

# The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications‡

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## Summary

Six islands, each less than a hectare in area, were isolated in about 1913 from the mainland of central Panamá by the rising waters of Gatun Lake. By 1980, the diversity of trees on all but one of these islands was far lower than on mainland plots of comparable size. A restricted subset of tree species has spread on these islands, notably *Protium panamense*, *Scheelea zonensis*, *Oenocarpus panamanus* and *Swartzia simplex*. We constructed a null model to predict how chance would change tree diversity and the similarity of tree species compositions of different islands, assuming that each mature tree has equal chances of dying and/or reproducing, regardless of its species. This model cannot account for the diminished diversity of the changes in vegetation on these islands: some factors must be favoring a particular set of tree species.

Two factors, exposure to wind and absence of mammals, seem needed to bring about the vegetation changes observed on these small islands. Their vegetation shows many signs of wind damage and of adaptation to resist wind, reflecting its exposure to dry season winds and storm winds sweeping across the lake from the west. Their most common tree species appear to have spread because mammals rarely visit these small and isolated islands. Seed of these common species are normally much eaten by mammals and do not need burial by mammals to escape insect attack.

A thorough grasp of plant–animal interactions is needed to understand the events that have taken place on these islands. Identifying those 'keystone animals' essential for maintaining plant diversity is a necessary element of reserve design and forest management in the tropics.

*Keywords:* diversity; habitat fragmentation; forests; plant–animal interactions; reserve design; null models

## Introduction

The enormous diversity of tropical trees is one of the great mysteries of biology. A plethora of possible explanations, some stressing biotic interactions, some not, have been suggested for this

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diversity. Each explanation seems to have evoked a plausible opposite (Leigh, 1990a). Resolving this confusion is essential. Our ignorance of what mechanisms preserve species diversity can render a reserve program utterly useless. Understanding what factors promote the coexistence of species is crucial for those seeking to maintain species diversity in small reserves.

By destroying intervening habitats, people often isolate tracts from formerly intact, natural communities (Diamond, 1984). Isolation can prevent or drastically reduce immigration into such a tract, but populations in the tract still fluctuate, and sometimes disappear, in response to environmental variation. The number of species in such a tract accordingly tends to decline after isolation. In small tracts, species diversity can drop markedly within a human lifetime. What can we learn about the factors which maintain tree diversity from the rate at which species disappear from newly isolated tracts of different sizes, or the order in which they do so?

A first step towards an answer is to construct a model of the decline in diversity on isolated tracts, based on Hubbell's (1979) null hypothesis that a tree's prospects of mortality or reproduction are not affected by its species. This model ignores those biotic interactions and environmental variations which affect species differentially. To be specific, we will model the changes in diversity of trees on isolated plots of forest, and changes in similarity or 'codominance' of tree species composition between pairs of isolated plots. We will use this model to judge whether the decline of tree diversity on islands in central Panamá, isolated about 1913 by the rising waters of Gatun Lake, and the similarity in their current tree species compositions, could have occurred by chance. We will then consider what the match – or the discrepancy – between observed facts and our null model's predictions suggests about the factors which maintain the diversity of tropical trees.

Diversity presupposes opportunities for at least transient coexistence. Does the stability of tropical environments promote tree diversity (Leigh, 1990b)? If so, do stabler tropical environments allow specialization of different species to different microhabitats with less risk of extinction (Ashton, 1989), or do stable tropical environments allow herbivore populations to build up, unhindered by winter or overly severe dry seasons, to the point where 'pest pressure' on more common species makes room for the rare (Gillett, 1962; Janzen, 1970; Connell, 1971)? Or, on the other hand, does environmental variability promote coexistence, by allowing different species a reproductive advantage in different years (Chesson and Warner, 1981), or by providing a range of sizes of tree fall gap for different species to specialize to (Strong, 1977; Putz, 1984)? Will the null model, as Hubbell (1979) first appeared to hope, suggest that none of these elaborate hypotheses was necessary, or will it serve as the lie that shows us the truth, by helping us choose among these contradictory explanations?

## **The model**

### *The questions*

Our null model must answer the following three questions: if only chance is involved.

- (i) How quickly does the tree diversity on small plots of known size decline when they are isolated from a larger forest of known diversity and species composition?
- (ii) How similar will the species compositions of two such islands be after a given amount of time?
- (iii) How rapidly does the species composition on an island change over a tree's lifetime?

### *The assumptions*

We can predict that the expected value of the 'codominance' (see below) between the species compositions of two isolated plots remains unchanged without recourse to detailed modelling.

To predict the effects of chance on the decay of diversity, or the changes in species composition, of an isolated island, requires, however, a specific model and a thicket of auxiliary assumptions. To calculate the decay of an isolated island's tree diversity and the degree of change in its species composition, we employ Moran's model of a multi-allelic locus in a haploid population (Moran, 1962; Karlin and McGregor, 1962), letting each allele represent a different species. We consider the neutral case where all alleles, that is to say, all tree species, are equally fit and mutually replaceable. To be specific, we assume that

- (i) Plot  $j$  has a constant number  $N_j$  of mature trees.
- (ii) Trees on this plot die one by one, averaging one death every  $1/N_j$  time units, where time is measured in tree generations. Thus, if the tree death rate is 3.3% per year, and a tree generation is 30 years, one tree dies every year on a plot with 30 trees, and one tree dies every month on a plot with 360 trees.
- (iii) Each death removes a mature tree randomly chosen from those alive on the plot just beforehand.
- (iv) Each dead tree is replaced by the young of a tree chosen at random from among the mature trees living on this plot just before the tree being replaced died. This young tree is assumed to mature immediately after the tree it replaces dies.

These assumptions seem very restrictive. Yet the results are nearly the same for any model where (a) all mature trees have identical prospects of death or reproduction, regardless of their species, (b) dispersal within an island is at random, with no immigration from other islands, and (c) only a small proportion of an island's trees die in any one year, and episodes of death happen regularly enough so that death rates per capita of mature trees on each island, averaged over two or more tree generations, are essentially the same for all islands.

Thus, if  $D$  trees die every  $D/N$  tree generations, rather than one by one, the model's results are essentially the same, so long as  $D$  is far smaller than  $N$  (Appendix A). Our model's independence of such details as whether trees die one by one, or several at a time, should not surprise anyone who has seen the same diffusion equation serve to approximate population genetics models in which individuals die one by one, and those in which successive generations are entirely distinct (Moran, 1962; Karlin and McGregor, 1964).

Small violations of these assumptions should make little difference over the span of a few generations (although they might be decisive in the longer term). Assuming that a tree's seeds are dispersed at random over its island is unlikely to be seriously misleading on islands 100 m in diameter or less, such as ours. The time it takes for successful seedlings to mature can allow the number of species of mature tree on an island to increase, when seedlings of a dead parent mature. Again, in Gatun Lake, some seeds must travel from one island to another. Immigrant seeds, however, must be vastly outnumbered by the seeds which are produced on the island. Neither delayed maturity nor immigration should greatly influence our measures of diversity or similarity if we choose them so that each species contributes in proportion to its abundance.

Nevertheless, our model embodies one dangerous carrier assumption. For the sake of a very necessary symmetry, we assume, not only that there is no meaningful difference between species, but also that there is no meaningful difference between mature trees of the same species. In fact, a larger tree must have more chance than a smaller conspecific of providing the seedling to replace a tree that has just died. Size differences within a species (like any other factor increasing variance among individuals in reproductive output, Crow and Kimura, 1970) has the same effect as lowering the number of individuals within that species. To bracket the error, we predict changes in tree diversity as if trees attained maturity (and an equal share in plot reproduction) at 10 cm diameter at breast height (dbh, diameter 1.3 m above the ground), and as if trees attained reproductive maturity only at 20 cm dbh.

*Definitions*

To answer our questions, we must define two quantities. First, we measure the relative dominance in species composition on plot  $j$  at time  $t$  by  $F_j(t)$ , the probability that, at time  $t$ , two individuals sampled randomly with replacement from plot  $j$  are the same species. Then

$$F_j(t) = \sum_{i=1}^n x_{ij}^2(t)/N_j^2 \quad (1)$$

where  $n$  is the total number of tree species on our system of plots at the time of fragmentation,  $N_j$  is the total number of mature trees on plot  $j$  (assumed constant), and  $x_{ij}(t)$  is the number of (mature) trees of species  $i$  on plot  $j$  at time  $t$ .  $F_j$  is the inverse of Simpson's (1949) measure of diversity.

Second, we measure the relative codominance in the species composition of plots  $j$  and  $k$  at time  $t$  by the probability  $F_{jk}(t)$  that two trees chosen randomly at time  $t$ , one from plot  $j$  and one from plot  $k$ , are of the same species. Then

$$F_{jk}(t) = \sum_{i=1}^n x_{ij}(t) x_{ik}(t)/N_j N_k \quad (2)$$

The codominance  $F_{jk}(t)$  of the plots  $j$  and  $k$  depends both on the species compositions of the two plots and on the relative dominance of each. If, for example, the species compositions of plots  $j$  and  $k$  are identical, so that  $x_{ij} = x_{ik}(N_j/N_k)$ , then  $F_{jk} = F_j = F_k$ . One measure of the similarity in species composition on these two plots (Horn, 1966) is  $2F_{jk}/(F_j + F_k)$ : this is 1 when their species compositions are identical, and 0 when they share no species in common.

*Predictions of the null hypothesis*

**A. Codominance.** However one may choose to model it, Hubbell's null hypothesis implies that, on an isolated island, the expected value of  $x_{ij}(t)$  is  $x_{ij}(0)$ , since, 'on the average', each tree just exactly replaces itself. Hubbell's hypothesis also implies that changes in the species compositions of different isolated islands reflect independent chance events. The expected value of  $x_{ij}(t)x_{ik}(t)$  is therefore  $x_{ij}(0)x_{ik}(0)$  for every species  $i$ , at all times  $t$ . The expected value of  $F_{jk}(t)$  is therefore  $F_{jk}(0)$ .

$F_{jk}$  nevertheless varies with time. Hubbell's hypothesis implies that, in the absence of speciation, each plot will eventually be taken over by a single species. The probability that species  $i$  eventually takes over plot  $j$  is  $x_{ij}(0)/N_j$  (Kimura, 1962, p.717; Feller, 1968, p.399); the probability that species  $i$  eventually takes over both plot  $j$  and plot  $k$  is  $x_{ij}(0)x_{ik}(0)/N_j N_k$ . The probability that plots  $j$  and  $k$  will eventually be taken over by the same species is thus  $F_{jk}(0)$ . With this probability, codominance between islands  $j$  and  $k$  will eventually be one; otherwise, it will be 0. Only the average codominance over many pairs of plots should remain roughly unchanged.

