

Can Neutral Theory Predict the Responses of Amazonian Tree Communities to Forest Fragmentation?^{*}

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ABSTRACT: We use Hubbell's neutral theory to predict the impact of habitat fragmentation on Amazonian tree communities. For forest fragments isolated for about two decades, we generate neutral predictions for local species extinction, changes in species composition within fragments, and increases in the probability that any two trees within a fragment are conspecific. We tested these predictions using fragment and intact forest data from the Biological Dynamics of Forest Fragments Project in central Amazonia. To simulate complete demographic isolation, we excluded immigrants—species absent from a fragment or intact forest plot in the initial census but present in its last census—from our tests. The neutral theory correctly predicted the rate of species extinction from different plots as a function of the diversity and mortality rate of trees in each plot. However, the rate of change in species composition was much faster than predicted in fragments, indicating that different tree species respond differently to environmental changes. This violates the key assumption of neutral theory. When immigrants were included in our calculations, they increased the disparity between predicted and observed changes in fragments. Overall, neutral theory accurately predicted the pace of local extinctions in fragments but consistently underestimated changes in species composition.

Trees provide the architectural basis for forest ecosystems, generate most of their primary productivity, and provide the foundation for much of their biodiversity. In Amazonian forests, tree diversity can exceed 280 species (≥ 10 cm diameter at breast height [dbh]) per hectare (Gentry 1988; Oliveira and Mori 1999), among the highest values seen anywhere on earth.

Unfortunately, Amazonian forests are being cleared and fragmented at an alarming—and accelerating—rate (Laurance et al. 2001a, 2004). To learn how habitat fragmentation affects forest ecosystems, the Biological Dynamics of Forest Fragments Project (BDFFP) was established in 1979 near Manaus, Brazil, in forest as diverse as any in Amazonia (Lovejoy et al. 1983, 1986; Laurance et al. 2002). To study tree communities, permanent 1-ha plots were established between 1980 and 1990 in areas soon to become fragments and in nearby intact forest. These plots have been regularly censused since. They show that fragmentation has a large impact on the mortality, recruitment, biomass, and community composition of rain forest trees (e.g., Laurance et al. 1997, 1998a, 1998b, 2000, 2001b, 2006; D'Angelo et al. 2004; Nascimento and Laurance 2004; Nascimento et al. 2006).

Here, we use Hubbell's (2001) neutral theory of forest dynamics and diversity as a null hypothesis for predicting the impact of fragmentation on diverse Amazonian forest. Neutral theory uses simplifying assumptions to develop precise, far-reaching predictions that bring a wealth of seemingly unrelated phenomena within the scope of a common theoretical framework. It is constructed in strict parallel with the neutral theory of population genetics (Leigh et al. 2004a), which is based on the assumption that the alleles in a population are selectively equivalent (Kimura 1983). By assuming that all mature trees, regardless of their species, are competitive equivalents, Hubbell's theory makes plausible predictions about species-area curves (Durrett and Levin 1996), the relative abundance of tree species on plots of different sizes (Bram-

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son et al. 1996; Hubbell 2001), and the rate of species turnover in space (Chave and Leigh 2002; Condit et al. 2002). Hubbell (2001) emphasizes the potential relevance of neutral theory for predicting community responses to habitat fragmentation, but to date there have been very few empirical tests of such predictions (e.g., Leigh et al. 1993).

In this study, we use Hubbell's (2001) neutral theory to generate predictions about the impact of forest fragmentation on the species diversity, species composition, and rate of local extinctions of mature (≥ 10 cm dbh) trees. We derive these predictions using the approach embodied in Moran's (1958, 1962) neutral model of genetic drift and compare them with observations from experimental forest fragments and intact forest (control) plots in central Amazonia. Although we focus on how well neutral theory predicts the initial effects of fragmentation, some of our results bear on the applicability of neutral theory to tropical forest ecology as a whole.

Study Area and Methods

This BDFFP study area spans about 1,000 km² and is located 80 km north of Manaus, Brazil (2°30'S, 60°W), at 50–100 m elevation. The topography consists of flat or undulating plateaus interspersed by many steeply eroded gullies. Rain forests in the area are not seasonally inundated. Annual rainfall varies from 1,900 to 3,500 mm, averaging 2,600 mm. There is a pronounced dry season from June to October (Laurance 2001), with the driest quarter of the year averaging 346 mm of rain. The forest canopy is 30–37 m tall, with emergents to 55 m. The dominant soils in the study area are xanthic ferralsols, which are heavily weathered, acidic, and very poor in nutrients such as P, Ca, and K (Chauvel et al. 1987). Rates of natural tree mortality in these nutrient-starved forests are low relative to most forests elsewhere in the Neotropics, averaging about 1.2%/year (Laurance 2001).

The study area is surrounded by large expanses (>200 km) of continuous forest to the west, north, and east. In the early 1980s, a series of forest fragments were isolated (by distances of 70–1,000 m) from the surrounding forest by clearing the intervening vegetation to establish pastures in three large (~5,000 ha) cattle ranches. Fragments were fenced to prevent encroachment by cattle. Reserves ranging from 1 to 1,000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Parts of the three ranches were later abandoned; *Cecropia*-dominated regrowth prevails in areas that were cleared but not burned, and *Vismia*-dominated regrowth prevails in pastures that were repeatedly burned (Mesquita et al. 2001).

Long-term changes in tree community dynamics and

composition are being assessed in the BDFFP study area, using a network of 1-ha permanent plots in which all trees (≥ 10 cm dbh) are being monitored. Our study is based on data from 30 plots, 17 of which are arrayed across nine forest fragments (four of 1 ha, three of 10 ha, two of 100 ha), with the remaining 13 in intact forest (table 1). These plots, a subset of a larger plot network, were selected to represent different distances from the forest edge for each fragment and to minimize pseudoreplication. Multiple plots within a single fragment were combined for analyses.

All plots were first censused between 1980 and 1990, then recensused three to five times, with the most recent census completed in June 1999. During the initial census, trees in each plot were marked with numbered aluminum tags and mapped. During recensuses, all new trees (≥ 10 cm dbh) were mapped and marked, and all dead and damaged trees were recorded. On average, 95.4% of all trees in each plot were identified to species or morpho-species level, using sterile or fertile material collected from each tree. Voucher specimens for each tree are maintained in the BDFFP Plant Collection, Manaus, Brazil. At the BDFFP, individual 1-ha plots average over 250 tree species (table 1), and a 9-ha square had 702 species among 5,271 identified trees.

