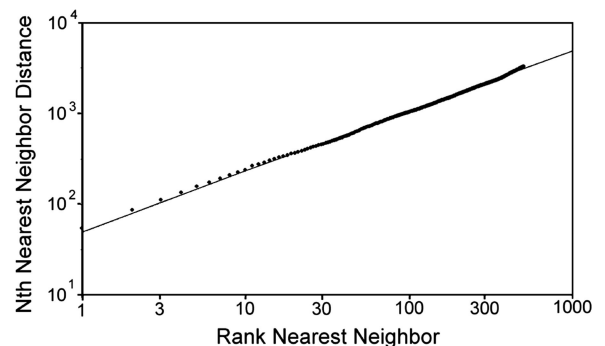


Fig. 5. Landscape-level relationship between the mean distance to the *n*th nearest conspecific neighbor of a focal plant and the rank of nearest neighbor for the rare canopy tree *Tabebuia guayacan* (Bignoniaceae) over the 15.2 km² area of BCI, Panama. Power-law relationship for *T. guayacan* adults: $\log_{10}(\text{distance to } n\text{th nearest neighbor}) = 1.7099 + 0.6586 \log_{10}(\text{rank nearest neighbor})$, $R^2 = 0.998$.

Table 1. Estimated tropical tree species' ranges as a function of species abundance in the Brazilian Amazon (total area: 4,652,400 km²)

Species abundance	Range area, km ²	Fraction of Brazilian Amazon
1.0×10^1	2.076×10^{-2}	4.467×10^{-9}
3.0×10^1	9.878×10^{-2}	2.125×10^{-8}
1.0×10^2	5.459×10^{-1}	1.174×10^{-7}
3.0×10^2	2.598×10^0	5.589×10^{-7}
1.0×10^3	1.436×10^1	3.069×10^{-6}
3.0×10^3	6.834×10^1	1.470×10^{-5}
1.0×10^4	3.772×10^2	8.115×10^{-5}
3.0×10^4	1.797×10^3	3.866×10^{-4}
1.0×10^5	9.935×10^3	2.137×10^{-3}
3.0×10^5	4.728×10^4	1.017×10^{-2}
1.0×10^6	2.613×10^5	5.621×10^{-2}
3.0×10^6	1.244×10^6	2.676×10^{-1}
1.0×10^6	1.244×10^6	2.676×10^{-1}

several decades? We can now attempt to answer this question, at least to a first approximation, by confronting our calculations of relative species abundance and range sizes with maps of projected loss of forest cover in the Amazon. Detailed maps produced by Laurance *et al.* (3) consist of two graphical scenarios of the future of the Brazilian Amazon. One scenario they considered “optimistic” (Fig. 6*a*) and the other “nonoptimistic” (Fig. 6*b*). They evaluated current and pending road-building projects, agricultural development and urbanization, logging, and mining, and then they classified land use into four categories: “heavy-impact areas” (shown in black), “moderate-impact areas” (red), “light-impact areas” (yellow), and “pristine areas” (green). There is a marked increase in the percentage of area in black, red, or yellow, and loss of area in green, in going from the optimistic to nonoptimistic scenarios. The percentages of area in the four land-use categories under the optimistic scenario were 36.7%, 16.1%, 23.1%, and 24.1% for black, red, yellow, and green, respectively. Under the nonoptimistic scenario, however, these percentages become: 49.4%, 25.4%, 21.0%, and 4.2%,

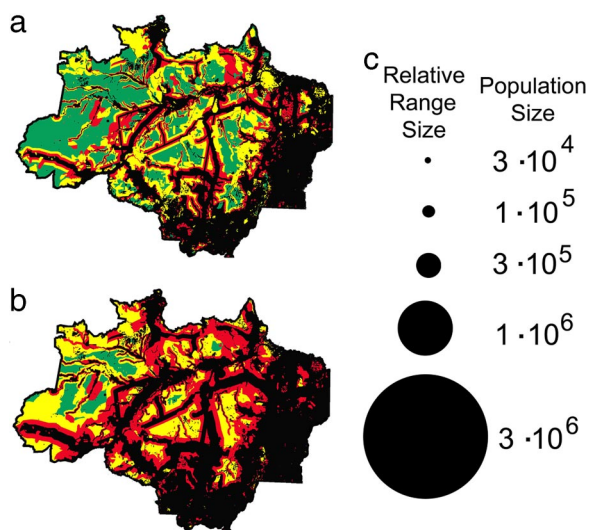


Fig. 6. Scenarios of the future of the Brazilian Amazon [after Laurance *et al.* (3)]. (a) Optimistic scenario. (b) Pessimistic scenario. Black, heavy-impact areas; red, moderate-impact areas; yellow, light-impact areas; green, pristine areas. See text for description of these impacts. (c) Relative sizes of species ranges for some highly abundant species, on same scale as maps of the Brazilian Amazon.

