

MAMMALS, EDGE EFFECTS, AND THE LOSS OF TROPICAL FOREST DIVERSITY

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Abstract. Relative to the surrounding mainland forests, a subset of tree species dominates wind-exposed, forested islands in Gatún Lake, Panama. We explored how tree diversity in these fragments has been affected by (1) impoverishment of the mammal community and (2) changes in abiotic conditions following island formation ca. 90 years ago. To test effects of changes in the mammal community, we assessed seed and seedling survival for nine tree species in five forests: small islands with no mammals; small islands with spiny rats but no larger mammals; medium islands (intermediate mammal community); Barro Colorado Island (intermittently present puma and jaguar); and mainland forests (intact mammal community). To test effects of abiotic stress, we chose experimental sites at wind-exposed, wind-protected, and interior forest sites. We predicted that fragments with less diverse mammal communities would be characterized by (1) fewer seeds dispersed and cached, (2) lower long-term seed survival, and (3) higher rates of seedling herbivory by mammals. Where alteration of the environment has caused greater exposure to dry-season winds, we predicted that (4) germination and seedling establishment and (5) dry-season seedling survival would be low. Further, we expected that (6) dry-season seedling survival would increase if soil moisture levels were raised, but that (7) wet-season seedling survival is independent of wind exposure.

In the larger forests, seed and seedling survival were low, and differences in mammal community composition had little effect. Small islands that supported only rats had the same low seed survival as larger forests. Elimination of all mammals resulted in much higher seed survival, and slightly higher seedling survival. Germination and seedling survival were lower at wind-exposed than at protected sites, but irrigation had no effect on dry-season seedling survival. It appears that the dominant species on Gatún Lake fragments have passed through a series of filters: seeds must first avoid being eaten by spiny rats, survive the first dry season, and then avoid seedling herbivory by rats. Biotic and abiotic factors determine seedling survival in tropical forests; synergistic changes in these factors can thus lead to dramatic losses of diversity.

Key words: *agouti*; Barro Colorado Island, Panama; *Dasyprocta* spp.; edge effects; irrigation experiments; island biogeography; *Proechimys semispinosus*; *Protium panamense*; seed dispersal; seedling herbivory; spiny rat; tropical forest diversity.

INTRODUCTION

Why are intact tropical rain forests so species rich? Although many mechanisms have been proposed, including niche differentiation (Ashton 1969), pest pressure (Janzen 1970), intermediate disturbance (Connell 1978), chance (Hubbell and Foster 1986), and forest productivity (Phillips et al. 1994), the answer to the diversity question still eludes ecologists. In this paper we attempt to shed light on the question by addressing the complement: why are fragmented tropical forests so species poor?

It is well documented that ecosystem fragmentation lowers species richness (MacArthur and Wilson 1967, Laurance 1997). Although ecologists have often noted that particular species disappear following fragmentation, there are few mechanistic explanations of why (but see Leigh et al. 1993, Terborgh et al. 1997, 2001). Apart from the simple answer that a fragment is too small to support a viable population of a species, we have rarely been able even to guess the mechanisms underlying fragmentation-induced species loss. This information gap is especially acute for tropical forests: we do not know which of the processes that maintain the diversity of intact forests are so altered by fragmentation that local extinctions result.

Some of the more obvious changes that follow tropical forest fragmentation are abiotic. Near fragment edges, the forest becomes warmer, better lit, and less humid (Fetcher et al. 1985). Edge creation alters the microclimate in ways that harm some species, increas-

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ing mortality rates and decreasing recruitment (Laurance et al. 1998). For example, seedling abundance in an Australian fragment varied depending on whether or not the edge was exposed to prevailing winds (Turton and Freiburger 1997). Changes in a fragment's abiotic environment thus can directly affect seedling recruitment, and in the long term can affect tree species diversity.

Indirect biotic changes also occur in a fragmented forest. Differences in herbivore foraging patterns caused by fragmentation-induced changes in mammal community composition can lead to changes in seedling recruitment (Dirzo and Miranda 1991, Wright and Duber 2001). Putz et al. (1990) hypothesized that differences in mammal community composition have influenced tree diversity on islands in Lago Gatún, Panama. Specifically, a lack of seed-eating mammals on small islands may have allowed increased recruitment of mammal-preferred tree species, resulting in changes in forest composition (Terborgh 1992). Moreover, in intact forests, mammals such as agouti (*Dasyprocta* spp.) often disperse and bury seeds, some of which survive to germinate (Smythe 1989). In fragments where mammals are absent, or where mammals have been lost to hunters, such dispersal does not occur. Mammal community composition thus may play an important role in the maintenance or loss of tree species diversity.