Table 1: Numbers of identified trees (≥ 10 cm dbh) during the first and last censuses (N_1 and N_2), the number of species among them (S_1 and S_2), the interval between the first and last censuses (T) in months, and the annual mortality rate (m) for a representative subset of forest fragments and intact forest plots in central Amazonia

Plot	N_1	S_1	N_2	S_2	T	m
1-ha fragment 1104.1	580	276	556	269	209	1.0844
1-ha fragment 2107.1	694	284	739	285	183	2.6623
1-ha fragment 2108.1	646	253	768	266	183	3.8313
1-ha fragment 3114.1	587	251	586	258	181	3.0557
1 ha in 10-ha fragment 1202.3	558	243	519	231	208	1.9664
3 ha in 10-ha fragment 2206 ^a	1,997	494	2,099	507	183	2.3650
4 ha in 100-ha fragment 3304 ^a	2,647	550	2,571	556	170	1.3377
Intact forest ha 1101.1	548	254	515	246	218	1.1792
Intact forest ha 1105.1	617	245	614	251	204	1.2328
Intact forest ha 1109.1	556	231	511	224	204	1.6179
Intact forest ha 1201.3	616	224	535	208	215	1.6864
Intact forest ha 1301.4	583	267	566	265	164	.6846
Intact forest ha 3402.7	550	258	569	271	156	.6063

Note: See appendix D in the online edition of the *American Naturalist* for the complete data set.

^a Numbers of trees and species for each fragment are pooled from one to four plots, treating the data as a single large plot.

Generating Neutral Theory Predictions for Forest Fragments

The fundamental premise of Hubbell's neutral theory of forest dynamics and diversity is that the prospects of death or reproduction for a tree are never influenced by the species to which it or its neighbors belong. The formalism used to derive predictions is that of the neutral theory of allele frequency change at a multiallelic locus in a haploid population. This formalism employs four specific assumptions. First, all mature trees are fundamentally the same; that is, each mature tree has identical prospects of dying or reproducing. Second, the overall density of mature trees in any community is constant. Therefore, if one species increases, at least one other must decrease (a zero-sum game). To be specific, if a tree dies, it is immediately replaced by the instantly maturing offspring of a living tree in the community. Third, the environment is uniform (or, at the least, temporal or spatial variation in environmental conditions does not favor some species over others). Fourth, each new tree has the same tiny probability v of being a new species.

Although these assumptions are unrealistic (e.g., Harms et al. 2000, 2001; Hubbell et al. 2001; Clark and McLachlan 2003; Gilbert and Lechowicz 2004; Wills et al. 2006), neutral theory provides a valuable null hypothesis by which to test for effects of differences among species (Leigh et al. 2004a, 2004b). Here, we derive testable predictions of rates of local extinction, the decline of tree diversity, and the change in species composition in recently isolated forest fragments. We use the neutral theory to probe whether environmental conditions in fragments favor some tree species over others or alter aspects of the whole community.

We model the neutral theory of tree diversity using Moran's (1958) neutral model of genetic drift for a multiallelic locus in a haploid population in which each new mutation gives rise to an entirely new allele (Ewens 2004). In the Moran model, each haploid individual has one gene at this locus, so we equate genes with individual trees, alleles with species, and new mutations with new tree species.

We apply this model to an isolated forest fragment with N trees. We assume that the fragment is small enough that we can ignore dispersal limitation so that any tree in the fragment is equally likely to be the parent of a new tree (Hubbell 2001). Let successive time steps be separated by $1/N$ of a tree generation, where a tree generation is defined as the time required for N trees to die in this fragment. At each time step, let a tree be chosen at random to die, and let another (which could be the same tree) be independently chosen to be the seed parent of the dead tree's replacement. Thus, the number of trees in a particular

species cannot change by more than one individual per time step. This model assumes that each mature tree will be pollinated, no matter how isolated it may be. In addition, in testing the theory, we count a tree as being mature when it attains 10 cm dbh—which in reality can take several decades after its seed germinates—even though the theory assumes that this tree matures instantly when its predecessor dies.

All neutral predictions derived below were confirmed with simulations using the initial censuses from the BDFFP fragment and control plots. All simulations were run 10,000 times at three time intervals that encompassed the time elapsed (in tree generations) between the first and last censuses of these plots. When converted to tree generations (by dividing the total number of tree deaths by the initial number of trees in each plot), the elapsed number of tree generations in our plots ranged from 0.15 to 0.58. To ensure that our predictions were accurate over this range of values, we ran separate simulations for 0.33, 0.5, and 1.0 tree generations.

Neutral Prediction 1: Extinction Rates

To calculate the rate of extinction of tree species from a fragment, first consider the probability that a species represented in an isolated fragment by one mature tree at time 0 is extinct by time t . If t is small enough that the number of mature trees of this species at time t is likely to be a small proportion of the total number of mature trees in the fragment, we may use the method of branching processes (Harris 1963) to calculate the probability that it is extinct by time t . This method assumes that trees of this species die and reproduce independently of each other.

Let a tree alive at time t have probability dt of dying by time $t + dt$ and probability dt of bearing one instantly maturing young by this time, where time is measured in tree generations. We use the method of generating functions (see app. A in the online edition of the *American Naturalist*) to calculate the probability $E_1(t)$ that a species represented in the fragment by one mature tree at time 0 is extinct by time t . We find that $E_1(t) = t/(1 + t)$. As the death and reproduction of different trees are independent events, the probability $E_j(t)$ that a species represented in the fragment by j mature trees at time 0 is extinct by time t is $E_j(t) = t^j/(1 + t)^j$.