**B. The decline of diversity.** To learn how fast diversity on isolated plots declines, let  $F_j^*(t, s)$  be the expected value of  $F_j(t)$ , given its value at an earlier time  $s$ . To calculate  $F_j^*(t, s)$  in terms of  $F_j(s)$ , we first calculate the expected change over a minute time interval  $dt$  in  $G_j(t)$ , the probability that two *different* trees sampled from island  $j$  at time  $t$  are of the same species.  $1 - G_j(t)$ , the probability that the two sampled trees are of different species, is

$$\sum_{i \neq k}^n x_{ij}(t) x_{kj}(t) / N_j(N_j - 1) = [1 - F_j(t)] / (1 - 1/N_j) \quad (3)$$

Since  $t$  is measured in tree generations, the expected lifetime of a tree in these time units is 1. Thus, for the exponential life table implied by the Moran model, the probability that a given, preassigned, tree dies during the time interval  $dt$  is  $dt$ . Thus, the probability that one of our two sampled trees dies between times  $t$  and  $t + dt$  is  $2dt$ . In this case the probability is  $1/N_j$  that the replacement of the dead tree is the young of the survivor, and therefore belongs to the same species, while the probability is  $(1 - 1/N_j)[1 - G_j(t)]$  that the dead tree is replaced by the young of a tree of a species different from that of the survivor. If we let  $G_j^*(t + dt, t)$  be the expected value of  $G_j(t + dt)$ , given its value at time  $t$ , then

$$1 - G_j^*(t + dt, t) = [1 - G_j(t)] [1 - 2dt + 2dt(1 - 1/N_j)] \quad (4)$$

$$= [1 - G_j(t)] [1 - 2dt/N_j] \quad (5)$$

Since  $1 - G_j$  is a constant multiple of  $1 - F_j$ , it follows that

$$1 - F_j^*(t + dt, t) = (1 - 2dt/N_j) [1 - F_j(t)] \quad (6)$$

and

$$F_j^*(t, 0) = 1 - [1 - F_j(0)] \exp - 2t/N_j \quad (7)$$

Equation (7) gives the expected change in the value of  $F_j$  with time as predicted by our null model. Crow and Kimura (1970) derive a related equation at the bottom of their page 101.

*C. Changes in species composition on an isolated plot.* Consider an island with  $N$  mature trees, where successive generations of mature trees are distinct, and where the parents of each generation are chosen by sampling  $N$  individuals with replacement from the trees of the generation previous (the number of times a parent is sampled is the number of offspring it contributes to the next generation). Here, the probability that a given tree has  $n$  mature offspring is

$$(1 - 1/N)^{N-n} (1/N^n) N!/(n!(N-n)!),$$

which is nearly  $e^{-1/n!}$  if  $n \ll N$  (Fisher, 1958, p. 82). The mean and variance in the number of offspring of individual trees are both 1. If, in generation  $t$ , species  $i$  is represented by  $n_i(t)$  mature trees, the probability distribution of the species composition of generation  $t + 1$  is obtained by supposing that the number of trees of each species  $i$  in generation  $t + 1$  independently follows a Poisson distribution with mean  $n_i(t)$ , subject to the condition that the total number of trees is  $N$  (Karlin and McGregor, 1964; Bulmer, 1965, p. 139). To estimate the probability that the differences observed in species composition between generations  $t$  and  $t + 1$  could occur by chance, lump rare species into categories  $z$  such that the number  $n_z(t)$  in each category  $z$  at generation  $t$  totals at least 5. If the number  $n_z(t + 1)$  of trees of category  $z$  in generation  $t + 1$  is normally distributed with mean and variance  $n_z(t)$ , we may conclude with Bulmer (1965) that

$$\sum_z [n_z(t + 1) - n_z(t)]^2/n_z(t),$$

being the sum of squares of independent normal variates, each with unit variance, follows a  $\chi^2$  distribution with one less degree of freedom than there are categories  $z$  at generation  $t$ .

In the Moran model, the probability that a tree has  $n$  mature offspring in its lifetime is roughly  $1/2^{n+1}$ : if one expands the 'generating function'  $f(s) = 1/(2 - s)$  in the power series

$$f(s) = p_0 + p_1s + p_2s^2 + \dots,$$

then the coefficient  $p_n$  of  $s^n$  in this expression is the probability that it has exactly  $n$  mature off-

spring (Leigh, 1990c, p. 173). Here, the variance in number of offspring per parent is 2: this is most easily found by evaluating  $f''(s) - f'(s) + [f'(s)]^2$  for  $s = 1$  (Harris, 1963, p. 6; Leigh, 1990c, p. 172). More generally, if a tree has a probability  $dt$  of dying and an equal probability of producing a single successful young during the time interval  $dt$ , then a tree alive now has probability  $p_n(t) = t^{n-1}/(1+t)^{n+1}$  of having exactly  $n$  ( $n \geq 1$ ) living descendants (which may include itself)  $t$  generations later (Feller, 1968, p. 480, problem 11). This probability is the coefficient of  $s^n$  in the generating function

$$f_t(s) = [t - s(t-1)]/[t + 1 - ts]$$

(Leigh, 1990c, p. 173). When  $t = 1$ ,  $f_t(s) = 1/(2-s)$ : the probability distribution of a tree's lifetime number of mature offspring is just the distribution of a tree's number of descendants (including itself) alive one tree-generation later. The variance in the number of a tree's descendants alive  $t$  generations later is  $2t$ . Let us again lump rare species into categories such that the number  $n_z(t_0)$  of trees in each category  $z$  at time  $t_0$  is at least 5. Then the joint distribution of trees over these categories at time  $t_0 + t$  is nearly that obtained if the distributions of the descendants alive at time  $t_0 + t$  of each tree living at time  $t_0$  are independent, each with generating function  $f_t(s)$ , subject to the condition that the total number of trees is exactly  $N$ . For a given value of  $n_z(t_0)$ , the variance in  $n_z(t_0 + t)$  is  $2tn_z(t_0)$ . If  $[n_z(t_0 + t) - n_z(t_0)]^2/2tn_z(t_0)$  approximates the square of a normally distributed variate with unit variance for all categories  $z$ , then the distribution of

$$\sum_z [n_z(t_0 + t) - n_z(t_0)]^2/2tn_z(t_0)$$

is approximately  $\chi^2$  with one less degree of freedom than there are categories  $z$ . For  $n \leq 12$ , the probability distribution generated by  $[f_t(s)]^5$  for  $t = 1/2$ , is very similar to that generated by a Poisson distribution with mean 5 (Appendix B).

#### *The null hypothesis and reality*

What might we learn by testing this null model? Consider first the codominance  $F_{jk}$  between different plots. If the vegetation of our mainland plots is representative of the vegetation of the islands before they were isolated from each other, the null hypothesis implies that the average codominance between the vegetation of different small islands should be equal to the average codominance among mainland plots. Unexpectedly high codominance among the small islands would occur if island conditions were favoring a few species at the expense of the rest. Study of the favored species could tell us whether they have responded to changes in their physical environment, or whether they were 'released' by the absence of herbivorous mammals from these small islands. Unexpectedly low codominance among the small islands would occur either if their vegetation was originally more heterogeneous than our mainland plots suggest, or if isolation has allowed vegetation to differentiate more completely in response to differences between islands.

Now let us consider changes in tree diversity on these islands. Diversity would decline unexpectedly rapidly if some factor (perhaps seed-eaters or seedling-browsers?) which maintains tree diversity on the mainland is much reduced on the islands, or if some factor which decreases diversity on the islands (such as destructive winds sweeping across the lake) is much less effective on the mainland. On the other hand, diversity on these islands would decline unexpectedly slowly when a tree is nonrandomly likely to be replaced by a conspecific, as if tree species were adapted to particular, permanent, features of their microhabitats.

## Testing the model: methods

### *The plots*

To assess the changes in the tree species compositions of small islands after their isolation from the mainland in about 1913, we compared (Fig. 1, Table 1) the tree species composition of seven islands in Gatun Lake, with between 57 and 3000 trees apiece 10 cm dbh and over, with those of four plots with 250 trees apiece along the shores of the mainland Bohio Peninsula, and a hectare each of young and old forest from the Forest Dynamics Plot on Barro Colorado Island (Foster and Hubbell, 1990). The Bohio Peninsula is a steep ridge, covered by secondary forest of various ages. Before the creation of Gatun Lake, physical conditions on this peninsula were presumably very similar to those on the hilltops that became islands, and we assume that their vegetations were likewise similar.

As we were interested in natural mortality and regeneration on isolated plots, we sought islands which were continuously forested since they were isolated from the mainland. To this end, we chose islands surrounded by the stumps of drowned trees. Aerial photographs, some taken as early as 1927 (see, for example, Chapman, 1929, plate facing p. 4), indicate that these islands have indeed been forested ever since their isolation. A portion of the Bohio Peninsula was cleared and planted in bananas in the 1920's. Disease destroyed the plants, and the plantations were abandoned in the early 1930's (Oscar Kidd, personal communication). Our mainland plots on this peninsula, however, suffered little human disruption after 1913.

### *The data*

In 1980, we counted and identified all trees and palms over 10 cm dbh on each of the six smallest islands, and 500 such trees on the largest island, Almendras (called Dipteryx Island in Putz *et al.*, 1990), using plant names from Croat (1978). For each mainland plot on the Bohio Peninsula, we enumerated 250 trees and palms in a 20 m wide strip along the lake edge. Between November 1988 and December 1989, we recensused the small islands, and measured the length and width of each small island in order to estimate its area. We also censused a tract on the northern end of Almendras Island, the end most exposed both to dry season winds and rainy season storms, to assess the effect on island vegetation of exposure to these winds. Individuals with multiple stems were included if their total basal area (total stem cross-sectional area 1.3 m above ground) exceeded the basal area of a single stem with a dbh of 10 cm.

### *Analyses of the data*

*Making predictions from the null model.* We assume that when the islands were first isolated, their vegetation was similar to that of the Bohio mainland plots.

We tested the null model's prediction that preventing migration between plots should not affect the average codominance among plots by comparing the average codominance among the six smallest islands with the average codominance among the Bohio mainland plots, both for trees over 10 cm dbh, and trees over 20 cm dbh. As the islands were scattered over a wider area than the Bohio plots, one might expect the average codominance among islands to be lower, at the time of isolation, than the average codominance among the Bohio mainland plots.

To predict the decline in diversity (increase in relative dominance) of trees on the small islands since the time of isolation, we need to know the time, in tree generations, since these islands were isolated, and the initial relative dominance of these islands' vegetation.

