Neutral theory as a predictor of avifaunal extinctions after habitat loss

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The worldwide loss of natural habitats leads not only to the loss of habitat-endemic species but also to further and protracted extinctions in the reduced areas that remain. How rapid is this process? We use the neutral theory of biodiversity to answer this question, and we compare the results taken with observed rates of avifaunal extinctions. In the neutral model, we derive an exact solution for the rate of species loss in a closed community. The simple, closed-form solution exhibits hyperbolic decay of species richness with time, which implies a potentially rapid initial decline followed by much slower rates long term. Our empirical estimates of extinction times are based on published studies for avifaunal extinctions either on oceanic islands or in forest fragments, which span a total of six orders of magnitude in area. These estimates show that the time to extinction strongly depends on the area. The neutral-theory predictions agree well with observed rates over three orders of magnitude of area (between 100 and 100,000 ha) both for islands and forest fragments. Regarding the species abundance distribution, extinction times based on a broken-stick model led to better agreement with observation than if a log-series model was used. The predictions break down for very small or very large areas. Thus, neutrality may be an affordable assumption for some applications in ecology and conservation, particularly for areas of intermediate size.

extinction debt | faunal relaxation | biodiversity loss | extinction rates

The primary driver of extinction in terrestrial environments today is habitat loss (1, 2). In particular, the loss of large portions of tropical rainforest through land conversion was estimated to lead to rates of species extinction hundreds of times higher than the background rate (3). However, the ensuing extinctions will not be realized immediately, because most of the species found in the destroyed habitat are also found in the remaining area. Instead, extinctions occur in the course of the following decades, centuries, or even millennia after the initial habitat contraction. This process has been called faunal relaxation (4). Another term used is extinction debt, which refers to the degree to which the species richness exceeds the species-carrying capacity of the diminished area (5, 6). A good understanding of this phenomenon is required to explain why the extinctions forecasts are not immediately observed.

Empirically, extinction is difficult to observe, because we must establish the absence of an organism simultaneously everywhere before we can be sure that it is extinct. As a result, organisms thought extinct frequently pop up again in subsequent surveys (7). Despite this, a large body of empirical work related to extinction debt has been assembled (review by Kuussaari et al.) (6), including various workarounds using natural experiments (4, 8, 9), microcosms (10), and historical data (11, 12). An important and still unresolved part of the picture is to find the dynamic model of extinction in the community context that can provide a background estimate for how fast extinctions occur after habitat loss and how the parameters of this relaxation depend on the size and isolation of the remaining habitat.

The first person to deal with the phenomenon of extinction debt was Diamond (4), who introduced the term faunal relaxation to equilibrium to describe the gradual loss of species after a re-

duction in the size of islands because of sea-level rise. Diamond (4) introduced a model for species richness motivated by island biogeography. In this model, species were effectively independent and had constant rates of extinction and colonization, leading to an exponential pattern of relaxation as a function of time. By fitting the model to observed patterns of species richness, Diamond (4) was able to estimate relaxation times for various islands. The term extinction debt first appeared in 1994 in a paper by Tilman et al. (5) that modeled the multispecies metapopulation dynamics in a grid of habitat patches. These authors (5) pointed out that extinction may happen many generations after habitat loss, although the more discussed (and controversial) result of their paper was that species that were better competitors would suffer earlier extinction. Their results regarding extinction debt were mainly qualitative (5). A metapopulation approach was also used by Hanski and Ovaskainen (13), who derived a dynamic theory for the metapopulation response of a multispecies community to environmental changes through the metapopulation capacity approach. Their theory is applicable to species that inhabit an archipelago of small islands separated by a large sea of nonhabitat area and requires some structural assumptions about rates of colonization and local extinction.

