

Effects of habitat disturbance on tropical forest biodiversity

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It is widely expected that habitat destruction in the tropics will cause a mass extinction in coming years, but the potential magnitude of the loss is unclear. Existing literature has focused on estimating global extinction rates indirectly or on quantifying effects only at local and regional scales. This paper directly predicts global losses in 11 groups of organisms that would ensue from disturbance of all remaining tropical forest habitats. The results are based on applying a highly accurate method of estimating species richness to 875 ecological samples. About 41% of the tree and animal species in this dataset are absent from disturbed habitats, even though most samples do still represent forests of some kind. The individual figures are 30% for trees and 8–65% for 10 animal groups. Local communities are more robust to disturbance because losses are partially balanced out by gains resulting from homogenization.

deforestation | lambda-5 index | mass extinction | multiton subsampling | species extinction

The current mass extinction will play out largely in tropical forests because the Earth's terrestrial biodiversity is heavily concentrated in these ecosystems (1–3). Global climate change may prove to be catastrophic for tropical trees (4) and other organisms (5). However, the most pressing immediate problem is massive and accelerating deforestation (6–9), which removed about 5% of global cover in the decade between 2000 and 2010 (10) and has had severe impacts even inside protected areas (11). Moreover, 88.5% of the Earth's land surface is unprotected, and 20% of threatened species have ranges falling entirely outside protected areas (12). The situation in the tropics is likely to be even worse.

There is noteworthy literature on the effects of habitat destruction on species richness in local and regional ecosystems across the globe (6–9), but surprisingly little is known about what might happen in terms of range-wide species extinctions as the remaining primary forest cover asymptotes on zero. This paper uses field-based ecological samples and rigorous statistical methods to quantify the amount of extinction that might be expected as disturbance proceeds. The samples document 11 organismal groups of keen ecological interest spread across the world's tropical forest habitats (Fig. 1 and Table S1).

Instead of using sample data, global estimates of potential species extinction have tended to rely either on expert opinion (4) or on extrapolations that combine observed species-area relationships with expected or actual deforestation rates (e.g., refs. 1, 6). Actual extinctions are well-documented only for vertebrates (13). Even the underlying estimates of global diversity in certain groups have depended on indirect extrapolation methods of various kinds, such as scaling up from local-scale plot data (14) or from richness ratios between taxonomic levels (15). These methodologies yield disparate results and have individually come under strong criticism (15). With a few important exceptions (e.g., refs. 6-8, 16-18, and local-scale analyses reviewed in ref. 19), most researchers have also tended to focus on trees, mammals, birds, and a few other groups such as dung beetles (e.g., ref. 9). Finally, although important meta-analyses of local data have been carried out, most have used raw species-richness values (6, 7, 20), and no study has attempted to compare local and global species richness based on strictly comparable estimates that are controlled for sample-size effects.

Ecologists do make extensive use of methods that remove sampling biases, but such research has focused almost entirely on local samples. Many of these standardization analyses (8, 17, 18, 21) have used species counts interpolated to a least common denominator level by means of the long-established method of rarefaction (22, 23), which is problematic because rarefaction compresses differences between samples (24).

However, the compression problem can be solved using methods of either interpolation or extrapolation. Four different approaches are used in this paper (Methods). Two are analytical subsampling methods that seek to make samples comparable by drawing them down to the same completeness level based on expected counts of species sampled exactly once. One of these is called "shareholder quorum subsampling" (24) or "coverage-based rarefaction" (25), and the other is called "multiton subsampling." The other two methods extrapolate the total number of species by considering counts of those found exactly once or twice. The first method (26), called "Chao 1" when applied to within-sample data and "Chao 2" when applied to among-sample incidence data, is very well-known (27). The second, called the " λ_5 " or "lambda-5" extrapolator, has not been reported previously. Analyses presented in the main body of this text focus on the λ_5 method because it is particularly accurate when counts of individuals are uneven. However, global-scale Chao 1 and λ_5 estimates are extremely similar, and none of the results depend qualitatively on the choice of methods.