If we know how many species are represented in the fragment by j mature trees apiece for all j (the distribution of mature trees over species) and the probability $E_j(t)$ that a species with j mature trees in the fragment at time 0 is extinct from it by time t , we can calculate the total number of species dying out from the fragment within t tree generations. If there are $S(j)$ species with j trees apiece at the initial census (time 0), and if each of these species has an

independent probability $E_j(t)$ of dying out by time t , we may calculate confidence intervals (CIs) for the number of these species dying out by time t if we remember that the probability $p(j)$ that $N(j)$ of these species die out by time t is given by the binomial distribution

$$p(j) = \left\{ \frac{S(j)!}{N(j)! [S(j) - N(j)]!} \right\} [E_j(t)]^{N(j)} [1 - E_j(t)]^{S(j) - N(j)}.$$

In 1-ha tropical forest plots of Abraham et al. (1996) and Leigh (1999), and in 1-ha plots of the BDFFP, the distribution of trees ≥ 10 cm dbh over species approximates a log series, especially for species with few trees (table 2). In the log series, the number $S(j)$ of species with j trees apiece is $\alpha x^j/j$, where α is Fisher's α (Fisher et al. 1943). The dynamics in a plot of species with few trees there, like the dynamics of very rare alleles (Fisher 1930; Gillespie 1991), is dominated by chance. The log series applies to rare species in a plot because migration into the plot of species previously absent, and dispersal outside the plot of young of trees in it, crudely approximate the role played by mutation in genetics models and by speciation in Hubbell's (2001) metapopulation (E. G. Leigh, unpublished manuscript). Approximate log series in these small plots neither imply nor deny the wider validity of the neutral theory.

If $S(j) = \alpha x^j/j$, the total number S of species on the plot or fragment is

$$S = \alpha x + \frac{\alpha x^2}{2} + \frac{\alpha x^3}{3} + \dots = \alpha \ln \left(\frac{1}{1-x} \right).$$

Moreover, if $S(j) = \alpha x^j/j$, the number $N(j)$ of trees in species with j trees apiece is $jS(j) = \alpha x^j$, and the fragment's total number N of trees is

$$N = \alpha x + \alpha x^2 + \alpha x^3 + \dots = \frac{\alpha x}{1-x}.$$

Therefore, $x = N/(N + \alpha)$, and $S = \alpha \ln [(N + \alpha)/\alpha]$.

In a fragment with N mature trees at time 0, the neutral theory predicts that if $t \ll N$, then $E_j(t)$, the probability that a species represented in the fragment by j trees at time 0 dies out from that fragment by time t , is p^j , where $p = E_1(t) = t/(1+t)$. If the distribution of trees over species follows the log series, then the total number $E(t)$ of tree species lost by the fragment within t tree generations is $S(1)E_1(t) + S(2)E_2(t) + S(3)E_3(t) + \dots$. If $S(j) = \alpha x^j/j$, then $E(t)$ is

Table 2: Fisher's α , $x = N_i/(N_i + \alpha)$, and the predicted and observed numbers of tree species represented by one ($S[1]$), two ($S[2]$), and three ($S[3]$) trees ≥ 10 cm dbh apiece, in four 1-ha fragments and a single 1-ha plot in a 10-ha fragment

	Plot ^a				
	1104.1	2107.1	2108.1	3114.1	1202.3
Area (ha)	1	1	1	1	10
α	210	180	155	169	169
x	.7365	.7951	.8085	.7781	.7671
$S(1)$ pre	155	143	125	132	130
$S(1)$ obs	159	162	135	156	133
$S(2)$ pre	57	57	51	51	50
$S(2)$ obs	58	50	57	47	44
$S(3)$ pre	28	30	27	27	26
$S(3)$ obs	23	27	27	21	24

Note: The suffixes "pre" and "obs" indicate the number predicted by the log series and the number observed.

^a Predicted values of $S(1)$, $S(2)$, and $S(3)$ are, respectively, αx , $\alpha x^2/2$, and $\alpha x^3/3$, the values expected from the log series. N_i is the number of trees ≥ 10 cm dbh recorded in the initial census.

$$\begin{aligned} \sum_{j=1}^{\infty} \alpha \frac{x^j p^j}{j} &= \alpha \ln \frac{1}{1-px} \\ &= \alpha \ln \frac{N + \alpha}{N(1-p) + \alpha}. \end{aligned} \quad (1)$$

This formula applies to small plots and fragments in our study area because $t < 0.5$ and $S(j)E_j(t) \approx 0$ for $j > 3$, while the log series applies for $j \leq 3$.

To summarize, neutral theory predicts that the rate at which tree species will become locally extinct in a fragment (the number of species lost per generation) increases in a predictable way with the mortality rate of trees. In a neutral world, species are lost only via random death and recruitment. According to the neutral theory, no species is inherently favored by fragmentation, so abundant species usually disappear far less quickly than rare ones.

Neutral Prediction 2: Changes in Species Composition

Consider a species represented at time 0 by j mature trees in an isolated fragment that has $N(0)$ mature trees at this time, where $j \ll N(0)$. With probability $j/N(0)$, one of these trees dies at the next time step, and, with equal probability, one will produce a single, instantly maturing young at this time. As there are $N(0)$ time steps per tree generation, the species undergoes an average of $2j$ instances of death or reproduction per tree generation, an average of $2jt$ in t tree generations. Each instance has an equal probability of being a birth or a death, nearly independently of all the other instances (if there is a constant number of mature trees in the fragment, there is a slight negative correlation among these instances in whether a birth occurs). Just as

the mean square difference between the numbers of heads and tails in $2jt$ tosses of a fair coin is $2jt$, so the mean square change in a fragment during time t in the number of trees of a species represented by j trees at time 0 is $2jt$. The expected value of the sum of the mean squared population changes of all tree species in the fragment during time t is thus $2N(0)t$.

To determine confidence limits about the sum Σ of the mean square changes in the populations in the fragment, we begin by calculating the variance in this quantity. If we assume that each tree in the fragment at time t has a probability dt of dying by time $t + dt$ and an equal probability of producing a single, instantly maturing young by that time, independently of all the others, then the variance in the square of the change in the number of trees during time t in a species with j trees at time 0, the fourth moment about the mean change minus the square of the variance (Feller 1971, p. 48), is $2jt + 8j^2t^2 + 24jt^3$ (app. A). If species n has j_n trees at time 0, then the variance in Σ should be nearly the sum of the corresponding quantity for each species, or

$$2N(0)(t + 12t^3) + 8t^2 \sum_{n=1}^S j_n^2 = 2N(0)(t + 12t^3) + 8[tN(0)]^2 F(0), \quad (2)$$

where S is the number of species in the fragment and $F(0)$ is the relative dominance in the fragment at the initial census (eq. [5]).