To assess the duration of a tree generation, we recall Foster and Brokaw's (1982) estimate that the expected lifetime of a canopy tree on the windward edge of the old forest on Barro

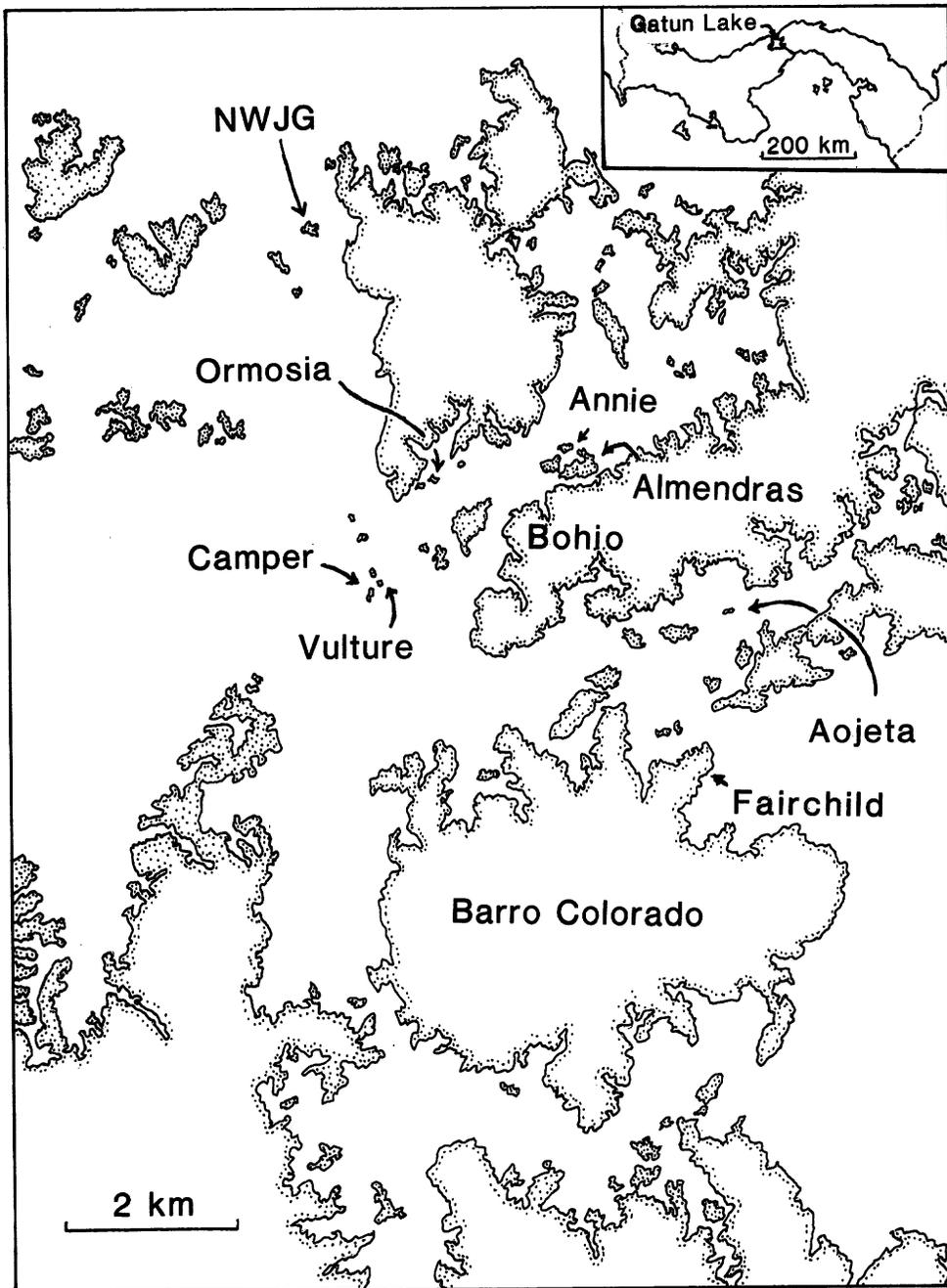


Figure 1. Map of Gatun Lake showing the locations of the islands studied. The inset indicates the position of Gatun Lake within the Republic of Panama. Our islands correspond to the numbers on Fig 1 of Adler and Seamon (1991) as follows: Almendras = 13, Annie = 15, NWJG = 37, Ormosia = 10, Aojeta = 7, Camper = 20, Vulture = 19. Their estimates of the areas of small islands, obtained by planimetry from maps, are larger than ours, which were obtained by direct measurement of length and width of the islands concerned.

Table 1. Numbers of trees, basal areas, and numbers of tree species on islands in Gatun Lake and selected mainland plots nearby (1980 censuses except where otherwise indicated).

Site	Number of trees with dbh $\geq$		Basal area (m <sup>2</sup> ) of trees with dbh $\geq$		Number of species with dbh $\geq$	
	10 cm	20 cm	10 cm	20 cm	10 cm	20 cm
Vulture Island	59	32	2.93	2.59	10	7
Camper Island	125	58	5.87	4.89	19	14
Aojeta Bay Island	128	64	6.99	5.84	26	17
Ormosia Island	135	61	8.53	7.38	32	24
NWJG Island	340	102	10.61	7.02	25	17
Annie Island	399	152	15.89	12.08	37	30
Almendras Island						
Central plot (1980)						
Total	498	181	33.38	28.54	77	48
Leeward half	249	83	17.50	15.03	53	32
Windward half	249	98	15.88	13.51	56	35
Windward tip (1989)						
Sheltered part	133	53	8.24	7.07	37	28
Exposed part	118	34	4.37	3.08	23	18
Bohio Mainland						
Leeward Trees	500	201	30.22	25.31	70	55
Leeward Plot 1						
Total	250	105	15.57	13.18	44	34
1st half-plot	125	50	8.12	6.98	35	24
1st 1/4-plot	62	28	4.61	4.06	21	16
Leeward Plot 2						
Total	250	96	14.65	12.13	54	37
1st half-plot	125	49	10.41	9.18	36	25
1st 1/4-plot	62	23	5.70	5.13	25	17
Windward Trees	500	205	43.87	39.33	58	42
Windward Plot 1	250	102	18.76	16.51	44	33
Windward Plot 2	250	103	25.11	22.82	45	32
Barro Colorado Island Forest Dynamics Plot, 1985 census						
Ha 6.4 (young)	584	181	24.76	18.25	76	47
Ha 7.0 (mature)	402	149	42.29	38.43	90	53

Colorado Island's central plateau is 60 years. To be conservative, we assume that on our islands, a tree generation lasts 30 years.

Even when trees of each species are distributed at random over a large plot  $A$ , so that sampling the  $N$  trees on a small subplot  $a$  is equivalent to sampling  $N$  trees (without replacement) at random from the large plot  $A$ , the relative dominance  $F_a$  among subplot  $a$ 's trees is not an unbiased estimate of relative dominance on  $A$  (Rosenzweig and Abramsky, 1985). It would be an overestimate, for the same reason that relative dominance among the sample of each new generation from the gametes of its parents is higher, on the average, than among the individuals of the parental generation (Crow and Kimura, 1970, p. 101). The effect is more pronounced when the plot is spatially heterogeneous. We therefore infer the initial relative dominance  $F_i(0)$

among the trees on island  $j$  from the relative dominance (in 1980) among trees on a mainland plot of comparable size. To facilitate comparison with islands of different sizes, we divided each mainland plot into two half-plots – the first 125, and the last 125, trees counted on the plot – and also into four quarter-plots of 62 trees each (the last two trees from each full plot were omitted from the quarter-plots). Vulture Island was compared with mainland quarter-plots, Ormosia, Aojeta Bay and Camper Islands with mainland half-plots, and NWJG and Annie Islands with mainland full (250-tree) plots.

We predicted the relative dominance  $F_j$  among trees over 10 cm dbh, and among trees over 20 cm dbh, on island  $j$ , in 1980 and 1989, assuming that the island's initial value  $F_j(0)$  was the average of the 1980  $F_j$ 's for Bohio mainland plots of comparable size. To predict the 1980 values for  $F_j$ , we assumed that the number of trees over 10, and over 20 cm dbh, on island  $j$  remained unchanged since 1910. To predict the 1989 values of  $F_j$ , we set the number of trees on island  $j$  equal to the smaller of the two numbers counted in 1980 and 1989.

To see if diversity on the small islands was continuing to decline or if, instead, there were signs that it was approaching an equilibrium level, we compared the relative dominance in 1980 and in 1989 of the vegetation on each small island.

To learn whether the chance replacement of dead trees by young of the survivors could cause the changes observed on our islands between 1980 and 1989, we applied a  $\chi^2$  test to the differences between species abundances observed in 1989 and the abundances expected had each species on the island the same proportion of trees in 1989 as in 1980. Species were arranged in alphabetical order, lumping rare species (and species likely to be mistaken for each other) to make expected abundances of all categories five or more. Were successive generations distinct, as in the models of Fisher (1930) and Wright (1931), the  $\chi^2$  would allow us to assess the chance that one generation arose simply by randomly sampling, with replacement, parents from the generation previous. In the Moran model, the  $\chi^2$  test, as described in textbooks, allows us to assess the probability that the change in species composition over half a tree generation could occur by chance. As only one third of a tree generation elapsed between 1980 and 1989, the  $\chi^2$  thus overestimates the probability that chance could account for the changes observed.

*Interpreting possible outcomes of the tests.* Have the destructive winds that now sweep across Gatun Lake affected the vegetation on our islands? There are two ways to test for such effects. The first is to compare the average codominance  $F^*_{W,j}$  between windward mainland Bohio plots and the six smallest islands, with the average codominance  $F^*_{L,j}$  between leeward Bohio plots and the six smallest islands. If the codominance between the small islands and the windward plots is significantly higher, this suggests that dry season winds have significantly altered the species composition of the vegetation on the small islands. The second test is to compare the average codominance  $F^*_{AW,j}$  between the windward tip of Almendras Island and the six small islands with the average codominance  $F^*_{LW,j}$  between these islands and the plot in the center of Almendras: if the former is higher, it would appear that the winds have helped to shape the vegetation of these small islands.

## Results

### *Codominance among island plots*

The average codominance among the tree species compositions of the six smallest islands is much higher than the average codominance among mainland full plots (Tables 2, 3). In 1980, the codominance among trees  $\geq 10$  cm dbh, and among trees  $\geq 20$  cm dbh, averaged over all pairs of mainland full plots, was  $F^*_{jk(10)} = 0.0458 \pm 0.0070$  and  $F^*_{jk(20)} = 0.0303 \pm 0.0029$  (mean  $\pm$

Table 2. Relative dominance for each plot, and relative codominance for all pairs of plots, 1980 census,  $F_{jk(10)}$  above,  $F_{jk(20)}$  below.