Disturbance has large effects at both local and global scales (Figs. 2, 3, and 4*A* and Tables S2 and S3). Local losses are >22% in pastures and croplands, and plantations and secondary forests are both >18% less rich than primary forests (Fig. 2 and Table S2). Indeed, although secondary forests are sometimes thought to

Significance

Biologists believe that a major mass extinction is happening in the tropics. Destruction of forests is a key reason. However, there are no solid predictions of the percentage of species that will go extinct as more and more forests are disturbed. This paper provides estimates based on extrapolating the respective numbers of species in disturbed and undisturbed habitats. It uses a large global database of species inventories at particular sites. Trees and 10 groups of animals are analyzed. All the disturbed habitats put together include 41% fewer species than the undisturbed forests. This proportion varies among groups but is always substantial. Furthermore, disturbed local communities are dominated by widespread species such as rats and electric ants.

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Data deposition: The data have been archived at the Ecological Register (ecoregister.org/? page=data).

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Fig. 1. Spatial distribution of 875 tropical forest samples including either animals or trees that were drawn from the Ecological Register. The tropics of Cancer and Capricorn are indicated. The pattern mirrors the known distribution of field-based research campaigns in the tropics (19), but this dataset is more dispersed than the one used in a recent, related study (8) because the number of consulted references is greater (605 for the tropics alone vs. 284 for the globe).

foster high diversity (19), the data here suggest that they are nearly as depauperate as plantations (Fig. 2 and refs. 7 and 21). Just as surprisingly, forest fragments and forests disturbed by factors such as hunting, selective logging, and grazing are not significantly less rich than primary forests. Thus, although small protected areas are often valuable reservoirs of diversity, they are more effective when there is no history of intense tree removal.

Increasing the level of disturbance would have strong effects on the global diversity of individual groups (Fig. 3). The term "global diversity" is used here to mean the overall richness estimate obtained by pooling all the local-scale species lists. Loss curves vary in shape in addition to scale, pointing to real biological differences among groups that have implications for conservation. The tree curve (Fig. 3A) is at first linear and then climbs steeply starting at about a 60-70% disturbance level, suggesting that there is a tipping point for this one group. The bat curve (Fig. 3B) is also somewhat exponential. Semiexponential curves are seen in simulation (SI Methods, Simulated Loss Curves) when species have relatively broad spatial distributions (Fig. S1 D-F). Asymptotic or linear trends are produced instead when geographic ranges are small relative to the scale of habitat disturbance (compare Fig. 3 *B–D* with Fig. S1 A–C). Thus, variation in curve shapes points to variation in range sizes among groups: Those exhibiting asymptotic trends presumably have smaller average extents and therefore are at greater risk of mass extinction. The simulation and empirical results also highlight the need to break up large-scale habitat disturbances by retaining fragments and corridors (SI Methods, Simulated Loss Curves). Finally, the negative values for mosquitoes at intermediate disturbance levels presumably reflect the invasion of disturbed forests by species adapted to open habitats, transiently increasing the size of the species pool. In any case, complete disturbance would ultimately lead to net species loss of mosquitoes. The overall implication is that any substantial loss of primary forests will result in numerous extinctions across many groups.

Indeed, expected global losses given complete disturbance are >18% in every single group except large mammals and mosquitoes and are >28% for seven groups in total (Figs. 3 and 44 and Table S3). The higher percentages generally apply to groups such as lizards and ants that have poor dispersal ability. Of concern, the various sampling biases discussed below might have depressed all the percentages. For example, the 30% estimate for trees (Table S3) combined with the fact that very few tree samples fall in moderately to highly disturbed categories (Table S1) suggests that this group is extinction resistant only in the sense that richness may be high in fragments and lightly disturbed forests. The only statistic that might well be liberal is the 28% figure for sample data derive from mist-netting studies that typically capture small understory species, which might be more vulnerable to extinction (28). In any case, none of the results are strongly dependent on the number of samples used in the calculations except in the case of mosquitoes (Fig. S2). The mosquito trend (Fig. S2D) is consistent with there being no strong effect of disturbance on this group. Estimates for the three mammal categories are particularly conservative (Fig. S2B). Local-scale patterns are different, but they still broadly confirm the alphal scale results (Fig. 4B and Table S4). In accord

birds (Table S3). It should be interpreted cautiously because the

firm the global-scale results (Fig. 4*B* and Table S4). In accord with the findings of multitaxon studies in individual systems (18) and with the global results (Fig. 4*A*), the local data suggest substantial differences among groups. One way or another, however, a large local footprint of disturbance is usually indicated (Table S4) because entirely pristine forests include more species