Is there a synergy between abiotic and biotic changes in fragments that further reduces tree diversity? The numerous small islands that were created during the 1912 construction of the Panama Canal provide a tractable study system for addressing this question. Most of these islands appear to have supported species-rich tropical forest immediately post-isolation, but they rapidly lost much of their species diversity. Many of the smaller islands were soon dominated by a restricted number of species: *Protium panamense*, *Oenocarpus mapora*, *Attalea butyracea* (formerly *Scheelea zonenensis*), and *Swartzia simplex*, with *Protium panamense* comprising ~60% of the stems on one island by 1980. Leigh et al. (1993) hypothesized that three mechanisms have contributed to this loss of diversity: exposure of adult trees to damaging windstorms; wind-induced changes in the islands' abiotic environment; and the alteration of the mammal community relative to intact forest.

Understanding the interplay of abiotic and biotic factors is likely to be critical for ensuring the maintenance of diversity in tropical forests. Although changes in a fragment's abiotic environment can profoundly affect seedling survival at the forest edge, such edge effects may be of little long-term importance in larger fragments. In contrast, if changes in mammal community composition drive changes in seedling dynamics, forest diversity even in large fragments may be at risk if hunting or other disturbances persist (Wright et al. 2000).

This paper experimentally explores the mechanisms of species loss proposed by Leigh et al. (1993). Our general hypothesis is that changes in fragments' biotic and abiotic environment (specifically, changes in the abundance and diversity of herbivorous mammals, and wind-induced changes in soil moisture) have had profound effects on seedling recruitment and tree diversity on these islands. We assessed seed and seedling survival under a variety of treatments in a range of different-sized fragments, and tested seven predictions. We predicted that in fragments with fewer mammal species (1) fewer seeds are dispersed and cached, (2) long-term seed survival is lower, and (3) seedling herbivory is higher than in fragments with more mammal species. Where a fragment's abiotic environment has been altered by increased exposure to dry-season winds, we predicted that (4) germination and early seedling survival is lower, and (5) dry-season survival of established seedlings is lower than at more protected sites. We also predicted that (6) during the severe dry season, seedling survival increases at exposed sites if soil moisture levels are raised, and (7) wet-season seedling survival does not differ between exposed and interior sites. Here, we test these predictions, show how changes in biotic and abiotic conditions have affected seedling dynamics, and demonstrate how these changes have reduced tree species diversity in Panamanian forest fragments.

MATERIALS AND METHODS

Our study sites were located in and around Gatún Lake, central Panama. Islands were formed in the lake during the construction of the Panama Canal, when rising waters of the Chagres river isolated forested hill-tops into numerous islands ranging in size from <1 ha to the 1500-ha Barro Colorado Island (BCI). Annual rainfall on BCI (9°10' N, 79°51' W) is 2600 mm, with a four-month dry season beginning in December. Strong dry-season winds blow across the lake from the north and northeast.

Tree and sapling diversity

On seven small (<2.2-ha) islands, we measured, identified, and permanently marked every tree with a diameter at breast height (dbh) >10 cm. We included all six islands on which we would conduct seed and seedling survival experiments, and the six small islands studied by Leigh et al. 1993 (five islands were common to both groups). Because we were interested in natural mortality and recruitment, we chose islands that, as far as could be determined, have been continuously forested since isolation in 1912. Stumps of drowned trees surround each island, and aerial photographs taken as early as 1927 suggest that the islands were still forested following construction of the Panama Canal (Leigh et al. 1993). Five islands were "exposed" to dry-season trade winds (i.e., >1 km of open water to the north and northeast), and two islands were "protected" from

winds by other land masses (i.e., <50 m of open water to the north and northeast). We also recorded tree species diversity on an exposed and a protected edge of each of two medium (3.5–17 ha) islands, three BCI peninsulas, and on a mainland peninsula (we analyzed these sites collectively as “large fragments”). At each large fragment, we measured, identified, and permanently marked the first 100 trees (dbh > 10 cm) encountered within 40 m of the forest edge.