The neutral theory of biodiversity by Hubbell (14) has prompted a resurgence of interest in community modeling of biodiversity. Its radical simplification of ecological reality has enabled progress in mathematical models of community structure (15, 16) but has also generated intense controversy (17–19). In the neutral theory, species are equivalent, and the community dynamics are driven by demographic stochasticity, dispersal limitation, and speciation. Empirically, the neutral theory by Hubbell (14) seems to work quite well for species abundance distributions (16, 20) but poorly for the fluctuations of population size (21) and species–area relations (22). However, with the adoption of spatially explicit models, it is likely that neutral theory will be in a better position to describe species–area relationships (23, 24); in fact, some progress has been reported in this area recently (25). Further concerns about neutral theory have been raised on specifically theoretical grounds. For example, Clark (19) argues that ecological uncertainty is intrinsically high-dimensional and cannot be described by "stochastic elements, perceived as neutral forces" (19). Despite its many limitations, the major attraction of neutral theory is that it may be used as a baseline from which explicitly ecological hypotheses can then be elaborated. Unlike many community theories, neutral theory is based on a dynamic process and hence, can generate time-explicit hypotheses as well as patterns. A number of studies have explored time-dependent aspects of neutral theory, such as

species lifetimes (17), community turnover (26), and delayed changes of species composition (27). Overall, however, the neutral theory literature has tended to neglect the time axis (22).

There have been few attempts to explore neutral predictions for species relaxation. There are two studies of tree diversity, one on and around Barro Colorado Island, Panama (28) and another in Manaus, Brazil (27), that deal with at most three generations. Also, on a relatively short timescale, Hubbell et al. (29) used neutral theory to forecast extinction rates of tree species in the Amazon using simulations over a variety of scenarios. At the other extreme, on geological timescales, Ricklefs (17) concluded that neutral theory could not explain the relative brevity of species lifetimes for birds. The goal of this paper is to fill in some of the gaps. The predictions of neutral theory are worth exploring, because it is a dynamic, relatively tractable theory of the community that is explicit at the population level and can, therefore, provide important insights. However, the neutral theory used here differs from that by Hubbell (14) in that there is no metacommunity: each community on an island or a fragment is assumed to be closed with neither immigration nor speciation. We here focus on a very simple situation in which immigration and speciation can be neglected. This simplification is important for two reasons. First, it allows us to derive a clear and simple formula, and second, it allows us to use the data from published studies of species relaxation, most of which do not provide estimates of immigration rates. In this paper, we use the neutral theory to obtain formulas for the dynamics of species relaxation on isolated habitat fragments or islands as a function of time, fragment size, and initial community structure.

Problem of Extinction Debt After Habitat Loss

Fig. 1 shows the essential problem in which we are interested. Initially, the habitat has an area A_0, which is reduced to a smaller size A.

Habitat loss, at time $t = 0$, is assumed to be instantaneous; subsequently, there is no regrowth, and it stays lost. We also assume that the area is contiguous and simple, and therefore, there are no special edge effects. Such a reduction of habitat area will necessarily lead to a reduction in the total number of individuals that can be supported by the habitat. Thus, the number of individuals in the community falls from N_0 to N and remains there. Typically, $N_0 - N$ will be proportional to the area lost. This reduction in the number of individuals also implies a reduction of the species richness that can be supported by the habitat: this falls from S_0 to S. However, the loss of species does not happen all at one time; it occurs in two phases: (*i*) $S_0 \rightarrow S_0'$ (some species are lost immediately, because all of their members are found inside the lost area) and (*ii*) $S_0' \rightarrow S(t) \rightarrow S_1$ (some species are lost gradually, because populations drift to low numbers and then to extinction). The difference $S(t) - S_1$ is the extinction debt, which is paid off as the community approaches its sustainable level of diversity by shedding excess species. During this final phase, because species whose populations have

fallen to lower levels will die off, more space is left for those species that remain. Therefore, with the collapse of the species-rich community S_0, there is consolidation to a few common species in the new community. Unless there is immigration or speciation, the eventual state of the community is fixation to a single species ($S_1 = 1$). Because of this, our theory is useful in situations where the focal habitat is isolated fairly well, and therefore, immigration can be neglected as a first-order approximation. As explained in *SI Text*, this is satisfied if the number of immigrants per generation is much smaller than the ratio $S(t)^2/N$, which means that it is less likely to hold at larger values of time. In this paper, we will not consider dispersal limitation or any other explicit aggregation of populations in space: all species are potentially present everywhere. This means that we do not consider the issue of endemicity (30). As a result, the initial loss of species is negligible: $S_0' \simeq S_0$.