	Mainland plots				7-ha Island			Small islands				
	Bo L1	Bo L2	Bo W1	Bo W2	Alm L	Alm W	Annie	NWJG	Ormosia	Aojeta	Camper	Vulture
Bohio	0.0684											
Leeward 1	0.0522											
Bohio	0.0762	0.1083										
Leeward 2	0.0295	0.0508										
Bohio	0.0371	0.0441	0.0534									
Windw 1	0.0402	0.0317	0.0581									
Bohio	0.0387	0.0457	0.0331	0.0502								
Windw 2	0.0288	0.0201	0.0315	0.0612								
Almendras	0.0625	0.0825	0.0343	0.0462	0.0801							
Ctr Leew	0.0258	0.0300	0.0266	0.0317	0.0533							
Almendras	0.0271	0.0316	0.0243	0.0288	0.0379	0.0377						
Ctr Windw	0.0134	0.0122	0.0205	0.0197	0.0284	0.0494						
Annie	0.0265	0.0261	0.0362	0.0674	0.0640	0.0620	0.4197					
Island	0.0189	0.0105	0.0372	0.0637	0.0594	0.0383	0.2984					
NWJG	0.0143	0.0098	0.0288	0.0565	0.0489	0.0542	0.3901	0.4148				
Island	0.0177	0.0127	0.0266	0.0573	0.0455	0.0253	0.2151	0.2397				
Ormosia	0.0068	0.0073	0.0080	0.0122	0.0124	0.0121	0.0513	0.1126	0.1176			
Island	0.0136	0.0186	0.0153	0.0216	0.0198	0.0075	0.0334	0.0672	0.0766			
Aojeta	0.0227	0.0222	0.0229	0.0411	0.0411	0.0390	0.2146	0.2069	0.0389	0.1514		
Island	0.0217	0.0223	0.0256	0.0426	0.0416	0.0206	0.1482	0.1411	0.0441	0.1479		
Camper	0.0226	0.0194	0.0265	0.0502	0.0468	0.0452	0.2790	0.2645	0.0462	0.1813	0.2456	
Island	0.0343	0.0377	0.0311	0.0544	0.0555	0.0215	0.1268	0.1479	0.0777	0.1684	0.2794	
Vulture	0.0409	0.0448	0.0178	0.0327	0.0451	0.0255	0.0319	0.0338	0.0284	0.0924	0.1341	0.2427
Island	0.0452	0.0475	0.0334	0.0628	0.0633	0.0201	0.1016	0.1544	0.0963	0.1914	0.3583	0.4961

Table 3. Relative dominance among trees of selected island plots, and relative codominance of trees of different island plots. Upper figure is for trees  $\geq 10$ , lower for trees  $\geq 20$  cm dbh. Data from 1989 census.

	Almendr. shelt.	Windward exposed	Annie	NWJG	Aojeta	Ormosia	Camper	Vulture
Windward Almendras Sheltered	0.1036 0.0583							
Windward Almendras Exposed	0.0780 0.0447	0.2540 0.1540						
Annie Island	0.0675 0.0403	0.2924 0.1636	0.3765 0.2282					
NW Juan Gallegos Island	0.0670 0.0406	0.3260 0.1918	0.4130 0.2406	0.4791 0.3082				
Aojeta Island	0.0564 0.0631	0.2121 0.1316	0.2648 0.1914	0.2912 0.2069	0.2213 0.2053			
Ormosia Island	0.0189 0.0283	0.0808 0.0377	0.0925 0.0591	0.1376 0.0708	0.0755 0.1102	0.1047 0.0708		
Camper Island	0.0501 0.0351	0.1382 0.0565	0.1574 0.1290	0.1698 0.1342	0.1554 0.1847	0.0503 0.0804	0.1510 0.2881	
Vulture Island	0.0423 0.0305	0.0345 0.0033	0.0182 0.1069	0.0132 0.1102	0.0864 0.1980	0.0268 0.1048	0.1533 0.3908	0.2778 0.6187

SEM), respectively. In contrast, the average codominances for all pairs of the six smallest islands were  $F_{jk(10)}^* = 0.1404 \pm 0.0288$  and  $F_{jk(20)}^* = 0.1381 \pm 0.0207$  in 1980, and  $F_{jk(10)}^* = 0.1404 \pm 0.0299$  and  $F_{jk(20)}^* = 0.1545 \pm 0.0228$  in 1989 (Tables 2, 3). The high codominance among the trees of the small islands was due almost entirely to the great abundance on these islands of the tree *Protium panamense* (Burseraceae) and the palm *Scheelea zonensis*.

#### Diversity of trees on the small islands

In both 1980 and 1989, relative dominance of trees over 10 cm dbh, and over 20 cm dbh, is higher – that is, diversity is lower – than predicted on all small islands except Ormosia (Table 4).

On the other hand, between 1980 and 1989 relative dominance *decreased* markedly among trees  $\geq 20$  cm dbh on Annie Island and trees  $\geq 10$  cm dbh on Camper Island. Some islands had more species of trees in 1989 than in 1980. Turnover of rare species was marked on some islands. Vulture lost three species and gained three others. Given the absence of vouchers, some of this ‘turnover’ may reflect calling some of the rarer trees by different names in the two censuses. Other ‘immigrants’ may represent growing saplings whose parents died before 1980. Others, however, like the Mango found on Ormosia in 1989, may have been introduced after the islands were isolated. Is diversity on these small islands beginning to stabilize?

The small islands suffered extraordinary changes in species composition between 1980 and

Table 4. Decay of diversity on small islands.

	$F_i$ (1910) (assumed)	$F_i$ (1980) Pre.	Obs.	$F_i$ (1989) Pre.	Obs.	Sign of $F_i$ (1989) - $F_i$ (1980)	$p$ (change, 1980-1989)
Vulture, trees $\geq$ 10 cm	0.0938 $\pm$ 0.0343	0.1627	0.2427	0.1728	0.2778	+	0.5 < $p$ < 0.75
trees $\geq$ 20 cm	0.0919 $\pm$ 0.0184	0.2151	0.4961	0.2528	0.6187	+++	not calculated
Camper, trees $\geq$ 10 cm	0.0788 $\pm$ 0.0266	0.1126	0.2456	0.1280	0.1510	--	$p$ < 0.005
trees $\geq$ 20 cm	0.0674 $\pm$ 0.0120	0.1395	0.2794	0.1852	0.2881	(+)	$p$ > 0.975
Aojeta, trees $\geq$ 10 cm	0.0788 $\pm$ 0.0266	0.1188	0.1514	0.1247	0.2213	++	0.25 < $p$ < 0.5
trees $\geq$ 20 cm	0.0674 $\pm$ 0.0120	0.1330	0.1479	0.1526	0.2053	++	0.25 < $p$ < 0.5
Ormosia, trees $\geq$ 10 cm	0.0788 $\pm$ 0.0266	0.1101	0.1176	0.1165	0.1047	-	0.1 < $p$ < 0.25
trees $\geq$ 20 cm	0.0674 $\pm$ 0.0120	0.1361	0.0766	0.1606	0.0708	(-)	0.1 < $p$ < 0.25
NWJG, trees $\geq$ 10 cm	0.0701 $\pm$ 0.0267	0.0828	0.4148	0.0844	0.4791	++	$p$ < 0.005
trees $\geq$ 20 cm	0.0556 $\pm$ 0.0049	0.0978	0.2397	0.1031	0.3082	++	0.01 < $p$ < 0.025
Annie, trees $\geq$ 10 cm	0.0701 $\pm$ 0.0267	0.0809	0.4197	0.0823	0.3765	-	$p$ < 0.005
trees $\geq$ 20 cm	0.0556 $\pm$ 0.0049	0.0834	0.2984	0.0897	0.2282	--	0.1 < $p$ < 0.25

Comparison of predicted with observed relative dominance  $F$  for each island  $j$  in 1980 and 1989, and change in  $F$ , and significance of change in species composition, during this period. +++ denotes a value of  $F_j$  (1989) -  $F_j$  (1980) of over 0.1, ++, a value of this difference lying between 0.05 and 0.1, +, a value between 0.01 and 0.05, and (-), a positive value less than 0.01; analogous conventions apply to the minus signs.  $p$  represents the probability that, if the species compositions of 1980 and 1989 on a given island represented successive distinct generations, a change of equivalent  $\chi^2$  value would have arisen by chance. The initial (1910) relative dominance is assumed to be the average relative dominance in mainland plots of comparable size. Thus, Vulture is assumed to have had, in 1910, the average of the relative dominances of the mainland quarter-plots (with 62 trees  $\geq$  10 cm dbh); Camper, Aojeta and Ormosia are assumed to have started with the average relative dominance of the mainland half-plots (with 125 trees  $\geq$  10 cm dbh apiece), and NWJG and Annie are assumed to have started with the average dominance of the mainland full plots (with 250 trees  $\geq$  10 cm dbh apiece).

1989. In four of eleven tests, changes were significantly greater than expected from the random sampling of one generation's trees from the generation previous; in nine of these eleven tests, changes were greater than the median change expected from such random sampling (Table 4). Yet the censuses were separated by only nine years. These changes reflect, not the chances of which species happened to supply the young replacing a newly dead tree, but the differential responses of different tree species to a violently changed environment.

#### *The effects of wind and isolation on island vegetation*

The tree species compositions of windward mainland plots were significantly more similar on the average, to those of the six smallest islands, than were those of the leeward mainland plots, as reflected by codominance among trees  $\geq 10$  cm dbh, and among trees  $\geq 20$  cm dbh (Table 2). In 1980, the average codominances of windward mainland plots W with islands  $j$  were  $F_{W,j(10)}^* = 0.0334 \pm 0.0052$  and  $F_{W,j(20)}^* = 0.0393 \pm 0.0048$  (mean  $\pm$  SEM) for trees  $\geq 10$ , and  $\geq 20$  cm dbh, respectively, while the average codominances of leeward mainland plots L with islands  $j$  were  $F_{L,j(10)}^* = 0.0220 \pm 0.0035$  and  $F_{L,j(20)}^* = 0.0251 \pm 0.0037$ . The greater similarity of island vegetation to that of the windward mainland plots suggests that a common factor is influencing both, although it is acting much more strongly on the islands.