At each site, we also randomly located and demarcated five 5 × 5 m plots and measured, identified, and tagged every sapling, shrub, and liana with dbh > 1 cm. We calculated abundance and species richness for each site, and compared the Shannon diversity index for each data set using factorial ANOVA with exposure and forest type (i.e., small islands vs. large fragments) main effects.

Experiments

To assess how seed and seedling survival are affected by differences in mammal community composition, we located 33 experimental sites in forests that supported five different mammal communities. To assess the effect of abiotic factors on survival, we located nine of these sites in the forest interior, 12 within 10 m of an “exposed” forest edge, and 12 within 10 m of a “protected” forest edge (definitions of exposed and protected as given previously). Specifically, sites were located as follows.

- 1) Small (<2.2 ha) islands with no mammals ($n = 3$ islands). These islands were exposed to dry-season trade winds (islands 15, 19, and 37 in Adler and Seamon [1991]).
- 2) Small (<2.2 ha) islands with only spiny rats, *Proechimys semispinosus* ($n = 3$ islands). One island was exposed to dry-season winds, and two islands were relatively protected by other land masses (islands 7, 10, and 43 in Adler and Seamon [1991]).
- 3) Medium-sized islands (3.5–17 ha) ($n = 3$) that lack deer, tapir, and large predators, but have the expected complement of small mammals (e.g., agouti, spiny rats, and squirrels) (Appendix A). On each island (islands 3 and 13 in Adler and Seamon [1991], and island 54 in Mangan and Adler [2002]) we undertook experiments at an exposed site, a protected site, and an interior site. The interior sites were as close to the center of the island as possible, although island geometry required that these sites were 40–50 m from the forest edge. This distance is greater than the 40 m invoked by Kapos (1989) as the zone into which the forest is influenced by the edge (but cf. Laurance et al. 1998).
- 4) Peninsulas on Barro Colorado Island (1600 ha) ($n = 3$) that support an intact mammal community (Glanz 1991) with jaguar (*Panthera onca*) and

puma (*Puma concolor*) as frequent visitors (Wright and Duber 2001). On each peninsula, we conducted experiments at an exposed, a protected, and an interior site.

- 5) Mainland forests surrounding Gatun Lake ($n = 3$). Whereas BCI and the small and medium islands have suffered minimal hunting, the otherwise-intact mammal faunas of mainland peninsulas were unprotected and suffered severe poaching until 1980 (Wright et al. 2000). On each peninsula (Bohio, Gigante, and Palenquilla), we undertook experiments at an exposed, a protected, and an interior site (interior sites on BCI and in mainland forests were in protected valleys >100 m from the forest edge).

Within each forest type, experimental site location was random, except that each site was under a closed forest canopy and had an area of level ground large enough for two mammal-exclosure cages and paired nearby control plots (same ground area, but uncaged). Cages were constructed of galvanized wire cloth (1.5 m high × 1 × 1 m), were open at the top, and were staked to the soil to prevent passage of burrowing mammals underneath. Although climbing mammals and large mammals such as deer had access through the open tops, Asquith et al. (1997) showed that disappearance/mortality of *Gustavia superba* seeds and seedlings from within similar cages was <10%, vs. 84–100% outside. Water, light, wind, and insects could pass through the cages.

Each cage was located in a similar light environment, as determined by the proportion of open canopy above each cage measured with a Spherical Crown Densiometer (Forestry Suppliers, Jackson, Mississippi, USA). The proportion of open canopy for cages and controls at each site were averaged, and the arc sine transformed means for each site were compared by ANOVA with main effects of forest type and location (edge vs. interior). As small islands lacked interior sites, we used two separate ANOVA to check each main effect individually. No difference was detected in light levels in the cages between forest types ($F_{3,26} = 0.57$, $P = 0.64$) or location ($F_{2,27} = 0.27$, $P = 0.76$).

We verified the presence/absence of spiny rats on each small island through trapping, but did not further census other mammals. Not only are accurate abundances of mammals extremely difficult to obtain (Wright et al. 1994), but also mammal populations vary over orders of magnitude in relatively short time periods (e.g., *Proechimys* on Gatun Lake islands, Adler 1996).

For experiments investigating the effects of mammal community composition, each small island was an independent sample. Each medium island, BCI, and each mainland peninsula had an exposed, a protected, and an interior site. Although the three sites located on each larger island or peninsula were connected by contig-

uous forest, sites were considered independent because the mammals of interest (*Proechimys*, *Dasyprocta*, *Agouti*, and *Sciurus*) have home ranges much smaller than the minimum distances between sites (Glanz 1991, Adler 2000).