Fig. 2. Differences in species richness among habitat disturbance categories. The vertical axis is the ratio of the median local-scale richness value in a category to median richness in undisturbed (= primary) forests, as extrapolated using the λ_5 equation (*Methods*). Data are shown on a log scale. Each bar represents the interquartile range for all samples in a category, regardless of the group. Data are standardized before any other calculation by being divided by the group median. Only categories with at least 20 samples are illustrated (Table S1).

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Fig. 3. Expected species losses given varying amounts of habitat disturbance. The x axis is the proportion of randomly drawn samples that represent disturbed habitats; the y axis is the proportion of species expected to be lost. Underlying estimates are based on the λ_5 equation. (A) Trees. (B) Mammals. All large mammal species were sampled by camera traps; terrestrial species of small mammals were sampled using various kinds of traps. (C) Other vertebrates. (D) Insects.

(Fig. 2 and Table S2). The data for a few groups do fall close to the line of unity (Fig. 4*B*), indicating minor or even reversed local effects of disturbance: For example, butterfly richness is a little above the line (Table S4). However, ratios are far from unity for trees, frogs, and dung beetles. Regardless of such details, these local-scale results are in accord with the expectation that highly disturbed tropical forests are depauperate (6, 7, 29).

Weaker responses at local rather than global scales are counterintuitive but are easily explained by a simple mechanism: Disturbed ecosystems are dominated by widely dispersed, highly abundant, and often invasive species such as the pig (*Sus scrofa*), black rat (*Rattus rattus*), cane toad (*Rhinella marina*), southern house mosquito (*Culex quinquefasciatus*), electric ant (*Wasmannia auropunctata*), and globe skimmer (*Pantala flavescens*). This fact can be demonstrated by examining incidence proportions (frequencies of presence across samples), which in almost every group are higher on average in disturbed settings (Fig. 5A). Another useful measure is average dominance (the frequency of the most common species), which again shows a strong and consistent signal (Fig. 5B). Because high species losses at local scales are masked by the spread of common species able to tolerate human impacts, the most important results in this paper are those pertaining to potential extinction at the global scale.

There are numerous reasons to believe that even the global estimates of richness loss are minimums. (*i*) Ecologists only infrequently study ecosystems that are highly unsuitable for the taxonomic groups of interest to them. Thus, the disturbed samples in this study tend to derive from suboptimal but still reasonably benign habitats. Indeed, only 10.7% of the samples (94 of 875) represent habitats that are completely deforested (Table S1). (*ii*) Many of



Fig. 4. Effects of complete habitat disturbance on global and local richness of tropical species. Estimates are based on the λ_5 equation; similar patterns are produced by other methods (Figs. S3 and S4). Points are ecological groups. Lines through points indicate 95% CIs based on simultaneous resampling of samples and of species records within samples. Lines of unity are also shown. (A) Global richness in undisturbed and disturbed original forest environments. (B) Local richness in undisturbed and disturbed original forest environments.

the disturbed habitat samples (157, 17.9%) actually come from forests that are not strongly impacted (Fig. 2). This category includes rural forests, fragments, and lightly disturbed forests (those currently subjected to minor disturbance or described as being disturbed in a general way). (*iii*) Some nominal primary forest samples may be misclassified as such because of underreporting of contextual information in the primary literature that was consulted. (*iv*) Many disturbed samples are reported in the same papers as matched primary forest samples and therefore are spatially proximate to large tracts of nearly pristine habitat. Thus, individuals of rare species in disturbed habitats may have dispersed into them. (v) Some groups are actually more diverse in open habitats and therefore may prosper when primary forests are degraded (17, 18). (vi) The analyses reported here do not account for overall extinction debt [i.e., the fact that many surviving species will go globally extinct within the next few decades or centuries because their overall population sizes are not viable (29)]. Specifically, small



Fig. 5. Effects of complete habitat disturbance on species incidence and dominance within samples. Points are ecological groups. Cls are not shown because they would be minimal, given the large sample sizes. (A) Median incidence of species. Incidence is the proportion of samples that include a particular species. (B) Median dominance within samples. Dominance is the relative abundance of the most common species.