The greater similarity of island vegetation to that of the windward mainland plots – relatively narrow strips along the windward shore of the Bohio peninsula – may reflect exposure to dry season winds, and/or to storms sweeping across the lake from the west. The central plot on the 7-ha Almendras Island is completely surrounded by forest and, indeed, vegetation on the windward half of this plot is rather less similar to that of the small islands than is vegetation on the plot's leeward half. In 1980, the codominances of the windward half of Almendras's central plot with the small islands were  $F_{AW,j(10)}^* = 0.0397 \pm 0.0184$  and  $F_{AW,j(20)}^* = 0.0222 \pm 0.0099$ , while the codominances of its leeward half with the small islands were  $F_{AL,j(10)}^* = 0.0431 \pm 0.0169$  and  $F_{AL,j(20)}^* = 0.0475 \pm 0.0159$ , respectively.

The vegetation on the exposed part of the windward tip of Almendras Island is very like that of the small islands (Table 3). In 1989, the average codominance between Almendras's exposed windward tip and the small islands was  $F_{EW,j(10)}^* = 0.1807 \pm 0.0521$  (mean  $\pm$  SEM) for trees  $\geq 10$  cm dbh and  $F_{EW,j(20)}^* = 0.0974 \pm 0.0338$  for trees  $\geq 20$  cm dbh. The relative dominance of trees  $\geq 10$  cm dbh on the exposed part of Almendras's windward tip,  $F_{EW(10)}$ , was 0.2540, which is close to the average, 0.2684, for the six small islands. The relative dominance of trees  $\geq 20$  cm dbh on the exposed section of the windward tip of Almendras was decidedly lower than on any of the small islands except Ormosia, but higher than on any mainland quarter-plot (for the least diverse of our 16 mainland quarter-plots of 62 trees  $\geq 10$  cm dbh apiece,  $F_{(20)} = 0.1384$ , compared with  $F_{EW(20)} = 0.1540$  for trees  $\geq 20$  cm dbh on the exposed section of Almendras's windward tip). Trees on the sheltered part of the windward tip of Almendras, like those in the center of Almendras, were as diverse as those on comparably sized mainland plots.

Unlike the trees on the Bohio mainland plots, the exposed trees on the windward tip of Almendras are on an island. Unlike the trees in the center of Almendras Island, trees on the exposed part of Almendras's windward tip are directly exposed to the wind. Both factors seem to be required to reduce diversity and to enhance the dominance of species like *Protium panamense* and *Scheelea zonensis*.

## Discussion

### *The causes of change in vegetation of the small islands*

What circumstances favored the spread of a restricted set of tree species on the small islands of

Table 5. Abundance of selected tree species on islands and mainland plots.

Species	Bohio Leeward 1980		Bohio Windward 1980		Almendras Center 1980		Almendras Sheltered 1989		Tip Exposed 1989		Annie Island 1980 1989		NWJG Island 1980 1989		Ormosia Island 1980 1989		Aojeta Island 1980 1989		Camper Island 1980 1989		Vulture Island 1980 1989		
	1980	1989	1980	1989	1980	1989	1989	1989	1989	1989	1980	1989	1980	1989	1980	1989	1980	1989	1980	1989	1980	1989	
<i>Astrocaryum standleyanum</i>	50	22	16	2	2	2	2	2	2	17	16	3	3	3	2	3	2	3	2	0	0	0	0
	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gustavia superba</i>	115	43	76	35	5	5	5	5	5	17	10	0	0	0	0	0	0	3	2	1	2	4	3
	11	6	5	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Luehea seemannii</i>	18	12	14	2	1	1	1	1	1	2	2	1	1	1	1	0	0	0	0	3	1	4	2
	16	9	11	2	1	1	1	1	1	2	2	1	1	1	0	0	0	0	0	3	1	4	2
<i>Oenocarpus panamanus</i>	0	0	3	0	5	5	5	5	5	3	13	76	82	42	34	3	2	3	2	0	0	0	0
	0	0	0	0	3	3	3	3	3	2	3	27	29	8	4	2	1	0	0	0	0	0	0
<i>Protium panamense</i>	8	40	33	13	56	56	56	56	56	256	282	204	314	9	17	41	43	52	23	1	0	1	0
	2	12	15	4	12	12	12	12	12	80	64	36	58	1	4	15	19	7	5	1	0	1	0
<i>Scheelea zonenis</i>	10	11	7	1	0	0	0	0	0	18	19	21	17	8	8	17	14	29	19	22	21	22	21
	10	11	7	1	0	0	0	0	0	18	19	21	17	7	7	17	14	29	19	22	21	22	21
<i>Spondias</i> spp.	24	35	7	4	3	3	3	3	3	2	1	0	1	5	5	1	1	1	0	1	0	1	1
	21	26	1	3	1	1	1	1	1	2	1	0	1	5	5	1	1	1	0	1	0	1	1
<i>Swartzia simplex</i>	26	11	24	9	10	10	10	10	10	0	2	0	0	1	2	14	10	15	20	17	22	17	22
	10	2	4	3	2	2	2	2	2	0	1	0	0	0	0	6	5	3	4	0	0	0	0
Totals,	500	500	498	133	118	118	118	118	118	399	470	340	470	135	126	128	103	125	96	59	59	59	59
all species	201	205	181	54	34	34	34	34	34	152	143	102	117	61	50	64	55	58	39	32	32	32	27

The date is the consensus year.  
 In each row, the upper number is the number of trees  $\geq 10$  cm, and the lower, the number of trees  $\geq 20$  cm, dbh.

Gatun Lake, even those which have been forested since well before they were isolated from the mainland? Why is tree diversity on these islands so very low? Why were the relative abundances of species still shifting so greatly even between 1980 and 1989 (Tables 2-4)? These changes cannot be accounted for by the vagaries of randomly sampling one generation's trees to choose the parents for the next. Isolation from the mainland, and direct exposure to dry season winds from the north and storm winds from the west, both seem to play an essential role in these changes. How might these factors work?

*Seedling regeneration.* Conditions on the small islands have apparently favored such species as *Protium panamense*, *Scheelea zonensis*, *Oenocarpus panamanus* and *Swartzia simplex* (Table 5). These species appear to be replacing themselves. On 9 April 1981, *Protium* and *Oenocarpus* seedlings were vastly more abundant, and *Swartzia* seedlings slightly more common, on Annie and Ormosia Islands than on two plots in the young forest of Barro Colorado Island (BCI). *Scheelea* seedlings, however, were more common in the BCI plots (Table 6).

To learn whether island conditions favored *Protium* regeneration, Herre planted seeds in young forest of Barro Colorado and on three small islands, including NWJG, on 3-7 October 1981. Four weeks later, germination and survival rates were highest on BCI, while NWJG had

Table 6. Numbers of seedlings of selected species on 50 m<sup>2</sup> plots on small islands and on Barro Colorado Island.

Plot	Numbers of seedlings per plot			
	<i>Protium</i>	<i>Oenocarpus</i>	<i>Scheelea</i>	<i>Swartzia</i>
Annie Island				
Plot 1	65	13	0	1
Plot 2	84	0	0	1
Plot 3	57	0	1	0
Plot 4	72	1	0	0
Plot 5	137	4	0	1
Ormosia Island				
Plot 1	9	81	4	0
Plot 2	5	19	0	3
Plot 3	13	71	2	1
Plot 4	145	144	0	18
Plot 5	85	33	0	0
Barro Colorado/Barbour Plot				
Plot 1	0	0	4	0
Plot 2	4	2	1	2
Plot 3	2	1	0	1
Plot 4	0	0	2	0
Plot 5	1	1	2	0
Barro Colorado/Knight-Lang Plot				
Plot 1	0	1	9	0
Plot 2	1	1	4	2
Plot 3	1	0	5	0
Plot 4	2	0	2	0
Plot 5	4	2	5	0

Samples taken 9 April 1981

Table 7. Survival of *Protium* seedlings at various sites.

Site	No. of seeds planted Oct 3-7	Number of living seedlings on			
		Nov 1-2	Jan 30-31	Mar 11-15	Mar 24
Barbour Pt, BCI	200	127	59	20	10
Ormosia Island	100	33	10	7	6
Annie Island	100	39	29	14	10
NWJG Island	68	1	1	1	1

Experiment began 3 October 1981 and ended 24 March 1982.

only one live seedling: in all, 73 of BCI's 200 seedlings, and 195 of the islands' 268 seedlings, died by early November (Table 7). During this period, BCI's death rate was significantly lower ( $\chi^2 = 61.5$ , 1 d.f.,  $p < 0.005$ ). By late March, 1982, however, the tables had turned: 117 of BCI's 127 early November seedlings, and 56 of the islands' remaining 73 seedlings, died by late March. During this period, BCI's death rate was significantly *higher* ( $\chi^2 = 9.43$ , 1 d.f.,  $p < 0.005$ ), as if island conditions favored established *Protium* seedlings.

*Effects of wind.* The forest on these small islands forms an irregular canopy 10-25 m tall, and is distinctly shorter than the forest on our mainland plots, that on the central plot of the 7-ha Almendro Island, or the old forest on the 1500 ha Barro Colorado Island. The dynamism of the forest on these islands – the great changes in number of trees, and sometimes in basal area, between censuses (Table 8) – suggests severe and continuing disruption by windstorms. These islands support an extraordinary number of trees per hectare (Table 9) – a characteristic shared by nutrient-poor forest and forest subject to frequent hurricanes (Stocker and Unwin, 1989), as

Table 8. Changes in the vegetation of small islands between 1980 and 1989.

Island	Area, ha (1 × w, m)	No. of trees		BA of trees		No. of species		
		≥10 cm	≥20 cm	≥10 cm	≥20 cm	≥10 cm	≥20 cm	
Vulture	80	0.095	59	32	2.93	2.59	10	6
	89	45×27	59	27	2.36	2.01	10	5
Camper	80	0.13	125	58	5.87	4.89	19	14
	89	100×15	96	39	4.63	3.74	22	11
Aojeta	80	0.16	128	64	6.99	5.94	26	17
	89	73×28	103	55	6.58	5.84	22	15
Ormosia	80	0.16	135	61	8.53	7.38	32	24
	89	60×35	126	50	7.81	6.63	33	24
NWJG	80	0.41	340	102	10.61	7.02	25	17
	89	95×55	470	117	12.84	7.46	29	19
Annie	80	0.63	399	152	15.89	12.08	37	30
	89	125×64	470	143	16.62	11.59	45	30

Table 9. Structural comparison of vegetation on small islands with that of selected mainland plots.