Abiotic environment

During the dry season (December–April), we measured wind velocity and soil moisture along two exposure gradients. Each gradient comprised two small exposed islands, one site on the exposed edge of a BCI peninsula, one site 40 m in from an exposed edge, one site on a protected edge of a BCI peninsula, one site 40 m in from the edge, and one interior forest site. Modal wind velocity (meters per second) was measured at 1 m height using an Omnisensor Air Velocity Meter (Model 1640, TSI, Saint Paul, Minnesota, USA) at each site for 10 min between 11:30 and 13:30 hours on at least four dry-season days in 1997. Wind velocity could not be measured at all of the sites on the same day, so sites measured each day were chosen randomly. Modal wind velocity values for each 10-min period were compared by ANOVA. We measured soil moisture content by collecting ~300 g of soil from the upper 15 cm of soil at each of these sites. Five samples for each site were pooled and weighed, dried for three days at 70°C (21.1°C), and then reweighed.

Tree species

We used nine tree species in seed and seedling survival experiments. Three of these species are common on small islands in Gatún Lake (Leigh et al. 1993) and also occur in intact forest. *Oenocarpus mapora* H. Karst (Arecaceae) (*Oenocarpus panamanus* Bailey) is a slender 8–20 m monoecious palm, common on BCI. Its 2.0–2.5 cm fruits are blackish-green (Croat 1978). *Protium panamense* Rose (Burseraceae) is usually <12 m tall and is abundant on BCI. Its fruits are 2–3 cm drupaceous capsules, that turn red at maturity and contain a white, fleshy mesocarp surrounding one or two 0.5 cm diameter green seeds (Croat 1978). *Swarzisia simplex* (SW.) Spreng. (Caesalpiniaceae) is a 15-m tree that is relatively common on BCI. Its fruits are orange pods, 2.5–5 cm long, that enclose a white aril and a single smooth 2–3 cm diameter black seed.

The other six study species are relatively uncommon on the small Gatún Lake islands studied by Leigh et al. (1993). *Calophyllum longifolium* Willd. (Clusiaceae) is a 35 m tall canopy tree, frequent in the BCI forest (and actually very common on a small, unstudied island). Its fruits are round, green, ~3 cm in diameter, with a thin fleshy exocarp surrounding a single large seed (Croat 1978). *Gustavia superba* (H.B.K.) Berg. (Lecythidaceae) is a small (10–15 cm dbh) pioneer tree common in the secondary forest understory on BCI. Its large fruits (150–600 g) contain 5–50 seeds, each 3–15 g (Sork 1987). *Astrocaryum standleyanum* Bailey (Arecaceae) is a monoecious 15 m tall palm, common

in young forests and on steep ravines. Its fruits are orange, 4–4.5 cm, and are held in a massive, pendant cluster (Croat 1978). *Virola nobilis* A. C. Smith (Myristicaceae) is a canopy tree. A fibrous capsule dehisces to expose a gray 2 cm diameter seed enclosed by a red aril 1 mm thick (Howe 1993). *Dipteryx panamensis* (Pitt.) Rec. & Mell (Leguminosae) is a common, large (40–50 m) canopy tree. Its drupes have a thin exocarp and a hard, thick-walled endocarp that encloses a single, 4 cm diameter seed (DeSteven and Putz 1984). *Prioria copaifera* Griseb. (Fabaceae) is a common canopy tree in seasonally inundated forest, but also occurs on BCI on well-drained upland soils. Its single-seeded woody legumes are >8 cm in diameter (Dalling et al. 1997).

Seeds of all species are consumed by mammals, and may be dispersed and buried by agouti, *Dasyprocta punctata* (e.g., Forget 1992, 1993). Prior to experiments, the mesocarp, fruits, and arils were removed from *P. panamense*, *S. simplex*, *G. superba*, *A. standleyanum*, and *V. nobilis*.

Mammalian seed dispersal and predation

Prediction 1: The ratio of seeds dispersed and cached by mammals per seed eaten is lower in fragments with less diverse mammal communities.—We assessed seed dispersal rates by attaching threads to seeds of eight species (not the small-seeded *P. panamense*) and following their fate. Eight seeds of each species were placed outside the enclosures on the forest floor at 33 sites, within a 2-week period for each species (May 1996–June 1997). Each seed was threaded with a 50 cm length of monofilament thread, to which was attached a 2 cm length of flagging tape to facilitate relocation (Asquith et al. 1999).