Simulating population changes using the Moran model shows that Σ is distributed according to a lognormal (see app. B in the online edition of the *American Naturalist*) with mean $\Sigma = 1.97N(0)t$ and variance

$$\sigma^2 = 1.97N(0)t + 1.97[2N(0)t]^2 F(0). \quad (3)$$

The mean M and variance S^2 of $\ln(\Sigma)$ are related to $M(\Sigma)$ and σ^2 by the equations

$$M(\Sigma) = \exp\left(M + \frac{S^2}{2}\right), \quad \sigma^2 = \exp(2M + S^2)(\exp S^2 - 1)$$

(Moran 1968, p. 317). Thus, $\ln(\Sigma)$ has a 95% chance of falling within the limits $M \pm 2S$, which is equivalent to

$$\frac{\exp -2\sqrt{\ln [1 + (\sigma/\mu)^2]}}{\sqrt{1 + \sigma^2/\mu^2}} < \Sigma < \frac{\exp 2\sqrt{\ln [1 + (\sigma/\mu)^2]}}{\sqrt{1 + \sigma^2/\mu^2}}. \quad (4)$$

In sum, if a tree has probability $1/N$ of dying and an equal probability of reproducing at each time step, the

mean square population change in a species with one tree at time 0 increases by $2/N$ per time step. If the fates of different trees are independent, the mean square population in a species with j trees at time 0 increases by $2j/N$ per time step, and Σ increases by 2 per time step. Thus, according to neutral theory, species composition changes progressively because nothing stabilizes it (Pandolfi 1996; Clark and McLachlan 2003).

Neutral Prediction 3: Decay of Diversity

In a forest fragment too small for speciation to be relevant over a few tree generations, new species never appear, but chance fluctuations in population size cause species to disappear, so diversity declines. How fast is this decline? To find out, set speciation rate $v = 0$. Let diversity be measured by the quantity $H(t)$, the probability that two trees sampled at random with replacement from the fragment at time t are of different species. Then $H(t) = 1 - F(t)$, where $F(t)$, the relative dominance (Leigh et al. 1993) in the fragment at time t , is the probability that two trees sampled at random with replacement from the fragment are of the same species. The quantity $H(t)$ is Simpson's index of diversity (Simpson 1949), which is commonly used in ecology. Let the proportion of trees in this fragment at time t that belong to species i be $x_i(t)$. Then

$$F(t) = \sum_{i=1} x_i^2(t). \quad (5)$$

The expected change in the relative dominance during one time step is the expected value of $F(t + 1/N) - F(t)$, where N is the total number of trees on the fragment. By definition, a time step includes one death and one recruitment. We therefore calculate the expected change in relative dominance caused by a single such death and replacement. If we assume that a newly dead tree is likely to be replaced by any other tree on the fragment, that is, if dispersal limitation can be ignored on a fragment this small, we find (see app. C in the online edition of the *American Naturalist*) that

$$F\left(t + \frac{1}{N}\right) - F(t) = H(t) - H\left(t + \frac{1}{N}\right) = \frac{2H(t)}{N^2}. \quad (6)$$

This assumption of panmictic dispersal is accepted by neutral theorists: Hubbell (2001, p. 86) assumes that if a newly dead tree on a 50-ha plot is not replaced by the young of a tree outside the plot, then every tree in the plot has an equal chance of providing the young that replaces it.

The probability that any two trees in the same fragment are conspecific increases over time because if one dies, the probability is $1/N$ that it will be replaced by the young of the other tree. Therefore, after Ns time steps (s tree generations),

$$\begin{aligned} H\left(t + \frac{Ns}{N}\right) &= H(t + s) \\ &= H(t) \left(1 - \frac{2}{N^2}\right)^{Ns} \\ &\approx H(t) \exp\left(-\frac{2s}{N}\right). \end{aligned} \quad (7)$$

The mean change $M(s)$ in F from time 0 to generation s is roughly $2[1 - F(0)]s/N$ if $s \ll N$. The variance $V(1/N)$ in the change of F over one time step, which is the mean square change in F minus the square of the mean change during one time step, is (app. C)

$$\frac{8(\sum_{i=1} x_i^3 - F^2)}{N^2} + \frac{4F(1 - F)}{N^4}. \quad (8)$$

If $s < 1$, the variance $V(s)$ in the change of F over Ns time steps (s tree generations) is Ns times the variance from a single time step. Simulations show that the change $\Delta F(s)$ in F over Ns time steps is close to normally distributed (app. B), so that the change in F has 95% probability of falling within the limits $\Delta F(s) \pm 2[V(s)]^{1/2}$.

To summarize, in a neutral world, tree diversity in an isolated fragment declines because the distribution of stems among species becomes less even with the passage of time, leaving more and more species with no representatives at all.

Testing Predictions of Neutral Theory

We tested these three predictions arising from neutral theory using our data for forest fragments and intact forest plots in central Amazonia. Because our predictions were generated by assuming that the fragments are fully isolated, we tested predictions 2 and 3 after excluding immigrant species (defined as those present in the final but not the initial census of a site) from our data. We cannot, however, exclude immigrants of species already present on the plot. An exchange of migrants, especially of commoner species, between a plot and its surroundings should stabilize species composition, just as it stabilizes genetic composition in the neutral theory of population genetics (Wright 1931). Our inability to exclude immigrants of common species

means that our neutral predictions should overestimate changes in fragments and intact forest plots.

Neutral theory measures time in tree generations, implying that the rate of change in a fragment is paced by the mortality rate of its trees. To test our neutral predictions, we equated the number of tree generations between the first and last censuses of a plot or fragment to the number of years between these censuses, multiplied by the average annual mortality rate of its trees.

Our tests assess the significance of deviations from neutral expectation for individual fragments or control plots in intact forest. For each of our three predictions, we also pooled observations from all fragments to test whether, as a group, fragments (or control plots) deviate from neutral predictions. Because the distributions of the variates we generated were not normal, we used nonparametric Mann-Whitney U -tests to evaluate the significance of these deviations. Findings for selected fragments and control plots are discussed below, with complete results for all sites provided in appendix D in the online edition of the *American Naturalist* (tables D1–D5).

Local Extinctions

First, we compare the proportions of species represented in a fragment or intact forest plot by one, two, and three trees (≥ 10 cm dbh) that die out by the final census with the neutral prediction that a species represented by k trees at time 0 has probability $E_k(t) = p^k$ of becoming extinct from it t generations later; p is the probability that a species represented by a single tree at time 0 is extinct at time t , where $p = t/(1 + t)$. If $E_k(t)$ consistently exceeds its predicted value for $k > 1$, but not for $k = 1$, we may conclude that the fates of conspecific trees in a fragment or intact forest site are correlated, contrary to the assumptions of neutral theory. We then test the neutral theory prediction that the total number of extinctions on a plot or fragment with N trees (eq. [1]) is

$$\alpha \ln \left[\frac{N + \alpha}{N(1 - p) + \alpha} \right].$$

Changes in Species Composition

For our second test, we calculate Σ_j for each fragment or intact forest plot j by summing the squared changes in numbers of trees (≥ 10 cm dbh) between the first and last censuses for each of its species, excluding immigrants absent from the first census, and compare this calculated Σ_j with the predicted value $1.97N_j(t)$, where $N_j(0)$ is the number of trees in the fragment or plot j at the initial census.