Island or plot		Number of trees per ha		Basal area per ha for trees $\geq 10$ cm dbh
		$\geq 10$ cm	$\geq 20$ cm	
Vulture	80	621	337	30.8
	89	621	284	24.8
Camper	80	962	446	37.6
	89	738	300	28.8
Aojeta	80	800	400	43.7
	89	644	344	41.1
Ormosia	80	844	381	53.3
	89	788	313	48.8
NWJG	80	829	249	25.9
	89	1169	291	31.3
Annie	80	633	241	25.2
	89	746	227	26.4
FDP, BCI (Ave.)		414	154	27.2
	(Ha 6.4)	584	181	24.8
	(Ha 7.0)	402	149	42.2
Tjibodas 2400 m		1516	n.d.	56.9

Figures for FDP are figures for the 1985 census of the 50 ha Forest Dynamics Plot on Barro Colorado Island, which consists primarily of mature forest. Hectare 6.4 is a hectare of secondary forest dominated by *Gustavia superba*, and hectare 7.0 is the hectare on that plot with the highest basal area. These figures were provided by Richard Condit on behalf of S. P. Hubbell and R. B. Foster. The figures for Tjibodas are figures from Yamada (1976) for forest on Mt Pangrango, Java: this forest, at 2400 m altitude, is 20 m tall.

well as stunted wind-blown forests of tropical mountaintops (Leigh, 1990d) and second-growth forest. Shaking by wind favors increasing trunk thickness at the expense of height growth (Holbrook and Putz, 1989). The need to develop stout, stiff trunks to resist the wind plays a major role in stunting montane forest (Lawton, 1982, 1984). Like montane forest, and unlike second-growth and nutrient-starved forest, the forest on most of these islands is characterized by a basal area (total cross-sectional area of tree trunks at breast height) per hectare which is considerably higher than the average for old forest on Barro Colorado Island (Table 9).

Thanks perhaps to storms opening up the canopy, the understory of our small islands struck us as much more clogged and tangled in 1989 than in 1980. On Vulture, the understory, open in 1980, has become a tangle of lianas and bamboo thickets. Ormosia was somewhat obstructed by fallen *Oenocarpus* stems, etc. while, on Annie, *Aechmea* has spread and, since 1986, the climbing bamboo *Chusquea* has created a tangle on the southwest side of the island.

*Oenocarpus panamanus*, an abundant palm on several of our small islands (Table 5), is also common in 'blowdowns' on Barro Colorado Island (De Steven, 1986: she calls this palm *O.*

*mapora*). *Protium panamense*, which has nearly 'taken over' some of our islands (Table 5) is, on Barro Colorado, a tree of second growth (Croat, 1978). Species which are unusually common on the small islands, e.g., *Protium panamense*, *Oenocarpus panamanus*, *Scheelea zonensis* and *Coccoloba manzanillensis*, are also common on the windward tip of Barro Colorado's Fairchild Peninsula (Putz *et al.*, 1990).

While netting birds on Almendro Island during the dry season, Wright noticed that while he was in the *Protium* forest on the windward tip of Almendro, the dry season trade wind whipped incessantly at his T-shirt, but when he entered the taller, more diverse forest nearer the center of that island, he found the air of the understory nearly still.

Finally, Ormosia, the one island where diversity was not lower than expected (Table 4), is the island best protected from the wind.

In sum, it appears that both storms and dry season trade winds influence the tree species composition of the small islands in Gatun Lake. How do windward mainland shores escape these effects?

*Animals.* Adler and Seamon (1991) surveyed all our islands for mammals. They caught mammals only on Almendras, which has a resident population of spiny rats, *Proechimys semispinosus*. Mammals sometimes reach these islands, but cause much less damage to fruits and seeds than on the mainland (Table 10). Has the absence of mammals affected the vegetation of our islands?

Although agoutis eat *Protium* seeds and *Oenocarpus* seedlings (P.-M. Forget, personal communication), and many mammals, especially agoutis, squirrels and peccaries, devour *Scheelea* seeds (Smythe *et al.*, 1982; Glanz *et al.*, 1982), the connection between mammal seed-eating and tree diversity is far from clear. De Steven and Putz (1984) and Sork (1987) report that survival of *Dipteryx panamensis* (Leguminosae) and *Gustavia superba* (Lecythidaceae) seedlings is manyfold higher on the mainland Gigante Peninsula than on the nearby Barro Colorado Island. Both papers relate this increased seedling survival to reduced mammal populations on the mainland, where hunting was then far more prevalent than on the better protected Barro Colorado Island (Glanz, 1991). Neither paper mentioned any connection between mammalian seed predation and tree diversity.

Mammals, however, do other things besides eating seeds. On Barro Colorado, only those seeds of the spiny palm *Astrocaryum standleyanum* which are buried by agoutis have any real prospect of eventually becoming mature palms, largely because, when an agouti peels the flesh from an *Astrocaryum* fruit and buries the seed, it protects that seed from bruchid weevils (Smythe, 1989). On this same island, seeds of *Virola surinamensis* (Myristicaceae) must be buried by agoutis to escape predation by *Conotrachelus* weevils (Forget and Milleron, 1991). Burial by agoutis may be essential to, or at least may greatly enhance, the survival prospects of seeds of many other species (P.-M. Forget, 1991 and personal communication). Bruchid beetles

Table 10. Proportions of fallen *Scheelea* seeds at different sites damaged by different factors.

Source of damage	Ormosia	Annie	NWJG	Bohio Pen.	BCI
Bruchid beetles	75.6%	78.2%	45.4%	18.6%	2.1%
Mammals	2.9%	12.4%	17.4%	65.3%	92.5%
Rotted endosperm	20.0%	7.6%	14.7%	11.7%	3.0%
Viable	1.5%	1.8%	22.5%	4.4%	2.4%

These data are based on fallen fruits collected in the first quarter of 1980. BCI is Barro Colorado Island.

devastate *Scheelea* seed crops both on Barro Colorado (Wright, 1983, 1990) and on our small islands (Table 10). Insects may be effective pests on these small islands: even the 0.1 ha Vulture Island supports a nest of leaf-cutter ants.

Do the trees that have spread on our small islands have seeds which do not require burial by mammals to escape insect attack? The seeds of *Protium*, *Oenocarpus* and *Swartzia* are not infested by specialized insect pests (S. J. Wright, personal observation, for *Protium* and *Oenocarpus*; P.-M. Forget, personal communication, for all three species). Moreover, on BCI, *Scheelea*'s bruchids cease activity well before *Scheelea* cease dropping fruit (Wright, 1990), halting their depredations just when mammal consumption of *Scheelea* seeds is most intense, thanks to the worsening shortage of other fruit in the forest (P.-M. Forget, personal communication). Do late-season *Scheelea* seeds on the small islands also escape bruchid attack? Have this 'immunity' to insect predators shared by *Protium*, *Oenocarpus* and *Swartzia*, and a 'safe season' for *Scheelea* seeds, allowed these species to dominate our small, mammal-free islands?

On the other hand, tree diversity is normal at the center of Almendras Island, even though vertebrate activity is much reduced there, and fruit such as *Sorocea*, which on Barro Colorado is normally eaten when ripe, on Almendras is left to rot on the branch (S. J. Wright, personal observation). It would appear that the reduced diversity we have observed on small islands requires destruction of pre-existing forest by storms, disturbance by dry season trade winds blowing upon its windward margins, and the absence of mammals, which favors a certain subset of species in the ensuing regeneration.

#### *Comparison with the minimum critical size of ecosystems project*

The most obvious parallel to our recently isolated islets in Gatun Lake are the even more recently isolated forest reserves, created north of Manaus, Brazil, by the conversion of the surrounding forest into pasture under the aegis of the INPA/WWF Minimum Critical Size of Ecosystems project (Lovejoy *et al.*, 1983, 1984, 1986). So far, this project has isolated reserves of 1, 10 and 100 ha apiece. None of these reserves was isolated earlier than 1980, so records of only the first few years after isolation are available. Nonetheless, changes promise to be even more drastic in these reserves than on our islands.

In Brazil, soon after a 10 ha reserve is isolated, daytime relative humidity is markedly lower, and daytime temperature in the shade up to 4.5 °C higher near its edge than 100 m into the forest. These changes are occasioned by hot dry winds blowing in from the surrounding clearing, as well as by increased isolation at the edge of the reserve. As second growth progressively screens the edges of the reserve, these differences become less marked, but they have already left their impact on the vegetation at the edge of the reserve (Lovejoy *et al.*, 1984; also see Kapos, 1989).

Tree mortality is higher in 1 and 10 ha reserves (2.6% per year for trees over 10 cm dbh during the first 2 years after isolation) than in continuous forest (1.5% per year: Lovejoy *et al.*, 1986). Most of these trees died standing. Many trees on the windward edge of the narrow buffer zone surrounding a 10 ha reserve, however, were blown down (Lovejoy *et al.*, 1984).

The Manaus plots were isolated in far more traumatic fashion than were our islands. The pasture surrounding the Manaus reserves is burned on occasion, scorching the neighboring forest (Lovejoy *et al.*, 1984) while Gatun Lake surrounds our islands with an even-temperated 'water bath'. The Manaus reserves contained 'virgin' forest (Lovejoy *et al.*, 1984, 1986), while our islands included second growth of various ages, perhaps less sensitive to 'edge effects'. Finally, between fires, 'weed trees' sprang up in the pastures, flooding parts of the Manaus reserves with invasive colonists (Lovejoy *et al.*, 1983, 1984), while Gatun Lake protected our islands from such

invasive weeds. Perhaps for these reasons, Lovejoy *et al.* (1984) expected their 10 ha reserves to be largely second growth ten years after isolation, while the forest in the interior of our 7 ha island appears quite normal.

On the other hand, the same shrubby second growth that flooded the Manaus plots with invasive weeds also allowed mammals to immigrate more easily than they could over water or open pasture (Lovejoy *et al.*, 1984).

In sum, the Brazil plots illustrate the impact on isolated 'woodlots' of nearby fires and hot, dry winds from the surrounding pastures. Physical factors apparently affected our small islands more slowly.

### Concluding remarks

The changes in the vegetation of these small islands since their isolation from the mainland reflect a complex interplay of factors. Leigh had expected this study to vindicate triumphantly Janzen's (1970) thesis that seed-eaters were essential to maintaining the diversity of tropical trees. In fact, these changes reflect an interaction between the destructive effect of wind, which enhances tree mortality, and isolation from the mainland, which reduces mammal activity, thus influencing the species composition of the regrowth. Neither factor could exert such an influence without the other's help.

Why did *Protium panamense* and its allies spread on our small islands? Only Pierre-Michel Forget's studies of seed dispersal on Barro Colorado Island allow us to essay an answer. He found that some seeds survive only if dispersed from their parents via birds or bats *and* protected against subsequent insect attack through burial by agoutis. Species whose seeds are not susceptible to insect attack figure largely in the regeneration on these islands. Are agoutis 'keystone animals' for neotropical tree diversity?