respectively. For our own analyses, we digitized the maps of Laurance *et al.* at a spatial resolution (pixel size) of 10×10 -km cells and classified each of these cells into one of the four land-use categories. We limit the analysis to the Brazilian portion of the Amazon because we do not have comparable maps for parts of the Amazon Basin that lie outside Brazil.

Calculating extinction risk for tree species in the Amazon is perhaps the most problematic and the most speculative part of the analysis, but it is a conservation issue of such paramount importance that we feel we must proceed. Whatever the accuracy of our extinction rate estimates, we believe that estimates informed by theory on the distribution of relative tree-species abundance and species range sizes are likely to be more accurate than estimates not based on such information. The two most difficult issues are: (i) we do not know where the species whose ranges we can estimate are physically located in the Amazon and (ii), perhaps more important, we do not know how each of these tree species will respond to each of the land-use categories.

Faced with these information challenges, we have taken the following approach. With regard to the first problem, the best we can currently do is to perform a large ensemble of stochastic simulations in which we assign locations of all species in the metacommunity randomly throughout the Brazilian Amazon and then average the extinctions results over these simulations. In each stochastic simulation, we assigned the centroids of the species ranges at random locations and then calculated the number of pixels of each land-use category that lay within the calculated range size for the species of a given abundance. For species with $<10^2$ individuals, calculated range sizes were smaller than a single pixel, and each of these was assigned to a single pixel of a single land-use category. We then computed the fraction of the species range that was within each land-use category. Range areas were originally calculated as circles whose radii were the mean distances to the n th nearest neighbor, but in our simulations, we allowed the compass orientation and shape to vary from circles to ellipses up to a maximum aspect ratio of 4:1 for species whose ranges exceeded 100 km² (minimum pixel size), with the long axis at a random angle with respect to north. The relative sizes of the Brazilian Amazon and some of the larger species range sizes are shown in Fig. 6*c* on the same scale as the maps in Fig. 6*a* and *b*.

With regard to the second problem—the responses of species to the land-use categories—we have run three extinction scenarios, the first of which we believe is most likely. The first scenario obeys a middle-of-the-road conservative rule of the three extinction scenarios—conservative in the magnitude of predicted extinction rates. The rule is that a species goes extinct if, and only if, its range lies entirely in heavy-impact areas. Of the four land-use categories, the heavy-impact areas, shown in black, are most likely to result in tree extinctions among species restricted to these areas because they have lost virtually all of their primary forest cover, and what forest remains is in very small, isolated, and highly disturbed remnants.

Although speculative, we think it is likely that the other land-use categories will have minimal impact on elevating species extinction above background rates. Despite the visually alarming appearance of the nonoptimistic scenario map (Fig. 6*b*), the descriptions of the land-use categories in on-line supplementary material to the paper by Laurance *et al.* (3) do not describe impacts that are likely to cause many, if any, tree-species extinctions, in our opinion. For example, light-impact areas (in yellow) still retain nearly intact primary forest cover ($>95\%$) but can “experience illegal gold-mining, small-scale farming, hunting, hand-logging, and nontimber resource extraction (e.g., rubber-tapping).” Even moderate-impact areas (in red) still have mostly intact primary forest cover ($>85\%$) but “contain localized forest clearings and some roads, and may be affected by logging, mining, hunting, and oil and gas exploration.” The

fourth land-use category, pristine (in green), is, by definition, the reference or “natural” state in which extinction occurs at background rates. These areas are described as having “fully intact primary-forest cover and are free from anthropogenic impacts aside from limited hunting, fishing, and swidden farming by traditional indigenous communities.”