After 14 days, we searched within a 10 m radius of the site to relocate threads and tapes. If the thread was relocated with the seed still attached and it had been moved and/or buried, secondary dispersal was indicated. If the thread alone was recovered, we assumed that the seed had been consumed. We tested this assumption by attaching similar threads to *A. standleyanum* seeds, which have an inedible endocarp (Asquith et al. 1997). Almost 80% (23 of 29) of the threads from which the seed had been removed were within a few centimeters of fragments of an opened endocarp, suggesting consumption by granivorous mammals.

For analysis, we excluded seeds that were not removed, seeds that were not recovered, and seeds whose thread was not recovered. We found no evidence that the small islands support scatter-hoarding mammals (but see Adler and Kestell 1998), so small islands were excluded from analysis. We also excluded *S. simplex* because none of its seeds were dispersed, and *D. panamensis* because only two of its seeds were dispersed in any forest type. Proportions of seeds dispersed at each site were ranked because some groups showed no variance (Conover and Iman 1981). The rankings were

analyzed by factorial ANOVA with main effects of species, forest type, and exposure (exposed edge, protected edge, forest interior).

Prediction 2: Long-term seed survival is lower in fragments with less diverse mammal communities.—After 2–4 months, we recorded the numbers of seeds at each site that were eaten, dispersed, or not moved. Proportions of seeds that were eaten were ranked before analysis by ANOVA (Conover and Iman 1981), with main effects of species, forest type, and exposure. Seeds for which neither seed nor thread was recovered were excluded from the analysis, because we did not know their fate. Small islands with and without spiny rats were included in the analysis. However, because small islands lack the three wind/drought exposure levels, the ANOVA design was not fully factorial. Therefore, the three-way interaction term, and one two-way interaction term (forest type and exposure level) were excluded from analysis.

Prediction 3: Seedling herbivory is higher in fragments with less diverse mammal communities.—Seedlings were transplanted from a growing house at BCI to exposed small islands and to exposed and interior sites in each of the three larger forest types. Two groups of three, two, and five seedlings, respectively, of *O. mapora*, *G. superba*, and *S. simplex* were transplanted to each of 22 sites in November 1996, and two groups of four *D. panamensis* seedlings were transplanted in the early wet season in June 1997.

Each seedling group was planted at least 3 m apart, and was protected from mammals by a wire enclosure cage. The number of established seedlings of each species was recorded in July 1997. Cages around one group of each species were then removed, such that those seedlings were then exposed to mammalian herbivores. The total number of surviving seedlings in each treatment was recorded at the beginning of the dry season (six months later). Proportions of seedlings surviving were ranked and analyzed by ANOVA (Conover and Iman 1981) with main effects of forest type, treatment, and exposure (exposed and interior). There was no difference in survival rates among species, so the totals for all species were pooled to increase sample size. Because the larger forest types (medium islands, BCI, and mainland peninsulas) had similar levels of seedling survival (84–88% in the cages, 81–90% in the open), these sites were also pooled before analysis. The three-way interaction term and one two-way interaction term (forest type and exposure level) were excluded from the analysis.

Seed germination and seedling survival

Prediction 4: Germination and early seedling survival are lower at exposed sites than at protected sites.—Between May 1996 and June 1997, we placed eight seeds of each of nine species in the 1-m² wire cages at each of 33 sites. All seeds of a given species were placed at all sites within a 2-week period. Germination and early seedling survival of *C. longifolium*,

G. superba, and *O. mapora* were recorded in October/November 1996, *P. panamense* in May 1997, and *A. standleyanum*, *D. panamensis*, *S. simplex*, and *P. copifera* in January 1998. By the end of the experiment (November 1998), too few seeds of *V. nobilis* had germinated to allow analysis. Proportions of seedlings of each species surviving at each site were arcsine-transformed before analysis. Because small islands lack the interior exposure level, they were excluded from the ANOVA, which compared germination in the three larger forest types, analyzing the main effects of species, forest type, and exposure.

Prediction 5: Survival of established seedlings during the season of abiotic (moisture) stress is lower at exposed than at interior sites.—Three, two, and five seedlings, respectively, of *O. mapora*, *G. superba*, and *S. simplex* were transplanted from the growing house on BCI into 1-m² wire cages at nine pairs of exposed and interior sites (on medium islands, BCI, and the mainland) in the late wet season (November 1996). These seedlings had established and were independent of their seeds. The number of seedlings at each site that were alive in January 1997 and that survived the dry season was recorded in May 1997. Proportions of surviving seedlings were arcsine-transformed and analyzed by ANOVA with exposure and species main effects.