We test for the significance of the deviation of Σ_j from the predicted value by asking whether Σ_j falls outside the confidence limits given by equation (4).

Changes in Tree Diversity

For our last test, we consider the relationship between the relative dominance F of each forest fragment or control plot j in its first and final censuses. Equation (7) implies that $F_j(t) = 1 - H_j(t)$ is $1 - H_j(0) \exp(-2t/N_j)$, which may also be expressed as $1 - [1 - F_j(0)] \exp(-2t/N_j)$, where N_j is the number of trees (≥ 10 cm dbh) in the fragment at the first census, and t is the number of tree generations between the first and last censuses. In each fragment, we compare the observed with the predicted values of $F_j(t)$ for the last census. Equation (8) predicts that when $t = N_s$, the standard deviation in the value of $H_j(t) = H_j(N_s)$ is very nearly

$$\sqrt{V(t)} = \sqrt{N_s \left[\frac{8(\sum_{k=1}^3 x_{jk}^3 - F^2)}{N^2} + \frac{4F(1-F)}{N^4} \right]},$$

where x_{jk} is the proportion of trees in fragment j at time 0 that belong to species k , and $F_j = F_j(0)$. We assess the significance of the divergence of the observed from the predicted value of $F_j(t)$ by asking whether this divergence exceeds $2[V(t)]^{1/2}$. Here again, we calculated this change excluding species that were present in the last census but not in the first census.

Results

Tree mortality rates were much higher in fragments than control plots ($t = 4.20$, $df = 10$, $P < .001$), causing large differences in neutral predictions for fragments relative to control plots (fig. 1; app. D). New immigrants (species present at the last census but absent from the first) arrived at a significantly faster rate in fragments than in control plots ($F = 35.31$, $df = 1, 19$, $P < .0001$; fig. 2A), which caused much larger changes in fragments than in control plots (fig. 2B; app. D). The elevated immigration rate in fragments was largely the result of many pioneer species colonizing the fragments (table 3).

Local Extinctions

Neutral theory accurately predicted the number of local extinctions of species initially represented by one (singleton) or two (doubleton) trees ≥ 10 cm dbh in control plots or the censused portions of fragments. The number of singletons dying out by the final census was lower than

predicted in seven of 13 control plots and in three of nine fragments—significantly lower than expected in one fragment, and never significantly higher than expected (table D2). Similarly, among doubletons, there was only one significant deviation from the predicted number of extinctions: one control plot lost too many.

Mortality rates differed markedly among the various plots and fragments, and extinction rate varied with tree mortality rate in remarkable accord with neutral theory predictions (fig. 3A; table D2), suggesting that we applied the neutral theory correctly and appropriately.

Predictions of extinctions from different control plots and fragments, based on a log-series approximation, were usually somewhat less accurate (table D3). Predictions were exact (within rounding error) for one fragment and three control plots, but they were underestimated for six of the remaining eight fragments and nine of the 10 remaining control plots.

Changes in Species Composition

When immigrants were excluded, the observed change in species composition was within a factor of two of the neutral theory prediction in 12 of 13 control plots and in six of nine fragments (table D4). Change was usually faster on plots with higher mortality, as neutral theory predicts (fig. 3B).

There was, however, a clear contrast between fragments and control plots. Change was slower than predicted in 10 of 13 control plots (perhaps from the stabilizing influence of the gain and loss of migrants of species already in the plot), whereas it was faster than predicted in seven of nine fragments, and significantly so in five. The prevalence of such rapid changes even without immigrants (table D4) suggests that fragmentation favors a species composition that is different from that in intact forest, implying that different tree species respond differently to environmental change.

The rate of change in species composition varied far more among control plots than predicted by neutral theory: this change was significantly slower than predicted in six control plots, and significantly faster in two. The significance of this result is enhanced if the exchange of migrants of commoner species stabilizes species composition.

When immigrants were included, the rate of change in species composition in control plots never deviated from the neutral prediction by more than a factor of two, but it changed over six times faster than predicted in three of nine fragments and over twice that predicted in three others. Although the neutral theory prediction is not meaningful if immigrants are included, this contrast is useful. Immigration accelerated changes in species composition far more in fragments than control plots (fig. 2B), inflating