Results

Mathematical Solutions. The distribution of S species in the community can be approximated by a diffusion process where species are found in proportions $x_1 \ldots x_S$, with $\mathbf{X} = (x_1, x_2, .., x_{S-1}, x_S)$. More details can be found in *SI Text*. The relative proportion x_j for each species j drifts in a random walk between absorbing states of 0 (extinction) and 1 (total dominance). This is based on the birth–death process for each species. At each step, each species may increase or decrease its share of the total community by $1/N$, where N is the total number of individuals in the community. Provided that the time interval Δt is short relative to the generation time τ, we can confine ourselves to changes of ± 1. If a change does occur, then the probability that it is a transition from species j to species i is (Eq. **1**)

$$\Pr\left[\mathbf{X} \rightarrow \left(\ldots, x_i - \frac{1}{N}, \ldots, x_j + \frac{1}{N} \ldots, x_S\right)\right]$$
$$= \frac{N x_i x_j}{\tau} \Delta t, \quad i, j \in 1, 2, \ldots, S, \quad i \neq j. \quad \textbf{[1]}$$

In this transition, the probability given by Eq. **1** is proportional to x_i, because it is the number of offspring available for colonization by species i. It must also be proportional to x_j, because that is the population of species j, one of which must die to make room for the extra member of species i. As discussed in detail in *SI Text*, this process leads to the following diffusion equation in the continuum limit (Eq. **2**):

$$\frac{\partial p}{\partial t} = \sum_{i=1}^{S-1} \frac{\partial^2}{\partial x_i^2}\left(\frac{x_i(1-x_i)}{N\tau} p\right) - \sum_{i=1}^{S-1}\sum_{j>i} \frac{\partial^2}{\partial x_i \partial x_j}\left(\frac{2 x_i x_j}{N\tau} p\right). \quad \textbf{[2]}$$

Here, $p(x_1, x_2, \ldots x_{S-1})$ is the distribution for the relative abundances in the different species $x_1, x_2, \ldots x_{S-1}$. For the last species, the abundance is given by $x_S = 1 - x_1 - x_2 - \ldots - x_{S-1}$. Eq. **2** can be solved explicitly for the uniform distribution, $p(x) =$ constant. This can be verified by substituting the function, $p = 1 \cdot \exp[-\mu t]$ into Eq. **2**, which yields $\mu = S(S-1)/N\tau$. In this case, the different species compositions of the community are equally probable, which corresponds to the broken-stick model by MacArthur (31, 32). Because this solution is everywhere, real and positive, then by the Perrin–Frobenius theorem, it is the eigenfunction corresponding to the dominant eigenvalue of the operator in Eq. **2**, and hence, all solutions will converge to this form (more details in *SI Text*). From this, we can conclude that the waiting times follow a negative exponential distribution with mean $N\tau/[S(S-1)]$. The waiting time for one of the S_0 species to go extinct has a mean $N\tau/[S_0(S_0-1)]$. The waiting time for the next extinction is then $N\tau/[(S_0-1)(S_0-2)]$ on average and
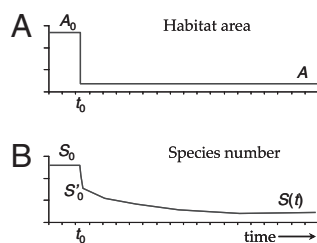

Fig. 1. The number of individuals in the community is proportional to the habitat area, which suffers the loss at $t = 0$ (*A*). This is gradually reflected in a loss in the total number of species in the community (*B*).

so on. Thus, the time required for the number of species to decrease from S_0 to $S(t)$ has a mean equal to (Eq. **3**):

$$t = \frac{N\tau}{S_0(S_0-1)} + \frac{N\tau}{(S_0-1)(S_0-2)} + \cdots + \frac{N\tau}{[S(t)+1]S(t)}. \quad \text{[3]}$$

This series can be summed by partial fractions to arrive at a simple result for $S(t)$.