Prediction 6: Seedling survival during the season of high moisture stress increases at exposed sites if soil moisture levels are raised.—Two 1-m² wire cages were placed at each of seven sites along the two exposure gradients. Into each cage, we planted 10 *O. mapora*, 8 *G. superba*, 12 *S. simplex*, and 7 *C. longifolium* seedlings in early November 1996. Numbers of established seedlings were recorded at the start of the dry season (January 1997). Seedlings in one randomly chosen cage at each site were irrigated with 36 L of lake water twice per week throughout the dry season. Lake water has extremely low total nitrogen and phosphate content (R. Stallard, *personal communication*), so the irrigation treatment did not add many nutrients to experimental plots. Gravimetric soil moisture in experimental cages was measured at 0–15 cm depth every 2 weeks during the dry season, and compared with ambient soil moisture levels in non-irrigated cages. Soil samples were taken for moisture analysis at least 3 days after the most recent watering. Dry season seedling survival was recorded in April 1997, and proportions of seedlings surviving on islands, at exposed sites, and at protected/interior sites were arcsine transformed and analyzed by ANOVA with species, exposure, and treatment main effects.

Prediction 7: Seedling survival during the season of low moisture stress (wet season) does not differ between exposed and interior sites.—As part of the mammalian herbivory experiment (test of prediction 3), seedlings of four species, *O. mapora*, *G. superba*, *S.*

TABLE 1. Fragment tree and sapling diversity at sites in Gatún Lake as measured by the Shannon Index, H .

Sites	n	Trees, H		Saplings, H	
		Mean	1 SE	Mean	1 SE
Exposed islands	5	1.77	0.17	1.88	0.30
Protected islands	2	2.91	0.13	1.71	0.30
Exposed mainland	6	2.64	0.19	2.69	0.15
Protected mainland	6	2.68	0.18	2.69	0.13

simplex, and *D. panamensis*, were transplanted to exposed and interior sites in each of the five forest types. Seedling survivorship was measured at the start (July 1997) and at end of the wet season (January 1998), and proportions of seedlings that survived were ranked and analyzed by ANOVA with treatment, exposure, and forest type main effects. This analysis tested for an effect of wet-season exposure on seedling survival.

RESULTS

Tree and sapling diversity

Protium panamense dominated the tree and sapling community on three of seven small islands, and at three of six exposed large fragments. *P. panamense* also dominated the sapling community at one protected site, whereas *Protium tenuifolium* dominated two small islands (Appendix B). *Oenocarpus mapora* dominated the tree and sapling community on one protected small island. *Attalea butyracea* dominated the tree community on one island, was second most dominant tree species on two small islands, and third most dominant species on two islands. *Swartzia simplex* was second most dominant species in two island tree communities, and fourth most dominant on one island.

In species-rich tropical forests, apparent diversity will tend to increase purely as a function of sample size when sample sizes are small. However, no positive relationship was detected between the number of stems and the number of species in the sapling plots: indeed, the sites with lowest diversity had some of the largest sample sizes. Tree diversity was higher at protected than exposed sites ($F_{1,14} = 10.2$, $P = 0.006$; Table 1). Islands had lower diversity than large fragments ($F_{1,14} = 10.0$, $P = 0.007$), but the forest type \times exposure effect was also significant ($F_{1,14} = 6.4$, $P = 0.02$). Exposure had a significant effect on diversity on small islands, but not in large fragments. Sapling diversity was significantly higher in large fragments than on islands ($F_{1,14} = 9.0$, $P = 0.01$), but no significant exposure ($F_{1,14} = 0.22$, $P = 0.65$) or interaction ($F_{1,14} = 0.15$, $P = 0.71$) effects were detected.

Small, exposed islands in Gatún Lake are dominated by a subset of mainland tree species, primarily *P. panamense*, *P. tenuifolium*, *A. butyracea*, *O. mapora*, and *S. simplex* (for dominance on other small islands, see Adler [2000]) On some islands, this dominance is profound, with *P. panamense* comprising >60% of the

trees on two islands, and *O. mapora* representing 60% of the saplings on one island. However, in comparison with six other forests around Gatún Lake, dominance on small islands is not as spectacular as it first appeared (Leigh et al. [1993] compared the islands with only one mainland peninsula). For example, *Gustavia superba* comprised 52% of the trees at a protected peninsula site and *Macrocnemum glabrescens* comprised 39% of the trees at a protected BCI site.