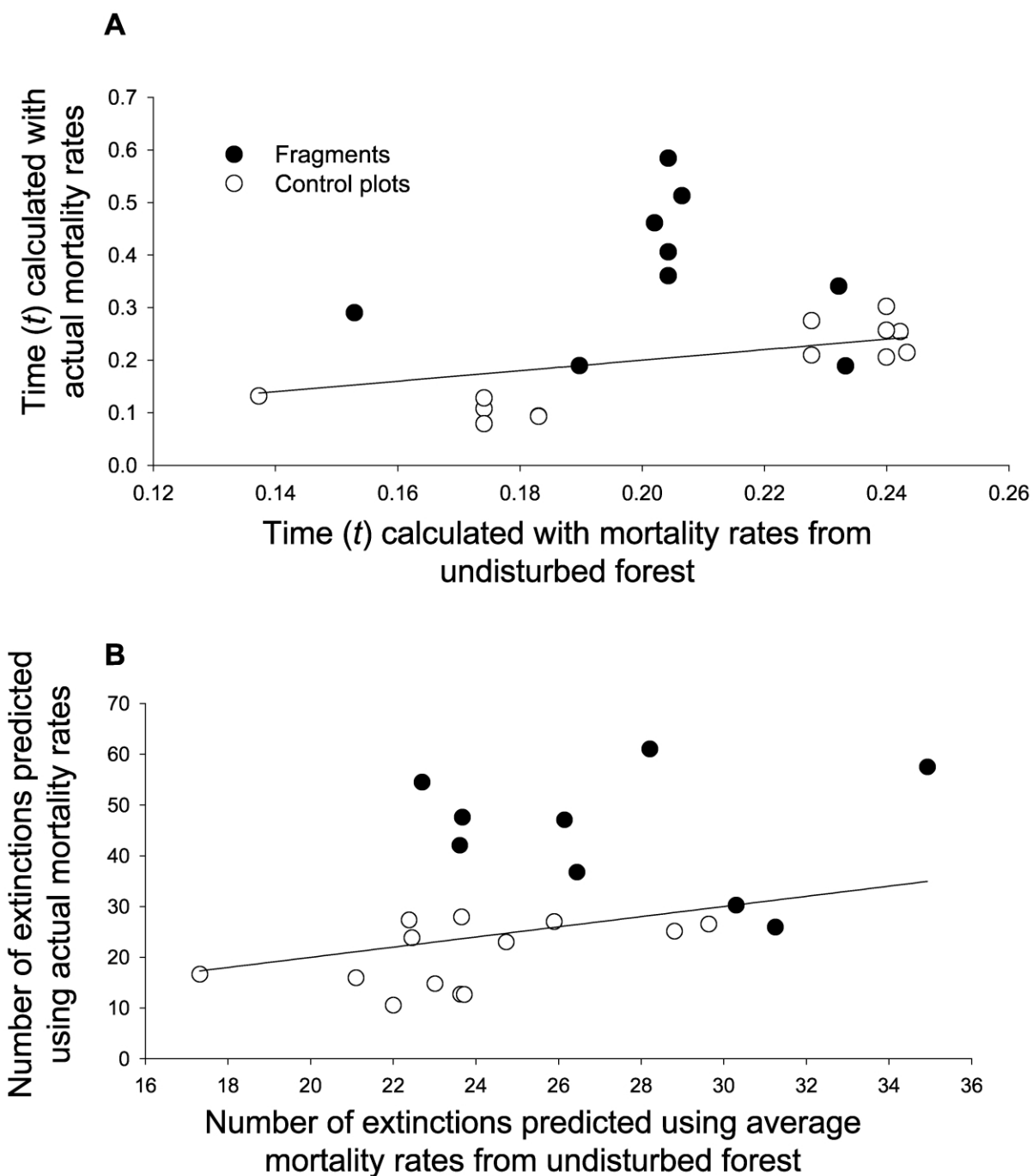


Figure 1: Effect of mortality rates on neutral predictions. Each point represents a fragment (*filled circles*) or control plot (*open circles*), and the line is 1 : 1, which is expected if there is no difference between measures. *A*, Time ($t = \text{mortality rate} \times \text{time between first and last census dates}$) used in neutral predictions calculated with average mortality rates from undisturbed forest and with the mortality rate of the fragment or control plot. *B*, Neutral predictions for the total number of local extinctions. Predictions were calculated using average mortality rates and mortality rates from individual fragments or control plots.

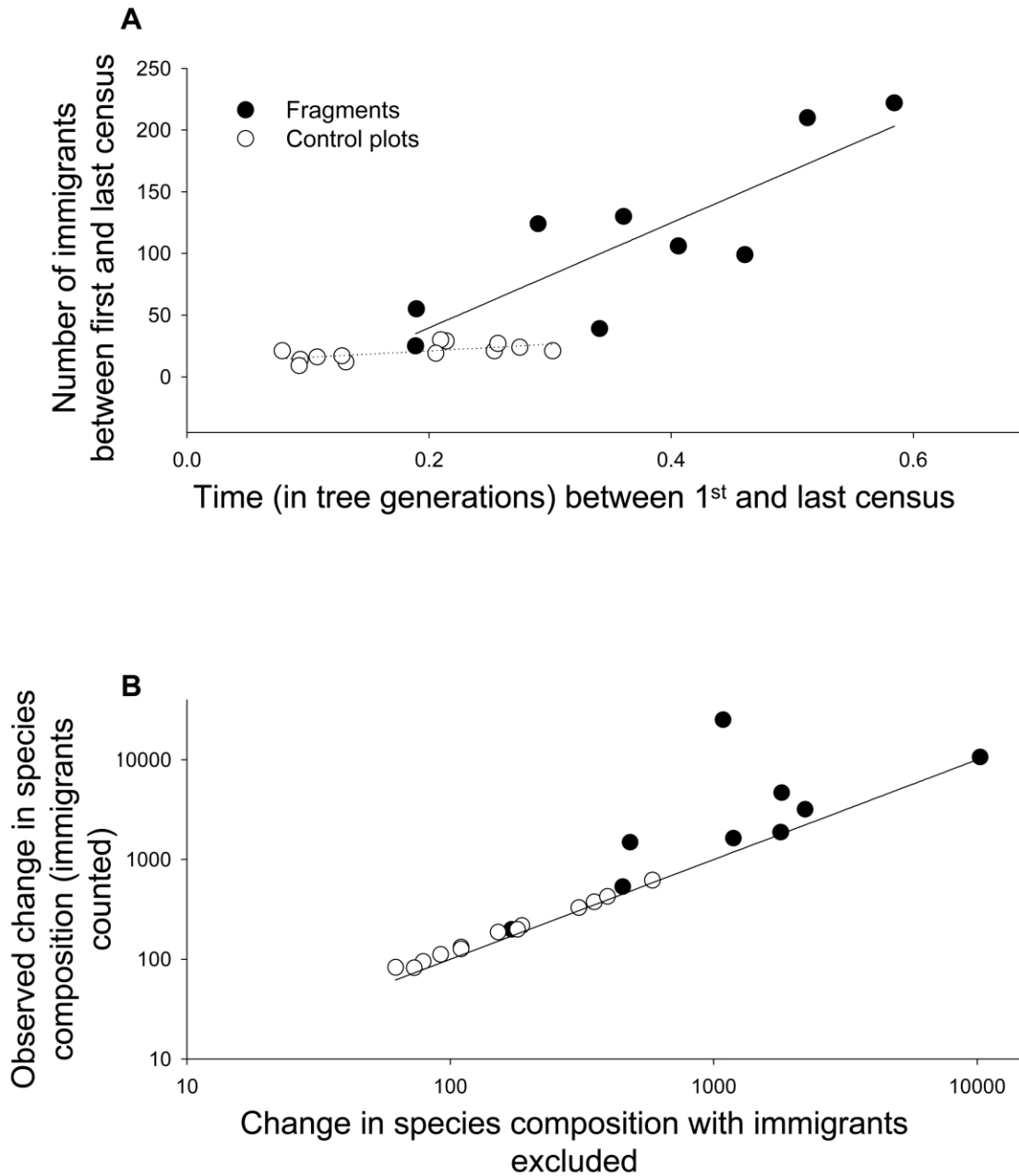


Figure 2: Effect of immigration on fragments (*filled circles*) and control plots (*open circles*). *A*, Number of immigrants as a function of time (*t*). Fragments and control plots have significantly different slopes ($P < .0001$). *B*, Effect of immigrants on the change in species composition (Σ). When immigrants are included, Σ increases on average by 23 in control plots and by 3,333 on fragments.

change 20-fold in a 10-ha fragment (no. 3209; table D4), partly as a result of immigration of many pioneers (table D3).