We define the half-life t_{50} as the time until the number of species falls to one-half of its initial value, that is, $S(t_{50}) = S_0/2$, where we have (Eq. **4**)

$$t_{50} = \frac{\tau N}{S_0}. \quad \text{[4]}$$

Here, τ is the number of years per generation, S_0 is the initial number of species, and N is the number of individuals. Eq. **4** is exact if it is interpreted as the arithmetic mean of half-life. We may adopt an approximation of this stochastic process by the deterministic model if the species number is large.

The result for the species number $S(t)$ can now be written (Eq. **5**)

$$S(t) = \frac{S_0}{1 + t/t_{50}}. \quad \text{[5]}$$

Here, t is time in years as in Eq. **4**, and S_0 is the initial number of species.

Thus, for much of the loss, species richness decays as $1/t$. The hyperbolic relaxation formula Eq. **5**, derived independently by Terborgh (8) but without explicit parameters, was used by Terborgh (8) to describe the process of competition between species in isolated fragments. In this hyperbolic decay of biodiversity, the eventual decline is slow, although the initial rate of loss may be very rapid. From Eq. **5**, the rate of decrease in the species number $(-1)dS/dt$ is equal to $S^2/\tau N$, which is proportional to the square of the number of existing species. Hence, the decay rate per species is $S/\tau N$ per year, indicating that each species experiences a rate of extinction proportional to the number of existing species. Thus, the more species there are initially, the faster will be the relative decline, because there are fewer individuals per species. Eq. **5** also states that the mean time for fraction δ of the initial set of species to go extinct is equal to $t_\delta = t_{50}(\delta/(1-\delta))$.

The neutral model described in this paper can be simulated using the Moran process (22, 33) (*SI Text*). This allowed us to test Eq. **5** for two different types of initial community structure: the broken-stick model by MacArthur (31) and the log-series model. The results are shown in Fig. 2.

The best agreement between the formula and simulations is when the initial community conforms to the broken-stick model by MacArthur (31), for which all configurations of species abundance have equal probability. This is expected, because the formula is derived under the assumption of $p = $ constant, which is exactly the assumption underlying the broken-stick model by MacArthur (31). Eq. **5** does a poor job of predicting species loss in communities with other structures, at least initially. This is especially true for highly skewed communities (a few species at high numbers and many species at low numbers) as described by a log-series model. At large values of time, the formula always agrees with the simulations. This is because the solution of Eq. **2** under the assumption of $p = $ constant is also the dominant eigenvalue of the operator, which has the slowest rate of decay. Disagreements are mainly because of initial structure, and these die off with the passing of time.

Comparison with Published Works. Observing and analyzing the avifaunas of Southwest Pacific islands, covering a size range from 0.36 to 3,000 mi^2, Diamond (4) noticed that large islands, which
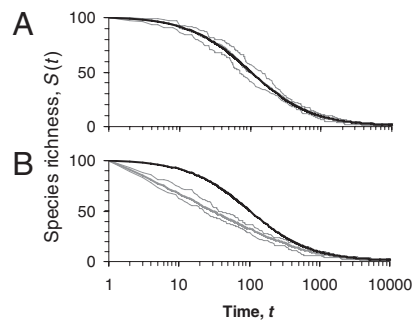
Fig. 2. The dynamics of species richness as a function of time (generations) after habitat loss as predicted by the neutral theory (Eq. **5**) and 10 simulations of the Moran (33) process. (*A*) Initial community composition is given by the broken-stick model by MacArthur (31). (*B*) Initial community composition is given by log-series model ($\alpha = 15.6$). In *A* and *B*, the black line denotes the predictions of Eq. **5**, whereas simulation results are shown in gray. The heavy gray line is the average of the simulations, whereas the thin lines denote their minimum and maximum values. The parameters are $S_0 = 100$ and $n = 10,000$.