In addition, the *P. panamense* of Leigh et al. (1993) actually appears to be two species, *P. panamense* and *P. tenuifolium*: this marginally increases the number of species in the subset dominating small islands, although these two congeners appear ecologically similar. Despite these caveats, exposed Gatún Lake islands exhibit lower species diversity and higher relative dominance of both trees and saplings than sites in larger forest fragments. In contrast, protected small islands, despite exhibiting very low sapling diversity, still maintain high tree species diversity.

Abiotic environment

Modal wind velocity differed significantly among sites ($F_{5,68} = 17.4$, $P < 0.001$; Appendix C): it was lowest at interior sites (0.53 m/s) and 40 m in from protected edges (0.55 m/s), and highest on small islands (1.89 m/s). Post hoc comparisons with an adjusted $\alpha = 0.025$ showed that sites 40 m from exposed edges were significantly less windy than exposed edges ($F_{1,68} = 6.31$, $P = 0.01$) and windier than protected edges ($F_{1,68} = 5.63$, $P = 0.02$). Throughout most of the dry season, soil moisture levels at the two exposed sites and on the small islands were lower than at the protected and interior sites (Fig. 1, controls).

Mammalian seed dispersal and predation

The ratios of seeds dispersed and cached per seed eaten by mammals did not differ among medium islands, BCI, and the mainland ($F_{2,103} = 0.1$, $P = 0.9$; Appendix D). Mammal community diversity was apparently unrelated to patterns of seed dispersal in these larger fragments (cf. Asquith et al. 1997). There were no differences between edges and interior sites ($F_{2,103} = 1$, $P = 0.4$), but there were differences among species ($F_{5,103} = 4.7$, $P < 0.001$). Mammals buried at least 59% of *Astrocaryum standleyanum* seeds on each of the medium islands, BCI, and the mainland. In contrast, no *S. simplex* seeds, and virtually no *Dipteryx panamensis* seeds, were buried.

The proportion of seeds eaten after 2–4 months did not differ between edge and interior sites ($F_{2,195} = 1.5$, $P = 0.23$), but there were differences between species ($F_{7,195} = 9.3$, $P < 0.001$; Table 2). Most species suffered high (>60%) predation where mammals were present, whereas <25% of *A. standleyanum* seeds were eaten across all sites. Forest types also differed ($F_{4,195} = 12.4$, $P < 0.001$): post hoc Bonferroni comparisons showed that small islands with no mammals had sig-