One can, however, erect a plausible second extinction scenario in which species could go extinct in moderate-impact areas at a higher than background rate, and even in light-impact areas. This is potentially the least conservative scenario, the one that predicts the most extinctions. Because the land-use categories are broad averages, they can potentially obscure local heterogeneity in the rate of loss of forest cover, so it is conceivable that a rare, localized endemic species may be eliminated in one of the cleared areas. In our second scenario, species still go extinct if their range lies entirely in heavy-impact areas. However, they can also go extinct if they have ranges that lie partially or wholly within moderate- or light-impact areas. The second-scenario rule is that there is a 15% probability of extinction of each cell occupied by the species in the red zone (because there is a 15% loss of forest cover in the moderate-impact areas) and a 5% probability of extinction of each cell occupied in the yellow zone (because there is a 5% loss of forest cover in the light-impact areas). These “coin tosses” per cell are assumed to be independent Bernoulli trials, so the probability of a joint event is the product of the per-cell probabilities. If the species has no range in green areas, and if it goes extinct in all of the cells it occupies in red and yellow areas (and it goes extinct in all black cells), then the species goes globally extinct.

The third scenario is at the other extreme, the most conservative hypothesis, predicting the lowest extinction rates. This scenario says that even if a species is restricted to the black zone, it has a nonzero chance of surviving. It is difficult to know what survival probability to give a species, but we assume that the larger the range of the species (more individuals), the greater the chance that some local population will survive in one of the forest fragments. For sake of argument, we assume in this scenario that a species has a 5% chance of surviving per black cell occupied. One could run many different versions of this scenario with different survival probabilities. A species whose range lies entirely within the black zone could nevertheless survive if it survives in at least one of the black cells it occupies.

Given these extinction scenarios, what are the predicted extinction rates? Fig. 7a shows the results for the middle-of-the-road extinction scenario 1. The qualitative pattern is that the probability of extinction is a logistic function of species abundance (range size), with high extinction probabilities for rare species, dropping to essentially zero probability for species above a critical population-size threshold of $\approx 10^6$ individuals. Below population sizes of $\approx 10^4$ individuals, the mean probability of extinction is close to the proportion of heavy-impact areas under Laurance *et al.*'s (3) optimistic and non-optimistic deforestation scenarios. This result is not unexpected because predicted range sizes of tree species with $<10^4$ individuals are small, <24 km². Under the nonoptimistic deforestation scenario 3,656 tree species (32.6%) are predicted to go extinct, but only 354 of these species have population sizes of $>10^5$ individuals, and only 42 species predicted to go extinct have population sizes of $>10^6$ individuals. But even under the optimistic deforestation scenario, 2,228 tree species (19.9%) are predicted to go extinct, of which 36 species have population sizes of $>10^5$ individuals. However, for the 3,248 species (29.0%) with $>10^6$ individuals apiece, there are no forecast extinctions under the optimistic scenario.

Extinction scenario 2 (results not shown) gave qualitatively similar results to scenario 1 because we made it hard to go extinct in moderate- to light-impact areas (all occupied cells in these areas had to go extinct, with fairly low probability of extinction