had either suffered significant area contraction or separation from the mainland at the end of the Pleistocene, were still supersaturated (more species-rich) compared with equivalent islands that had been isolated for much longer. He interpreted this difference as a delay because of the slowness of faunal relaxation; even after 10,000 y, the process had not reached its equilibrium. Using the framework of island biogeography, Diamond (4) fitted an exponential model that yielded estimates of relaxation time up to 17,600 y for the larger islands.

Terborgh (8) carried out a similar analysis on the avifauna of the West Indies, where similar patterns can be seen, and applied it in addition to the avifauna of Barro Colorado Island (BCI; data from Willis in ref. 34). The large islands of Trinidad, Margarita, Coiba, Tobago, and Rey, ranging in size from 249 to 4,828 km^2, all show signs of not having reached their equilibrium. In contrast to Diamond (4), Terborgh (8) used a model for species relaxation that "acknowledges interspecific competition" and for which survival rates of the "remaining populations increase as their competitors drop out" (8). The relaxation formula by Terborgh (8) has exactly the same form as the neutral result (Eq. **5**). Thus, neutral theory recovers a formula specifically introduced to include competition. Neutral theory goes further by providing an explicit value for the phenomenological rate constant introduced by Terborgh (8).

Extinction debt for forest fragments has been studied in Kenya's Kakamega rainforest (35) and Manaus, Brazil (36). Brooks et al. (35) considered four (smaller) forest fragments that had been isolated by the encroachment of agriculture. These fragments, ranging from 100 to 1,500 ha in size, had been isolated for 10–66 y. For these smaller patches, Brooks et al. (35) found relaxation times between 23 and 55 y, again using an exponential relaxation model. Ferraz et al. (36) analyzed even smaller forest fragments (1–100 ha) from the Biological Dynamics of Forest Fragments Project (BDFFP) system in Manaus, Brazil. Using various inferential techniques, they arrived at relaxation times between 1 and 16 y for fragments ranging in size from 1 to 100 ha.

Newmark (37) studied local extinctions of understory birds in the intermediate moist forests of the Eastern Usambara Mountains in Tanzania in a network of 10 habitat islands ranging in size from 0.1 to 521 ha and containing from 4 to 26 of 31 known species in the area. MacHunter et al. (38) studied avifauna loss for Australian birds, again in very small patches. Like Newmark (37), they did not express their results in terms of relaxation times. MacHunter et al. (38) present comparisons of species

richness between two separate sampling events, 22 y apart, in a network of 20 habitat relict patches ranging in size from 2.3 to 47.4 ha. By the time of the first sampling period, these had already been isolated for some time, and therefore, the surveys represent two snapshots at different moments in the relaxation process. Their data showed that average species richness declined by nine species per patch in the 22 y between the two sampling periods.

Fig. 3 assimilates the reported results of avifaunal relaxation using Eq. **8** (see *Methods*) and compares them with the predictions of neutral theory's Eq. **4** (Table S1). The island sizes range over six orders of magnitude from forest fragments less than 1 ha to large islands like Trinidad (4,828 km²).

Fig. 3A compares the relaxation times inferred from real data, T_{50}, with the predictions of neutral theory t_{50}. Points on the left tend to correspond to small areas, and points on the right tend to correspond to large areas (Fig. 3). For medium to large islands, the times forecast by the neutral model through Eq. **4** compare favorably with relaxation times estimated from the observed losses: the deviation from theory is no greater than the natural scatter, and there is no systematic deviation upward or downward (Fig. S1). Note the correlation in this panel is not an artifact of any mathematical similarity between Eq. **4** for t_{50} and Eq. **8**, the extrapolation model for T_{50}, because the burden of the large changes in magnitude is borne by A (Fig. 3B). However, at very small sizes, the neutral pattern of scaling seems to break down. This is clearly visible in Fig. 3A for $t_{50} \leq 100$ (corresponding to small fragments), where most points lie well above the line $T_{50} = t_{50}$. Here, relaxation times of 2–10 y are observed for fragments ranging in size 1–10 ha, whereas neutral theory predictions range from 3 to 0.2 y. This difference is unlikely to be