Decay of Diversity

When immigrants were excluded from the last census, the decline in diversity did not differ significantly from neutral

prediction in any fragment, whereas diversity declined more than predicted in 10 of 13 control plots, and significantly so in two (table D5). Neutral theory predicts that, by increasing the distance to neighboring forest, isolating a fragment reduces immigration to it, leading to a decline in its diversity. Nonetheless, when we included immigrants in our calculations, we found that diversity

Table 3: Pioneer species that invaded or increased in three 1-ha fragments

Species	Fragment and tree mortality (%/year)		
	2107.1 (2.66)	2108.1 (3.83)	3114.1 (3.06)
<i>Guatteria olivacea</i> (Annonaceae)		0 → 13	0 → 1
<i>Cecropia sciadophylla</i> (Moraceae)	0 → 1	0 → 39	0 → 29
<i>Pourouma guianense</i> (Moraceae)		1 → 10	
<i>Pourouma tomentosum</i> (Moraceae)	1 → 11		2 → 7
<i>Pourouma velutina</i> (Moraceae)	0 → 6		
<i>Croton lanjourensis</i> (Euphorb)		1 → 24	
<i>Mabea angularis</i> (Euphorbiaceae)	1 → 10	0 → 15	
<i>Inga heterophylla</i> (Leguminosae)	0 → 8	1 → 12	
<i>Inga paraense</i>		3 → 12	
<i>Inga pezizifera</i>	0 → 2	0 → 10	
<i>Bellucia dichotoma</i>	1 → 20		0 → 1
<i>Miconia burchellii</i>	0 → 13	0 → 27	0 → 1

Note: Arrows indicate the change in density (no./ha) of each species between the first (prefragmentation) and final censuses.

increased in four of our nine fragments (table D5). If immigrants are included, diversity should increase in about half of the control plots; in fact, diversity declined in 10 of the 13 control plots and significantly so in one.

Discussion

In a neutral world such as that envisioned by Hubbell (2001), species richness in isolated communities should gradually erode over time, with rare species disappearing via random demographic processes, much as rare alleles are lost stochastically in isolated populations via genetic drift. The expected rate of species loss in a habitat fragment is a function of the population sizes of its constituent species and their mortality rate, which is assumed to be constant among species and in all places. Over time, most forest fragments should become increasingly dominated by the species that were originally most abundant (Hubbell 2001).

In applying neutral theory to fragmented tree communities in Amazonia, we encountered two obvious departures from the idealized conditions postulated by Hubbell. First, tree mortality rates are not constant but are sharply elevated in fragments (Laurance et al. 1997, 1998b, 2000). This accelerated mortality increased local extinction

rates and the pace of change in species composition. When we used the actual mortality rate for each fragment (rather than the typical rate in intact forest) to generate our neutral predictions, we found that the theory accurately predicted the numbers of rare species (singletons and doubletons) that disappeared in the initial 1–2 decades after fragmentation (fig. 3; table D2). The theory also predicted, albeit less accurately, the total number of local extinctions from each fragment or control plot, given its Fisher's α , total number of trees, mortality rate, and time since the initial census (table D3). Thus, when modified to incorporate actual mortality rates, neutral theory was reasonably effective in predicting the pace of species loss.

In contrast, species composition often changed significantly more rapidly in forest fragments than predicted by neutral theory (fig. 3; table D4), even when predictions were based on the actual, elevated mortality rates in fragments. Habitat fragmentation alters the ecology of Amazonian forests in many ways, especially via increased light, desiccation stress, canopy disturbance, and biotic changes associated with the abrupt, artificial boundaries of forest fragments (Laurance et al. 2002). Different tree species vary greatly in their capacity to tolerate such changes (e.g., Metzger 2000; Wright et al. 2003), and the net result is rapid shifts in tree community composition, with light-loving pioneers often increasing dramatically at the expense of old-growth tree species (Laurance et al. 1998a, 2006). Hence, a fundamental tenet of neutral theory—that species are equivalent ecologically—is clearly violated, and the efficacy of the theory for predicting compositional changes in fragments appears limited.

A second way that our study area departed from the conditions hypothesized by Hubbell (2001) for fragmented systems is that, despite being physically isolated from other primary forest, our fragments were probably not entirely isolated functionally. Seed dispersers and pollinators of some rain forest trees, such as certain birds, bats, and insects, can traverse the matrix of cattle pastures and young regrowth that surrounds our fragments (Gascon et al. 1999; Laurance et al. 2002) and may thereby move propagules and pollen among sites. A subset of tropical tree species may be dispersed among fragments by wind (cf. Bacles et al. 2006). Forest fragments also probably received a substantial seed rain from pioneer and generalist trees that often proliferate in the surrounding matrix (Laurance et al. 2006; Nascimento et al. 2006). The net result is that, for a portion of all tree species, populations in fragments are not fully isolated demographically or genetically (Aldrich and Hamrick 1998; Dick et al. 2003; Bacles et al. 2006).

When we excluded species that had immigrated into our plots, species composition in control plots usually changed more slowly than predicted by neutral theory and