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populations in isolated forests will eventually be lost (30, 31), thus increasing the number of range-wide extinctions.

The most important point, however, is that many species may have already gone extinct because their ranges are now entirely deforested. These species were never in the sampling pools whose sizes have been estimated by extrapolating from the undisturbed habitat data. Furthermore, many species in otherwise pristine forests may have already gone extinct because of stressors not related to habitat destruction, such as hunting, interactions with invasive species, introduced epidemic diseases, pollution, and the direct effects of climate change. Thus, the current comparisons (Figs. 3 and 4) are between depauperate and very depauperate species pools. Given the rapid pace of deforestation throughout the tropics (10, 11), it therefore is conceivable that an event on the scale of a true mass extinction has already taken place. If recent, these losses may have gone unrecognized because the many rare species found in terrestrial communities are both at high risk of extinction and hard to sample on a regular basis. Regardless of this possibility, the current study paints a bleak picture of rapid, continuing loss of biodiversity even in a world where disturbed forests remain widespread.

Methods

Data. The sample data used in this study were downloaded from the relational Ecological Register database (ecoregister.org) on 15 March 2017 using standard criteria, and these particular flat files have been archived at the same site (ecoregister.org/?page=data). Samples were defined as lists of species with matched abundances, as reported in the original literature. The datasets included as many published papers as possible. Only samples located between 23.44° N and 23.44° S and representing originally forested habitats were drawn. Woodland and savanna environments were excluded. Samples deriving from the same equal-area latitude/longitude degree cell, published in the same study, and representing the same original and altered habitats were lumped by summing the counts of individuals for each species.

Habitat alteration categories were similar to those used in a related study of strictly local-scale patterns (8), except that a unidimensional system was used instead of a two-way system with use intensity as the second axis. The reasons are that (*i*) the two axes are interdependent, with urban systems, for example, being "intense use" by definition; and (*ii*) extremely detailed information on use is not normally reported in the primary literature. Furthermore, secondary forests, forest fragments <100 ha in area, and lightly disturbed forests were split into separate categories instead of subsetting secondary forests by stand age (again, because detailed information on stand age is normally lacking). Clearcuts and rural and suburban settings were also recognized as separate categories. Forests were classified as being lightly disturbed if they were said to be disturbed in a general way or if they were subjected to grazing, selective logging, or hunting. Together, the additional categories capture the consistently recoverable information on use intensity.

Samples were divided into 11 primarily taxonomic groupings (Table S1). Tree samples were restricted to inventories based on a lower size cutoff of approximately 10-cm diameter at breast height. Large mammal samples were strictly derived from camera trapping studies; terrestrial small mammal studies were based on physical trapping studies; bat and bird samples were based on mist-netting; ant samples were based on pitfall and Winkler apparatus collections; and dung beetle samples were based on pitfall trapping. Specifically indeterminate records, which formed a small minority in most cases, were included in the analyses. If multiple records of indeterminate species stemmed from the same publication and were spelled identically, they were considered to represent a single morphospecies, whereas informal names spelled identically but stemming from different references were considered distinct. Counts of morphospecies are 5,239 (trees), 301 (large mammals), 380 (small mammals), 241 (bats), 2065 (birds), 332 (lizards), 787 (frogs), 811 (mosquitoes), 2,479 (ants), 815 (dung beetles), and 1,715 (butterflies).

Richness Estimation Methods. Local analyses focused on counts of individuals within samples, whereas global analyses focused on counts of presences across samples. For example, if two samples respectively included species A and B and A and C, the respective presence counts would be 2, 1, and 1 for A, B, and C. Using presences in global analyses is standard procedure in the literature (e.g., ref. 24) and yields more accurate values in simulation.

Species richness was estimated using two extrapolation methods and two interpolation methods. The older extrapolation method (26) has two very

similar variants, called the Chao 1 index when applied to raw counts of individuals and the Chao 2 index when applied to counts of presences. There are two names because a sample size correction term is used with presence counts. The basic form is $S + s_0 = S + s_1^2/2s_2$ where S is the observed number of species, s_0 is the number of unsampled species, and s_1 and s_2 are the numbers of species respectively represented by exactly one or two individuals (i.e., the singletons and doubletons). Although the Chao indices assume that abundance distributions are nearly uniform, they are still wellestablished and widely used (27) and perform very well in simulation when this key assumption is met.