Fig. 3. Relaxation times inferred from empirical data (T_{50}) for avifaunal extinctions in various parts of the world. (A) T_{50} plotted against the relaxation time predicted by the neutral model (t_{50}) using Eq. **4**. The straight line denotes equality: $T_{50} = t_{50}$. (B) The same data for T_{50} plotted against area. The straight line denotes the empirical power law fit ($T_{50} = 4.35 \times A^{0.652}$). In A and B, the shaded + symbol denotes the relaxation time for Barro Colorado Island.

related to our assumption of broken-stick community structure. Log-series or lognormal distributions, because of their strong asymmetry, would result in even shorter predicted values for t_{50}, which is evident from Fig. 2B. Thus, for very small areas, the relaxation time predicted by neutral theory seems to be too short. At very large sizes, the neutral pattern of scaling also breaks down. Here, the prediction of neutral theory seems to be too long compared with relaxation times inferred from real data.

Fig. 3B shows that the predicted scaling pattern of relaxation time with island (or fragment) area A also agrees well with observation. This figure shows the inferred relaxation times as a function of area along with a power-law fit to the data. In this model, we assume that the ratio τ/S_0 either does not matter or is constant. Thus, on a doubly logarithmic scale, relaxation time T_{50} is a straight-line fit against area. The relation has the approximate form $T_{50} = 4.34 \times A^{0.65}$. This empirical power law shows a very clear pattern of increase of relaxation time with area ($R^2 = 0.90$), which is slower than neutral theory predicts ($T_{50} \propto A$) but faster than the proposed rough-scaling relation of $T_{50} \propto A^{1/3}$ proposed by Ferraz et al. (36) for a range of scales 1–10,000 ha. The disagreement with their results is because of the larger range of timescales and the contribution from other datasets, especially those of Newmark (37). It is also worth noting that the results for actual islands (West Indies, southwest Pacific, and BCI) are broadly consistent with those for habitat fragments isolated by deforestation.

The above analysis assumes a broken-stick species abundance distribution. For many tropical bird communities, it is likely to be appropriate (39, 40). However, for other types of organisms, it will be unsuitable, and a more skewed distribution, such as the log series (27) or canonical lognormal (32), might be appropriate. For the log-series distribution, Gilbert et al. (27) developed a formula that can be adapted (*SI Text*) to provide an analog of 4. As can be observed in Table S2, in contrast to the observations of Gilbert et al. (27) for trees, the log series-based formula is not a good one to use for relaxation times of avifauna, because it is always forecasting more rapid species relaxation than what is observed by a factor, on average, of 28.3.

Discussion

For large islands, the times t_{50} forecast by the neutral model through Eq. **4** compare well with observed losses, and therefore, neutrality would seem to be a reasonable assumption on scales between 100 and 100,000 ha.