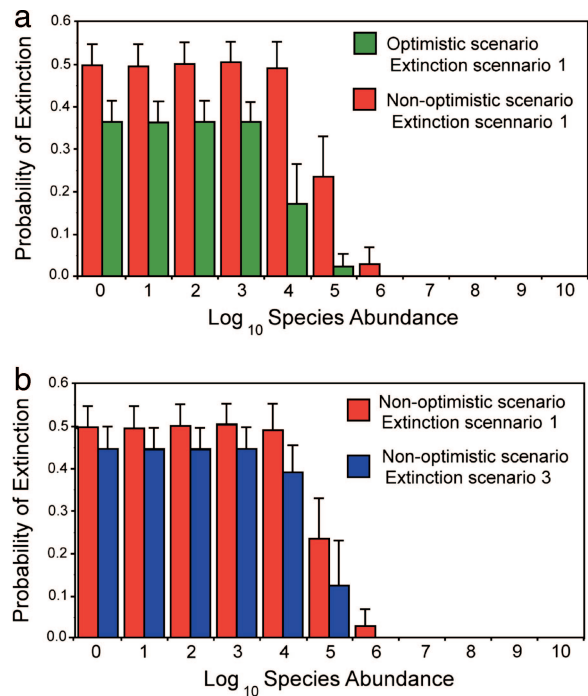


Fig. 7. Predicted extinction rates of tree species in the Brazilian Amazon under the optimistic and nonoptimistic scenarios of Laurance *et al.* (3) as a function of population size. The abundance bins (histogram bars) are labeled with the logarithm to the base 10 of the lower bound of abundance in the respective bin. (a) Extinction scenario 1: Species go extinct only if their entire geographic range is in heavy-impact areas (in black) on either the optimistic or the nonoptimistic scenarios of Laurance *et al.* (3). (b) Comparison of extinction scenarios 1 and 3. In extinction scenario 3, species manage to survive in heavy-impact areas if at least one occupied cell survives, with probability 0.05 per cell. Extinction scenario 2 (data not shown), in which species can go extinct if they have some portion of their range in areas other than heavy-impact, gave results very similar to extinction scenario 1.

in each cell: 15% and 5% per-cell extinction probability in moderate- and light-impact areas, respectively).

Extinction scenario 3 showed a significant “rescue effect” relative to scenario 1 for species with population sizes between 10³ and 10⁵ (Fig. 7b) even though the probability of survival of species in heavy-impact areas was small on a per-cell basis. A total of 3,085 species (27.5%) are expected to go extinct under extinction scenario 3, which is 571 fewer species than under extinction scenario 1, under the pessimistic case. There is also an $\approx 3\%$ improvement in the mean survival of species with $<10^3$ individuals, but the extinction rate of these rare species is still very high, $\approx 47\%$.

One question we cannot answer is how many of these extinctions have already taken place. At the time this article was written, we did not have a map of areas already deforested in the Brazilian Amazon. It is quite clear that much of the Atlantic forest in Amazonia is already gone. This fact is reflected by the scant change in heavy-impact areas in the eastern Amazon between the maps for the optimistic and nonoptimistic deforestation scenarios. Thus, our estimates of extinction rates due to future deforestation are likely to be overestimates because they include species that have already gone extinct.

Conclusions and Caveats

A controversy in recent years has been developing over the future of the Amazon. On the one side are scientists legitimately concerned with the rapid deforestation of the Amazon and the potential consequences for not only species extinction but also

for the loss of ecosystem services, such as climate amelioration, soil conservation, and the welfare of wildlife and other species that depend on the trees for their survival (3, 4, 24, 25). On the other side, however, are scientists who believe that the short-term extinction threat, particularly from human population growth, is greatly exaggerated, and that rates of deforestation are likely to decline in the future (26, 27). In retrospect, many of the predictions of tropical deforestation made in the 1970s and 1980s have not come to pass (28). For example, the eminent tropical forest ecologist and biogeographer, T. C. Whitmore (29) wrote, nearly three decades ago, that “the onslaught [on tropical forests] will continue to accelerate, reducing the forest to scattered fragments by A.D. 2000.” Although he was wrong on his dates, if one takes a longer view, one may worry that Whitmore’s dark vision will prove to be accurate.

The results of the present analysis paint a somewhat more complex and nuanced picture of the future of Amazon forests and its tree species. On the one hand, under all of the scenarios we considered, a large number of very common tree species will almost certainly survive habitat losses, whether one takes an optimistic or nonoptimistic view of deforestation in the Brazilian Amazon. This is the good news. However, it is not clear how many survivors of habitat loss will also survive the novel climates forecast for the Amazon, which include significantly warmer temperatures and more variability in rainfall, accompanied by longer and more severe droughts (10). The bad news is that large percentages of rare and endemic species will probably go extinct. The number of rare tree species at risk of extinction from habitat loss could be in the hundreds to several thousand. The actual number at risk is uncertain, because it depends on how many rare species really exist in the Amazon.

There are many caveats to this analysis. A central issue is whether Fisher’s logseries is the correct model of relative tree-species abundance in the Amazon tree metacommunity.

This assumption leads to the prediction of high species richness and many rare species and high extinction rates of rare species. In defense of the theory, there is strong support in the data on tree-species abundances across Central Panama (data not presented), and from the abundances of tree genera across Amazonia, that the logseries is the right model.

Another caveat is that the analysis considers only tree-species extinctions and not the potential extinction of other animal and plant (microbial?) species, that are likely to accompany habitat loss. There are also many complex biological interactions in tropical rainforests affecting the survival and reproduction of tropical tree species that might be seriously impacted by forest degradation long before complete deforestation occurs. For example, many tropical trees are bat-pollinated, and their successful reproduction depends on bats. What do we know about the susceptibility of bat communities to forest fragmentation?