The second extrapolation approach seeks to account for the fact that real abundance distributions are typically far from uniform. It stems from reformulating Chao's equation in terms of Poisson sampling. Let λ be the average rate of sampling per species across the dataset. The chance of failing to draw a species is then $e^{-\lambda}$ and that of drawing a singleton is $\lambda e^{-\lambda}$. If R is the unknown total number of species, then $s_0 = R e^{-\lambda}$ and $s_1 = R \lambda e^{-\lambda}$. It follows that $s_0/s_1 = 1/\lambda$, $\lambda = s_1/s_0$, and $s_0 = s_1/\lambda$. A generic richness estimate therefore would be $S + s_1/\lambda$. Chao's equation can be justified on this account because it assumes that λ (here called " λ_1 ") equals $2s_2/s_1$, which is easily proven to be valid because $s_2 = R \lambda^2 e^{-\lambda}/2$. However, the value of λ can be fixed in a number of other ways by exploiting relationships such as $S = R (1 - e^{-\lambda})$ and $N = R \lambda$ where N is the number of individuals. For example, we can define $\lambda_2 = (N - s_1)/S$ and $\lambda_3 = \ln(N/s_1)$ and justify both by using simple algebra. Another easily proved estimator is $\lambda_4 = -\ln[s_1/\lambda_4 S(1 - e^{-\lambda_4})]$, which can be computed recursively. It is interesting because it ignores N, but like all the estimators discussed to this point it is not particularly accurate.

The last estimator, $\lambda_{\text{5}}\text{,}$ is the most complex and the most robust. It is computed by a simple hill-climbing equation from the equality $\ln[N/(S - s_1)]$ $s_1/S = \ln[\lambda/(1 - e^{-\lambda} - \lambda e^{-\lambda})] \lambda e^{-\lambda}/(1 - e^{-\lambda})$. Although daunting, this equation has intuitive components. First, like Chao 1, it implies that sampling is poor when s_1 is large (because s_1 appears by itself as a numerator and also in the denominator term $S - s_1$). Second, it implies that sampling is good when S is large (because S appears in two denominator terms). This idea makes sense because we eventually must encounter all species as S grows. Third, and most importantly, it implies that sampling is actually poor when N is large because large samples are likely to include some highly abundant species, so they should also include very rare species that are unlikely to be found. All the prominent species-abundance distributions such as the geometric series. log series, and log normal also rest on the assumption that when the most common species are very common, the rarest species are very rare. To put these considerations simply, the purpose of the N term is to compensate for the downward bias of most λ -based estimators that results from their assumption of uniformity in abundance.

The λ_5 equation is emphasized throughout this paper because it outperforms all others in simulation by producing relatively unbiased estimates when abundances are very uneven. That said, the λ_5 method and the Chao indices do produce similar patterns when applied to the current data. The λ_5 estimates are a bit higher at the local scale, consistent with the expectation that this method will uncover more species when distributions are uneven but otherwise will yield the same values (Fig. 4*B* vs. Fig. S3*A*). Global-scale λ_5 estimates are slightly lower than Chao 2 estimates, but the differences are statistically insignificant for most groups (Fig. 4*A* vs. Fig. S4*A*). Values are more similar in this case because global presence–absence distributions tend to be quite flat and thus are more consistent with Chao 2's assumptions. The methods also yield very similar underlying richness estimates for the undisturbed and disturbed habitat categories at both scales (Figs. S5 *A* and *B* and S6 *A* and *B*).

The first subsampling method was originally called "shareholder quorum subsampling" (24) and is now often called "coverage-based rarefaction" (25). It was originally an algorithmic approach (24), but calculations here are based on exact equations (25). Its goal is to determine the expected richness at a certain sampling level such that Good's index of frequency distribution coverage equals a fixed target, called a "quorum" (24). The index is $1 - s_1/N$. The second subsampling method is also analytical and is called "multiton subsampling" (*SI Methods, Multiton Subsampling*). It is based on examining the ratio ($S - s_1$)/S where $S - s_1$ is the number of nonsingletons (i.e., multitons). To guarantee that it will rise monotonically with N, the observed ratio at a candidate sampling level N_i is multiplied by $N_i(s_{1,i} + 1)$ where $s_{1,i}$ is a candidate singleton count. An exact algorithm is used to find subsampled richness given a desired (target) multiton ratio.