Other studies also single out the enormously important role mammals (and birds) play in maintaining tree diversity in tropical forest. In the Côte d'Ivoire, elephants are primary, and often exclusive, seed dispersers for many tree species (Emmons, 1989). Where elephants have disappeared, some of these species are not regenerating (Alexandre, 1978). At the Estacion de Biología Las Tuxtlas, a 700 ha rainforest fragment near Vera Cruz, Mexico, populations of larger mammals have declined precipitously during the last 20 years. Seedling density is twice as high there, and diversity of understory plants three times lower, than in the far more extensive Lacandon rainforest in Chiapas, which has a slightly higher diversity of canopy trees, but a normal complement of mammals. The understory at Las Tuxtlas lacked any sign of vertebrate browsing, while signs of such browsing were obvious in the Lacandon Forest (Dirzo and Miranda, 1990, 1991).

Karr, 1990) of tropical forests. We have hardly begun to elucidate the variety of ways plant populations depend on animals for their very persistence. Yet, to design reserves or manage forests, we must identify and safeguard the 'keystone animals' for plant diversity, as well as the 'keystone plants' (Terborgh, 1986) for animal populations. The functioning of rainforests depends on innumerable intricate interrelationships (Corner, 1964; Jacobs, 1988; Leigh, 1991), which bring great joy to the naturalists who study them. Tropical foresters and reserve designers cannot afford to ignore them.

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## References

- Adler, G. H. and Seamon, J. O. (1991) Distribution and abundance of a tropical rodent, the spiny rat, on islands in Panama. *J. Trop. Ecol.* **7**, 349–60.
- Alexandre, D.-Y. (1978) Le rôle disséminateur des éléphants en forêt de Taï, Côte-d'Ivoire. *La Terre et la Vie* **32**, 47–72.
- Ashton, P. S. (1989) Dipterocarp reproductive biology. *Tropical Rain Forest Ecosystems, Biogeographical and Ecological Studies* (H. Leith and M. J. A. Werger, eds), pp. 219–40. Elsevier, Amsterdam, Holland.
- Bulmer, M. G. (1965) *Principles of Statistics*. Oliver & Boyd, Edinburgh, UK.
- Chapman, F. M. (1929) *My Tropical Air Castle*. D. Appleton & Co., New York, USA.
- Chesson, P. L. and Warner, R. R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* **117**, 923–43.
- Connell, J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (P. J. den Boer and G. R. Gradwell, eds), pp. 298–312. Centre for Agricultural Publication and Documentation, Wageningen, The Netherlands.
- Corner, E. J. H. (1964) *The Life of Plants*. World Publishing, Cleveland, OH, USA.
- Croat, T. B. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, CA, USA.
- Crow, J. F. and Kimura, M. (1970) *An Introduction to Population Genetics Theory*. Harper and Row, New York, USA.
- De Steven, D. (1986) Comparative demography of a clonal palm (*Oenocarpus mapora* ssp. *mapora*) in Panama. *Principes* **30**, 100–4.
- De Steven, D. and Putz, F. E. (1984) Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* **43**, 209–16.
- Diamond, J. M. (1984) 'Normal' extinctions of isolated populations. *Extinctions* (M. H. Nitecki, ed.), pp. 191–246. University of Chicago Press, Chicago, USA.
- Dirzo, R. and Miranda, A. (1990) Contemporary neotropical defaunation and forest structure, function and diversity – a sequel to John Terborgh. *Conserv. Biol.* **4**, 444–7.
- Dirzo, R. and Miranda, A. (1991) Altered patterns of herbivory and diversity in the forest understory: a case study of the possible consequences of contemporary defaunation. *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson, eds), pp. 273–87. Wiley, New York, USA.
- Emmons, L. H. (1989) Tropical rain forests: why they have so many species and how we may lose this biodiversity without cutting a single tree. *Orion*, Summer, 8–14.

- Feller, W. (1968) *An Introduction to Probability Theory and its Applications*, Vol. 1, 3rd Edn. Wiley, New York, USA.
- Fisher, R. A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford, UK.
- Fisher, R. A. (1958) *The Genetical Theory of Natural Selection*, 2nd Edn. Dover Press, New York, USA.
- Forget, P.-M. (1991) Comparative recruitment patterns of two non-pioneer canopy tree species in French Guiana. *Oecologia* **85**, 434–9.
- Forget, P.-M. and Milleron, T. (1991) Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* **87**, 596–9.
- Foster, R. B. and Brokaw, N. V. L. (1982) Structure and history of the vegetation of Barro Colorado Island. *The Ecology of Tropical Forest* (E. G. Leigh Jr, A. S. Rand, and D. M. Windsor, eds), pp. 67–81. Smithsonian Institution Press, Washington, DC, USA.
- Foster, R. B. and Hubbell, S. P. (1990) Estructura de la vegetación y composición de especies de un lote de cincuenta hectáreas en la isla de Barro Colorado. *Ecología de un Bosque Tropical* (E. G. Leigh Jr, A. S. Rand and D. M. Windsor, eds), pp. 141–51. Smithsonian Tropical Research Institute, Balboa, Panamá.
- Gillett, J. B. (1962) Pest pressure, an underestimated factor in evolution. *Systematics Assn Publ.* **4**, 37–46.
- Glanz, W. E. (1991) Mammalian densities at protected versus hunted sites in central Panama. *Neotropical Wildlife Use and Conservation* (J. G. Robinson and K. H. Redford, eds), pp. 163–73. University of Chicago Press, Chicago, IL, USA.
- Glanz, W. E., Thorington Jr, R. W., Giacalone-Madden, J. and Heaney, L. R. (1982) Seasonal food use and demographic trends in *Sciurus granatensis*. *The Ecology of a Tropical Forest* (E. G. Leigh, Jr., A. S. Rand and D. M. Windsor, eds), pp. 239–52. Smithsonian Institution Press, Washington, DC, USA.
- Harris, T. E. 1963. *The Theory of Branching Processes*. Springer-Verlag, Berlin.
- Holbrook, N. M. and Putz, F. E. (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum). *Am. J. Bot.* **76**, 1740–9.
- Horn, H. S. (1966) Measurement of overlap in comparative ecological studies. *Am. Nat.* **100**, 419–24.
- Hubbell, S. P. (1979) Tree dispersion, abundance and diversity in a tropical dry forest. *Science* **203**, 1299–309.
- Jacobs, M. (1988) *The Tropical Rain Forest*. Springer-Verlag, Berlin.
- Janzen, D. H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–28.
- Kapos, V. (1989) Effects of isolation on the water status of forest patches in the Brazilian Amazon. *J. Trop. Ecol.* **5**, 173–85.
- Karlin, S. and McGregor, J. (1962) On a genetics model of Moran. *Proc. Camb. Phil. Soc.* **58** (part 2), 299–311.
- Karlin, S. and McGregor, J. (1964) Direct product branching processes and related Markov chains. *Proc. Nat. Acad. Sci. USA* **51**, 598–602.
- Karr, J. R. (1990) Biological integrity and the goal of environmental legislation: lessons for conservation biology. *Conserv. Biol.* **4**, 244–50.
- Kimura, M. (1962) On the probability of fixation of mutant genes in a population. *Genetics* **47**, 713–9.
- Lawton, R. O. (1982) Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *Am. J. Bot.* **69**, 1224–30.
- Lawton, R. O. (1984) Ecological constraints on wood density in a tropical montane rain forest. *Am. J. Bot.* **71**, 261–7.
- Leigh Jr, E. G. (1990a) Introducción: ¿por qué hay tantos tipos de árboles tropicales? *Ecología de un Bosque Tropical* (E. G. Leigh, Jr., A. S. Rand and D. M. Windsor, eds), pp. 75–99. Smithsonian Tropical Research Institute, Balboa, Panamá.
- Leigh Jr, E. G. (1990b) Community diversity and environmental stability: a re-examination. *Trends Ecol. Evol.* **5**, 340–4.
- Leigh Jr, E. G. (1990c) Afterword. *The Causes of Evolution* (J. B. S. Haldane), pp. 130–212. Princeton University Press, Princeton, NJ, USA.
- Leigh Jr, E. G. (1990d) Tree shape and leaf arrangement: a quantitative comparison of montane forests,

- with emphasis on Malaysia and South India. *Conservation in Developing Countries: Problems and Prospects* (J. C. Daniel and J. S. Serrao, eds), pp. 119–74. Oxford University Press, Oxford, UK.
- Leigh Jr, E. G. (1991) Genes, bees and ecosystems: the evolution of a common interest among individuals. *Trends Ecol. Evol.* **6**, 257–62.
- Lovejoy, T. E., Bierregaard Jr, R. O., Rankin, J. M. and Schubart, H. O. R. (1983) Ecological dynamics of tropical forest fragments. *Tropical Rain Forest: Ecology and Management* (S. L. Sutton, T. C. Whitmore and A. C. Chadwick, eds), pp. 377–84. Blackwell, Oxford, UK.
- Lovejoy, T. E., Bierregaard Jr, R. O., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown Jr, K. S., Powell, A. H., Powell, G. V. N., Schubart, H. O. R. and Hays, M. B. (1986) Edge and other effects of isolation on Amazon forest fragments. *Conservation Biology: The Science of Scarcity and Diversity* (M. Soulé, ed.), pp. 257–85. Sinauer Associates, Sunderland, MA.
- Lovejoy, T. E., Rankin, J. M., Bierregaard Jr, R. O., Brown Jr, K. S., Emmons, L. H. and Van der Voort, M. E. (1984) Ecosystem decay of Amazon forest remnants. *Extinctions* (M. H. Nitecki, ed.), pp. 295–325. University of Chicago Press, Chicago, USA.
- Moran, P. A. P. (1962) *The Statistical Processes of Evolutionary Theory*. Clarendon Press, Oxford, UK.
- Putz, F. E. (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **65**, 1713–24.
- Putz, F. E., Leigh Jr, E. G., and Wright, S. J. (1990) Solitary confinement in Panama. *Garden Mag.*, March/April, 18–23.
- Rosenzweig, M. L. and Abramsky, Z. (1985) Detecting density-dependent habitat selection. *Am. Nat.* **126**, 405–17.
- Simpson, E. H. (1949) Measurement of diversity. *Nature* **163**, 688.
- Smythe, N. (1989) Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica* **21**, 50–6.
- Smythe, N., Glanz, W. E. and Leigh Jr, E. G. (1982) Population regulation in some terrestrial frugivores. *The Ecology of a Tropical Forest* (E. G. Leigh Jr, A. S. Rand and D. M. Windsor, eds.), pp. 227–38. Smithsonian Institution Press, Washington, DC, USA.
- Sork, V. L. (1987) Effect of predation and light on seedling establishment in *Gustavia superba*. *Ecology* **68**, 1341–50.
- Stocker, G. C. and Unwin, G. L. (1989) The rain forests of northeastern Australia – their environment, evolutionary history and dynamics. *Tropical Rain Forest Ecosystems, Biogeographical and Ecological Studies* (H. Leith and M. J. A. Werger, eds.), pp. 241–59. Elsevier, Amsterdam, Holland.
- Strong Jr, D. R. (1977) Epiphyte loads, treefalls, and perennial forest disruption: a mechanism for maintaining a higher species richness in the tropics without animals. *J. Biogeog.* **4**, 215–8.
- Terborgh, J. (1986) Keystone plant resources in the tropical forest. *Conservation Biology; The Science of Scarcity and Diversity* (M. Soulé, ed.), pp. 330–44. Sinauer Associates, Sunderland, MA, USA.
- Wright, S. (1931) Evolution in Mendelian populations. *Genetics* **16**, 97–159.
- Wright, S. J. (1983) The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent palm. *Ecology* **64**, 1016–21.
- Wright, S. J. (1990) Cumulative satiation of a seed predator over the fruiting season of its host. *Oikos* **58**, 272–6.
- Yamada, I. (1976) Forest ecological studies of the montane forest of Mt Pangrango, West Java II. Stratification and floristic composition of the forest vegetation of the higher part of Mt Pangrango. *South East Asian Studies* **13**, 513–34.