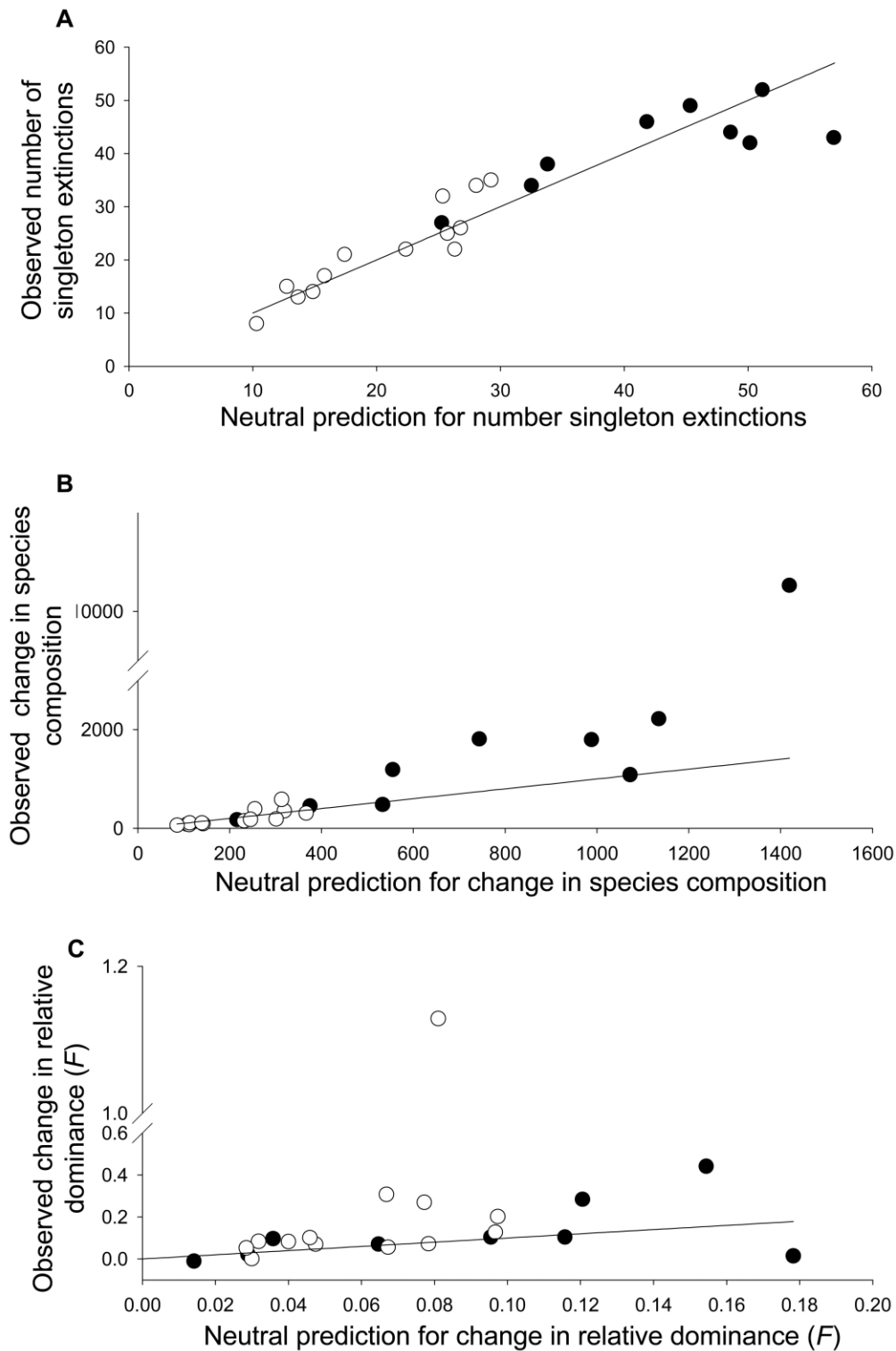


Figure 3: Difference between neutral predictions and observed changes when site-specific mortality rates are used and immigrants are excluded. Each point represents a fragment (*filled circles*) or control plot (*open circles*), and the line represents no difference between neutral predictions and observations (1 : 1). *A*, The number of local extinctions of species initially represented by one individual (singletons) is consistent with neutral predictions. *B*, The mean square change in species composition is significantly greater than predicted for fragments (Mann-Whitney U -test, $P < .04$), but not for control plots. *C*, The change in relative dominance (F), with numbers given at 100 times their actual value for simplicity of presentation. Control plots have a greater observed change in F than predicted (Mann-Whitney U -test, $P < .02$), but fragments show no significant difference.

significantly so in nearly half of the plots (table D4). This may reflect the stabilizing influence of the exchange of migrants of species already on the plot with its surroundings or the stabilizing density-dependent forces that promote local coexistence of different tree species (cf. Clark and McLachlan 2003; Wills et al. 2006). When immigrants were included, however, species composition changed two to six times faster than predicted in several fragments, but it was faster than predicted in only two control plots. Striking compositional changes in fragments were partially the result of elevated immigration of disturbance-adapted pioneer species (fig. 2; table 3).

As a result of a pronounced immigration of new species, local tree diversity rose significantly in three of our nine fragments (table D5). In contrast, tree diversity declined in forest fragments isolated by man-made reservoirs in Panama and Venezuela (Leigh et al. 1993; Terborgh et al. 2006). In Panama, fragmentation led to increased tree mortality on small islets in Lake Gatun (Leigh et al. 1993), much as we observed in Amazonian forest fragments. However, isolation by water virtually halted immigration to the islets, whereas in Amazonia, isolation by mosaics of pasture and young regrowth increased immigration by pioneers and did not entirely prevent immigration by other forest species. Notably, large differences between fragments and control plots in terms of the number of pioneer immigrants are inconsistent with the assumptions of neutral theory, which posits that species-level differences in dispersal ability do not occur and that different forest environments (e.g., the young regrowth surrounding fragments) should not favor a different species composition than does primary forest.

In sum, based on data from a large-scale study of Amazonian forest fragmentation, the neutral theory accurately predicted the number of local extinctions from fragments and intact forest control plots. The theory also correctly predicted that fragments and control plots with higher mortality experience increased local extinction and faster changes in diversity and species composition. However, the rate of change in species composition varied far more among fragments and control plots than is predicted by the theory. Moreover, even when immigrants were excluded and increased mortality controlled for, fragmentation still accelerated the rate of change in species composition substantially beyond that predicted, implying that different tree species have very different responses to environmental change. This conclusion accords with other evidence suggesting that ecological and life-history differences among tree species are both pervasive and important in allowing them to coexist (Chave et al. 2002; Leigh et al. 2004b; Wills et al. 2006).

In intact forests, tree species may be close enough to equilibrium—with recruitment balancing mortality on av-

erage—that their dynamics are nearly neutral in the short term, as Hubbell (2001) and Chave (2004) have suggested. Neutral theory, however, fails to predict many impacts of forest fragmentation because it fails to recognize the underlying differences among species, as evidenced by much faster compositional changes in fragments than predicted by the theory. In our study area, responses of different tree species to fragmentation are strongly influenced by their growth rates, seed-dispersal mechanisms, and tolerance of matrix habitats and disturbed forest edges (Laurance et al. 2006). These characteristics all affect the capacity of species to immigrate into, and persist in, forest fragments.

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