For smaller fragment sizes, Eq. **4** is a poor predictor of species loss rate, consistently underestimating the relaxation time. Why is this? One reason is that immigration, ignored in our model, is playing a more dominant role at this scale. In most empirical studies of extinction debt, immigration is neglected, and often, distances from the mainland are not provided. However, these distances range from less than 100 m to hundreds of kilometers, and therefore, this factor will have a serious effect. This is especially a concern for the data from Manaus (36). For example, for several of the fragments, the number of species is far in excess of a plausible equilibrium value. If we assume that the forest in Manaus can support ~10 pairs/ha, then Manaus/2107/Dimona, with an area of 1.8 ha, should support 18 pairs. However, the initial number of species is 86. A direct calculation of Eq. **4** with these data leads to a decay time t_{50} less than one generation. If the forest fragments were truly isolated, we would expect the species number to fall rapidly to something consistent with $n = 18$. However, even after isolation, the species numbers remain well above this value. Clearly, birds caught in such an area are not only those actually supported by that area but also visitors from adjoining areas. Thus, the most probable cause of the departure from neutrality for small fragments is that these are affected or even dominated by immigration. It is well-established that the isolation of these fragments is imperfect (discussed in
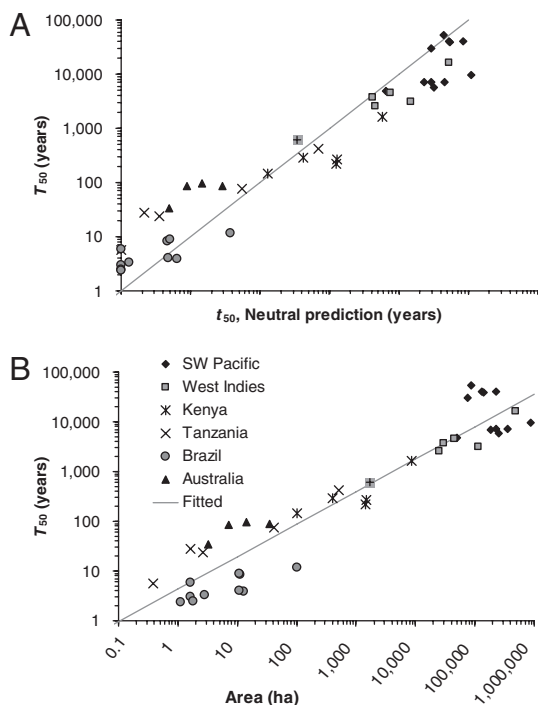
ref. 36), because a variety of species from different guilds are capable of dispersing over relatively long distances (41).

Another explanation is that, in smaller islands, stochastic effects play a greater role, causing the neutral assumptions to fail. Stochastic factors other than basic demographic stochasticity of population size are not considered in the neutral model. However, factors such as environmental stochasticity (climatic variability, changes in abundance of predator or prey species, etc.) are likely to play a greater role in survival probability for small fragments. Behavioral shifts are also likely to play a more important role in the breakdown of neutrality in small fragments. In Manaus, some species that remained in small fragments stopped foraging in mixed species groups entirely, a hugely different foraging strategy and obviously, very significant to survival (42).

The neutral formula also yields poor predictions of extinction time for very large areas. Some bigger islands such as Aru (4) seem to have relaxed much more rapidly than predicted. This was the conclusion of Ricklefs (17), who compared phylogenetic estimates of the global bird-species time to extinction with the predictions of neutral theory. He found that the observed waiting times to extinction (*ca.* 2 Myr) were much less than those predicted by neutral theory (typically 40–86 Myr). Thus, he inferred, drift is too slow to account for turnover in regional avifaunas. Thus, for large scales, our concern is the same as that of Ricklefs (17): neutral theory predicts excessively long relaxation times. However, for the southwest Pacific islands, there are other possibilities that might explain this divergence. First, S_0 might be significantly lower than the total lowland fauna $S_0 = 325$ assumed by Diamond (4) and adopted here. For example, for continental fragments, we might alternatively apply the species–area relation with a low exponent of $\gamma = 0.16$ (35) to estimate S_0. This leads to lower values of S_0 and hence, larger values of T_{50}. Also, for these larger islands with very large population sizes and slow relaxation stretching into evolutionary timescales, the closed-community assumption breaks down because of speciation as well as immigration. Finally, the spatially implicit treatment will cause problems on larger spatial scales and in situations where the geometry of habitat loss plays a major role. For very large areas, the assumption of perfect mixing will be more problematic, and localization of species and endemicity will become more important. So, our theory may be unsuitable for predicting species loss rates not only in large continental areas but also for the larger islands. Thus, the disagreements on larger scales may be because of this paper's specific assumptions rather than the assumption of neutrality itself.