## Appendix A

### *What if trees do not die one at a time?*

Suppose that recurrent disturbance kills  $D$  trees every  $D/N_j$  time units, and that these dead trees can be replaced only by the young of their survivors, as in the model of Hubbell. Let us now calculate  $1 - G_j^*(t + D/N_j, t)$ , where  $G_j(t)$  is the probability that two different trees sampled at random from island  $j$  at time  $t$  are of the same species, and  $G_j(t + D/N_j, t)$  is the expected

value of  $G_j$  at time  $t + D/N_j$  given its value at time  $t$ . We must consider two possibilities. The first possibility is that both trees survive this round of disturbance – in which case the probability they represent different species is unchanged. This outcome has probability

$$\frac{(N_j - D)(N_j - D - 1)}{N_j(N_j - 1)} = \frac{N_j(N_j - 1) - D(2N_j - D - 1)}{N_j(N_j - 1)} \quad (\text{A1})$$

The second possibility is that at least one tree dies. This outcome has probability

$$\frac{D(2N_j - D - 1)}{N_j(N_j - 1)} \quad (\text{A2})$$

If only one tree dies, the probability that it is replaced by the young of the survivor is  $1/(N_j - D)$  whereas, if both trees die, the probability is  $1/(N_j - D)$  that both replacements are descended from the same survivor. In either case, the probability is

$$\left[1 - \frac{1}{N_j - D}\right][1 - G_j(t)] \quad (\text{A3})$$

that at time  $t + D/N_j$ , the two trees are of different species. We thus conclude that  $1 - G_j^*(t + D/N_j, t)$  is

$$\begin{aligned} & [1 - G_j(t)] \left[1 - \left(1 - \left(1 - \frac{1}{N_j - D}\right)\right) \frac{D(2N_j - D - 1)}{N_j(N_j - 1)}\right] \\ & = [1 - G_j(t)] \left[1 - \frac{D(2N_j - D - 1)}{N_j(N_j - 1)(N_j - D)}\right] \end{aligned} \quad (\text{A4})$$

We accordingly conclude that

$$1 - G_j^*\left(t + \frac{D}{N_j}, t\right) = [1 - G_j(t)] \left[1 - \frac{D(2N_j - D - 1)}{N_j(N_j - 1)(N_j - D)}\right] \quad (\text{A5})$$

We may approximate Equation A5 by

$$\frac{d}{dt}[1 - G_j(t)] = \frac{2N_j - D - 1}{(N_j - 1)(N_j - D)}[1 - G_j(t)] \quad (\text{A6})$$

If  $D$  trees die every  $D/N_j$  time units, as in Hubbell's model, but if a tree which just died has the same chance of contributing young to the resulting gaps as a given tree which is still alive, then, if one or both of our pair of trees die, the probability that at time  $t + D/N_j$  both members of our pair have the same parent is  $1/N_j$ , rather than  $1/(N_j - D)$ . In this case,

$$1 - G_j^*\left(t + \frac{D}{N_j}, t\right) = [1 - G_j(t)] \left[1 - \frac{D(2N_j - D - 1)}{N_j^2(N_j - 1)}\right] \quad (\text{A7})$$

If, in Equation A7, we set  $D = 1$ , we obtain

$$1 - G_j^*\left(t + \frac{1}{N_j}\right) = [1 - G_j(t)] \left[1 - \frac{2}{N_j^2}\right] \quad (\text{A8})$$

which we may approximate by

$$\frac{d}{dt}[1 - G_j(t)] = \frac{2}{N_j} [1 - G_j(t)] \quad (\text{A9})$$

Equation A9 is Equation 5 of the text, which follows from the Moran model. Equations A6 and A7 tell us that if  $D$  is far smaller than  $N_j$ , Equation A9 is very nearly true.

## Appendix B

### *The $\chi^2$ distribution and the Moran model*

Can we use the  $\chi^2$  distribution to assess the degree of divergence between the tree species composition at generation  $t$  and that at generation  $t + 0.5$  under the Moran model? Under the Moran model, the generating function for the number of descendants at time  $t + 0.5$  of a tree alive at time  $t$  (including the original tree, if it is still alive) is approximately

$$f_{1/2}(s) = \frac{\frac{1}{2} + \frac{s}{2}}{\frac{3}{2} - \frac{s}{2}} = \frac{\frac{1}{3} + \frac{s}{3}}{1 - \frac{s}{3}} \quad (\text{B1})$$

The generating function for the number of descendants at time  $t + 0.5$  of a group of five trees living at time  $t$  is

$$[f_{1/2}(s)]^5 = \left( \frac{1}{3} + \frac{s}{3} \right)^5 \bigg/ \left( 1 - \frac{s}{3} \right)^5. \quad (\text{B2})$$

Were this latter distribution of Poisson distribution with a mean of 5, it would approximate a normal distribution closely enough for the purposes of the  $\chi^2$ . How closely does this distribution approach a Poisson distribution with mean 5?

To calculate the coefficients of  $s^i$  in the power series expansion of  $[f_{1/2}(s)]^5$ , our primary problem is evaluating  $1/(1 - z)^5$ , where  $z = s/3$ . We begin by recalling that

$$1/(1 - z) = 1 + z + z^2 + z^3 + z^4 + z^5 + \dots \quad (\text{B3})$$

Then we set

$$\begin{aligned} 1/(1 - z)^2 &= 1 + z + z^2 + z^3 + z^4 + z^5 + \dots \\ &\quad + z + z^2 + z^3 + z^4 + z^5 + \dots \\ &\quad + z^2 + z^3 + z^4 + z^5 + \dots \\ &\quad + z^3 + z^4 + z^5 + \dots \end{aligned} \quad (\text{B4})$$

$$1/(1 - z)^2 = 1 + 2z + 3z^2 + 4z^3 + 5z^4 + 6z^5 + \dots \quad (\text{B5})$$

If we multiply  $1/(1 - z)^2$  by  $1/(1 - z)$ , the coefficient of  $z^n$  in  $1/(1 - z)^3$  is the sum of the coefficients of  $z^i$ ,  $i \leq n$ , in  $1/(1 - z)^2$ , just as the coefficient of  $z^n$  in  $1/(1 - z)^2$  is the sum of the coefficients of  $z^i$ ,  $i \leq n$ , in  $1/(1 - z)$ . Extending the method, we may thus calculate  $1/(1 - z)^5$  by forming the following version of Pascal's triangle:

$$\begin{aligned} 1/(1 - z)^1 &= 1 + z + z^2 + z^3 + z^4 + z^5 + \dots \\ 1/(1 - z)^2 &= 1 + 2z + 3z^2 + 4z^3 + 5z^4 + 6z^5 + \dots \end{aligned}$$

$$\begin{aligned}
1/(1-z)^3 &= 1 + 3z + 6z^2 + 10z^3 + 15z^4 + 21z^5 + \dots \\
1/(1-z)^4 &= 1 + 4z + 10z^2 + 20z^3 + 35z^4 + 56z^5 + \dots \\
1/(1-z)^5 &= 1 + 5z + 15z^2 + 35z^3 + 70z^4 + 126z^5 + \dots
\end{aligned}
\tag{B6}$$

Here, each coefficient is the sum of the one just left of it, and the one just above it. Each coefficient is also the sum of the one just above it, and all the other coefficients to the left of that,

Table B1. The probabilities of a group of five trees living at time  $t$  leaving different numbers of descendants at time  $t + 0.5$  (Moran model) and  $t + 1$  (Wright-Fisher model).

$n$	Probability of 5 trees leaving $n$ offspring under	
	Wright-Fisher model	Moran model
0	0.00674	0.00412
1	0.03369	0.02743
2	0.08422	0.08230
3	0.14037	0.14937
4	0.17547	0.18798
5	0.17547	0.18025
6	0.14622	0.14192
7	0.10444	0.09698
8	0.06528	0.05972
9	0.03626	0.03399
10	0.01813	0.01819
11	0.00824	0.00927
12	0.00343	0.00479

The probabilities for the Wright-Fisher model are the probabilities of getting  $n$  events when the number of events is governed by a Poisson distribution with mean 5 (the appropriate probability distribution under the Wright-Fisher model for the number of offspring in the next generation of 5 mature individuals). The probabilities for the Moran model are the coefficients of  $s^i$ ,  $i \leq 12$ , in  $[f_{1/2}(s)]^5$ .

which was the principle by which we formed this family of power series. Once Pascal's triangle is involved in these calculations, the formula

$$\frac{1}{(1-x)^{N+1}} = \sum_{n=0}^{\infty} \frac{(N+n)!x^n}{N!n!}
\tag{B7}$$

follows from theorems proved by Pascal (1954) and known to the Chinese by 1300 (Needham 1959, pp. 134, 138). With this formula in hand, calculating the coefficients of  $s^i$  in  $[f_{1/2}(s)]^5$  is simply tiresome algebra. The results are similar to the corresponding probabilities from a Poisson distribution whose mean is 5 (Table B1).

## References

- Needham, J. (1959) *Science and Civilization in China*, Vol. 3, *Mathematics and the Sciences of the Heavens and the Earth*. Cambridge University Press, Cambridge, UK.
- Pascal, B. (1954) *Traité du triangle arithmétique*. Pascal, *Œuvres Complètes* (J. Chevalier, ed.). Gallimard, Paris, France.