The end-member richness ratios generated by the λ_5 equation (Fig. 4) are similar to those produced by the two interpolation methods (Figs. S3 *B* and *C* and S4 *B* and *C*). That said, the underlying values are substantially different (Figs. S5 *C*–*F* and S6 *C*–*F*). Again, the λ_5 results are emphasized in this paper

because this method builds in an explicit correction for the unevenness of abundance distributions, but the other three do not.

Loss Curves. In the analyses varying the proportions of undisturbed and disturbed samples (Fig. 3), each illustrated species loss value equals $1 - S_d/S_u$ where S_d represents the number of species estimated to remain at a given disturbance level and S_u represents the estimated number given no disturbance. The global estimate S_d at each level reflects a mixture of disturbed and undisturbed local samples. For example, at one extreme all samples are undisturbed, so $S_d = S_u$; at the other all are undisturbed; and at the midpoint 50% are in each category. The combined number of samples drawn at each step was fixed, with the quota equaling the smaller of the total counts in each category. Quotas were 40 samples (trees), 25 (large mammals), 46 (small mammals), 55 (bats), 44 (birds), 24 (lizards), 28 (frogs), 25 (mosquitoes), 32 (ants), 30 (dung beetles), and 26 (butterflies). To compute an individual S_d value, an appropriate number of samples in each category was drawn at random; the species list for each sample was bootstrapped (i.e., sampled with replacement); the presences were summed; and a global richness estimate for the combined presences was computed using the λ_5 equation. Each point in a given curve represents the median $1 - S_d/S_u$ value generated by 10,000 randomization trials.

Cls on Local Richness Estimates. The Cls (Fig. 4*B* and Figs. S3 and S5) were computed using a two-layer bootstrapping protocol. First, during each of 1,000 trials each sample's species list was bootstrapped up to the original richness level; the randomized abundances were used to obtain a richness estimate by means of the appropriate method; and the median richness across samples was found. Separate distributions of medians were computed for the disturbed and undisturbed data partitions. Second, the medians for the disturbed samples were sampled with replacement 10,000 times; the same was done with the undisturbed sample medians; the ratio of the two vectors was taken; and nonparametric Cls (based on percentiles) were then computed using the ratio vector. Because the Cls are nonparametric, some are seen to be asymmetrical in Fig. 4*B*.

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CIs on Global Richness Estimates. Calculations similar to those used in the losscurve analysis were used to obtain CIs for the global-scale data (Fig. 4A and Figs. S4 and S6). First, during each of 10,000 trials the list of samples itself was sampled without replacement down to the least common denominator level for the two disturbance categories (i.e., the relevant quota given in the list above). Because of computational limits, 1,000 trials were carried out when applying the two subsampling methods instead of the two extrapolation methods. Second, during each trial all the drawn samples in a given category were transformed to presences and summed; estimates were made using the four methods; and the standardized richness values were recorded in arrays. Third, the arrays of 10,000 richness values in each category were sampled with replacement 10,000 times, and the ratios were recorded. Finally, nonparametric Cls were computed from those data.

Incidence and Dominance Calculations. Incidence (Fig. 5A) was computed by taking the ratio of the number of samples including a given species (X_i) to the total number of samples representing the relevant group (X). However, raw ratios are somewhat upward biased when X is small because they have a lower bound of 1/X. Thus, a mild correction was used: X was incremented by 1 to produce the ratio $X_i(X + 1)$. This correction had no qualitative effect on the results. Cls on across-species medians are not shown because the extremely large sample sizes render them too small to illustrate meaningfully.

Dominance figures were computed directly from the species abundance data for the individual samples, with each sample yielding a single dominance value equal to the maximum abundance of any included species divided by the sum of abundances. Again, CIs are not illustrated (Fig. 5*B*) because sample sizes are so large.

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