Another issue is that the calculation of the number of tree species at risk also depends on how individual species will respond to different levels of forest disturbance and conversion. This unknown is undoubtedly the most challenging aspect of the present analysis. Although it is an old scientific chestnut, we must once again emphasize how important it is to support continuing basic science on tropical forests. We urgently need information on the biogeography, population sizes, comparative life histories, and environmental requirements of tropical tree species. As such data accumulate, we can not only make more accurate assessments of extinction risks, but also have more informed and intelligent suggestions for how to save tropical tree species and forests from extinction.

ACKNOWLEDGMENTS. We thank N. Pitman, O. Phillips, J. Chave, D. Sabatier, A. Duque, J.-F. Molino, M.-F. Prévost, R. Spichiger, H. Castellanos, P. von Hildebrand, and R. Vásquez for use of their unpublished plot data on the abundances of Amazonian tree genera. This work has been supported by grants from the National Science Foundation and in-kind support from the Smithsonian Tropical Research Institute.

- Pires JM, Dobzhansky TH, Black GA (1953) An estimate of the number of species of trees in an Amazonian forest community. *Bot Gaz* 114:467–477.
- Whitmore TC, Sauer JA, eds (1992) *Tropical Deforestation and Species Extinction* (Chapman & Hall, London).
- Laurance WF, et al. (2001) The future of the Brazilian Amazon. *Science* 291:438–439.
- Laurance WF, et al. (2002) Issues in Amazonian development. *Science* 295:1643–1644.
- Anonymous (2006) *Ecosystems and Human Well-Being. The Millennium Ecosystems Assessment* (UNDP, United Nations, New York).
- Ehrlich P, Ehrlich A (1981) *Extinction* (Ballantine Books, New York).
- Wilson EO, Peter FM, eds (1988) *Biodiversity* (Natl Acad Press, Washington, DC).
- Wilson EO (1989) Threats to biodiversity. *Sci Am* Sept 108–116.
- Thomas CD, et al. (2004) Extinction risk from climate change. *Nature* 427:145–148.
- Williams JW, Jackson ST, Kurtzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proc Natl Acad Sci USA* 104:5739–5742.
- Black GA, Dobzhansky TH, Pavan C (1950) Some attempts to estimate species diversity and population density of trees in Amazonian forests. *Bot Gaz* 111:413–425.
- Fisher RA, Corbet AS, Williams C (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *J Anim Ecol* 12:42–58.
- Preston FW (1948) The commonness, and rarity, of species. *Ecology* 29:254–283.
- Preston FW (1962) The canonical distribution of commonness and rarity. *Ecology* 43:185; 215:410–432.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ Press, Princeton).
- Volkov I, Banavar JR, Hubbell SP, Maritan A (2003) Neutral theory and the relative abundance of species in ecology. *Nature* 424:1035–1037.
- Volkov I, Banavar JR, Hubbell SP, Maritan A (2007) Patterns of relative species abundance in rain forests and coral reefs. *Nature* 450:45–49.
- ter Steege H, et al. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature* 443:444–446.
- Condit R, et al. (2002) Beta diversity in tropical forest trees. *Science* 295:666–669.
- Tuomisto H, et al. (1995) Dissecting Amazonian biodiversity. *Science* 269:63–66.
- Hubbell SP (1979) Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203:1299–1309.
- Condit R, et al. (2000) Spatial patterns in the distribution of tropical tree species. *Science* 288:1414–1418.
- Thompson HR (1956) Distribution of distance to nth neighbour in a population of randomly distributed individuals. *Ecology* 37:391–394.
- Laurance WF, Albernaz AK, Fearnside PM, Vasconcelos HL, Ferreira LV (2004) Deforestation in Amazonia. *Science* 304:1110.
- Brooks TM, et al. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conserv Biol* 16:909–923.
- Wright SJ, Muller-Landau H (2006a) The future of tropical forest species. *Biotropica* 38:287–301.
- Wright SJ, Muller-Landau H (2006b) The uncertain future of tropical forest species. *Biotropica* 38:443–445.
- Myers, N (1980) *Conversion of Tropical Moist Forests*. (National Academy of Sciences, Washington, D.C.).
- Whitmore TC (1980) in *Conservation Biology*, eds Soulé ME, Wilcox BA (Sinauer, Sunderland, MA), pp 303–318.