A number of further assumptions had to be made in this paper. Throughout, we assumed a generation time of 5 y, following the work of Ricklefs (17). We also assumed that the density of pairs in the region was 8.29 pairs/ha (39), a value which is close to that reported by Terborgh et al. (40) for Cocha Cashu, Brazil ($\rho = 9.55$ pairs/ha) and Hubbard Brook, New Hampshire ($\rho = 10.0$ pairs/ha). Ricklefs (17) used a value of 6 pairs/ha, but this was for passerines only. Both of these are likely to be subject to considerable variability, especially the density of individuals, ρ. Overestimation of either of these factors leads to an overestimation of relaxation time.

Acknowledging the limitations of neutral theory, the sheer simplicity of Eqs. **4** and **5**, and the fact that predictions agree rather well with observed extinction rates suggests that it can be a useful tool in conservation. It also shows the surprising relevance of the neutral model to ecological observation and species conservation, in particular, in contrast to the rather pessimistic view expressed by Clark (19). The results of this paper raise a number of interesting recommendations for further field studies in extinction debt. One is that the degrees of isolation and levels of immigration should be carefully recorded and reported, because these data lead to major changes in the faunal relaxation rates. With properly quantified patterns of immigration, it might also be possible to test some of the spatial versions of neutral theory. Another factor that should be observed is the species abundance distribution, because this strongly affects the initial rates of relaxation. A third and related direction for work is the extension of these tests to other taxonomic groups.

Methods

In comparing neutral predictions with published results, we note that the various authors have used different methodologies and systems of units, which must be harmonized. The predictions of neutral theory are twofold. First, through Eq. **5**, neutral theory predicts a hyperbolic rather than exponential decay. Second, given hyperbolic decay, the relaxation time is given by Eq. **4**, which can be written in terms of population density ρ and area A (Eq. **6**):

$$t_{50} = \frac{\tau \rho A}{S_0}. \qquad [6]$$

Most of the studies of relaxation only have available two points in time, and therefore, it is difficult to test hyperbolic vs. exponential decay given such data. However, if we assume a hyperbolic model (following Terborgh) (8), then Eq. **5** should hold if this is because of neutral relaxation rather than to other processes. This is the approach that we use.

The most common currency for quantifying relaxation rates has been the half-life, the time to lose one-half of the species present at isolation (4, 35, 36). This is the denomination that is used in this paper, where T_{50} denotes the half-life inferred from observations and t_{50} denotes the half-life predicted by theory.

In all calculations, we used years for the units of time. The units of population were breeding pairs. Following the work of Brooks et al. (35), we converted all area units to hectares.

Because authors did not observe T_{50} directly, this quantity must be inferred from the species richness at different times. Some authors used an exponential model of faunal relaxation (4, 35), for which the equation is (Eq. 7)

$$T_{50} = \frac{t}{-\ln\left[\frac{S(t) - S_{eq}}{S_0 - S_{eq}}\right]}. \qquad [7]$$

Here, t is the time elapsed since isolation, and $S(t)$ is the currently observed species richness. S_{eq} is the number of species expected at equilibrium (using species area relations relationships). The above equation is different from the formula used by Terborgh (8) assuming hyperbolic dynamics, which is (Eq. **8**)

$$T_{50} = \left[\frac{S(t)}{S_0 - S(t)}\right] \cdot t. \qquad [8]$$

For consistency, we use the latter equation throughout. Note that there is no equilibrium implicit in this equation. This follows from our assuming that both speciation and immigration are absent. Using Eq. **8**, T_{50} can be calculated on the basis of the number of species at two points in time and the length of time t between the two time points. If the neutral model is a good approximation for the mechanisms causing hyperbolic relaxation, then we expect that $T_{50} \simeq t_{50}$.

For two of the cited studies (37, 38), it was necessary to make some extra assumptions to compare their results with neutral predictions, because these studies did not estimate relaxation times, although the data do allow such a calculation. More information about the methods can be found in *SI Text*, where we derive an equivalence for their system.

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