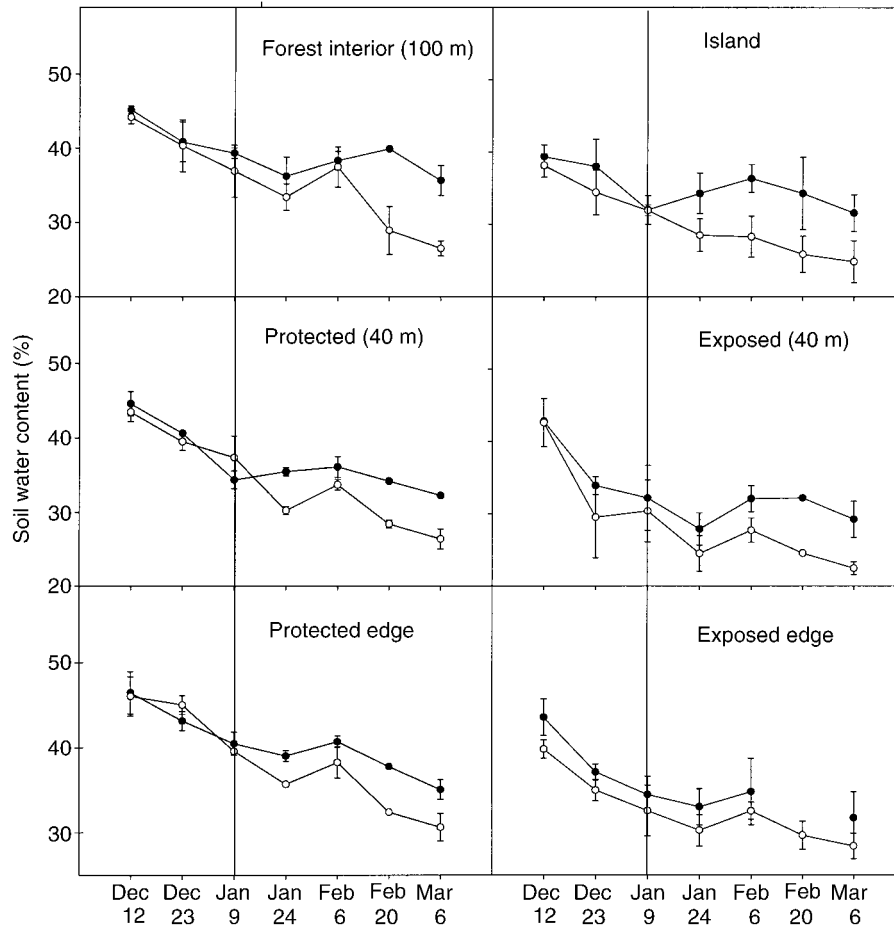


FIG. 1. Dry-season gravimetric soil water content for six different sites in Gatún Lake, Panama. For each site, percentage soil water content is shown for irrigated (solid circles) and control (open circles) plots. The vertical line represents the start of the irrigation experiment (9 January).

nificantly lower disappearance rates (<35%) than each of the other forest types (each comparison $P < 0.01$), but that no other forest types differed from each other. Thus, no differences were found between rates of seed survival after 2–4 months on medium islands, BCI, and the mainland. This suggests that even if components of the mammal community are absent or at reduced densities, other seed consumers will compensate. Fur-

thermore, rates of seed destruction after 2–4 months were virtually indistinguishable between the larger forest types and islands with rats only, even though the mammal communities in these forests are radically different.

In contrast, on small islands with no resident mammals, seed survival was high for all eight tree species. Seeds that would be consumed quickly by mammalian

TABLE 2. Proportion of unprotected seeds eaten during 2–4 months at sites in Panamá.

Species	Mainland		BCI		Medium islands		Small islands with rats		Small islands without rats	
	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE	Mean	1 SE
<i>O. mapora</i>	0.99	0.01	0.91	0.06	0.72	0.14	1.00	0.00	0.33	0.33
<i>A. butyraceae</i>	0.89	0.05	0.82	0.08	0.85	0.12	1.00	0.00	0.33	0.33
<i>G. superba</i>	1.00	0.00	0.92	0.04	0.81	0.10	1.00	0.00	0.33	0.33
<i>C. longifolium</i>	0.68	0.15	0.37	0.13	0.71	0.09	0.90	0.10	0.33	0.33
<i>V. nobilis</i>	0.97	0.02	0.94	0.05	0.69	0.16	0.38	0.31	0.33	0.33
<i>A. standleyanum</i>	0.25	0.10	0.15	0.07	0.23	0.08	0.19	0.19	0.11	0.11
<i>D. panamensis</i>	0.60	0.12	0.42	0.14	0.63	0.16	0.09	0.04	0.09	0.09
<i>P. copatifera</i>	0.83	0.10	0.87	0.07	0.80	0.10	0.67	0.33	0.00	0.00

TABLE 3. Mean number (and 1 SE) of protected seeds ($n = 8$ seeds per species) germinating and surviving at exposed, protected, and interior sites.

Site type	Species code							
	<i>Om</i>	<i>Pp</i>	<i>Ss</i>	<i>Gs</i>	<i>Cl</i>	<i>As</i>	<i>Dp</i>	<i>Pc</i>
Small islands								
Exposed	0.8 (1.5)	3.0 (1.4)	2.3 (2.2)	0.0 (0.0)	1.2 (2.5)	1.0 (1.4)	2.5 (1.7)	1.5 (2.5)
Protected	0.0 (0.0)	1.0 (0.0)	3.5 (2.1)	3.0 (4.2)	2.5 (3.5)	1.0 (1.4)	1.0 (1.4)	0.5 (0.7)
Medium islands								
Exposed	3.3 (2.9)	1.3 (1.2)	4.3 (1.5)	4.3 (3.1)	2.0 (3.4)	1.3 (1.5)	2.0 (1.7)	1.7 (1.2)
Protected	5.3 (2.1)	2.3 (0.6)	6.0 (1.0)	4.7 (3.2)	2.6 (2.3)	1.3 (0.6)	3.3 (1.2)	4.3 (2.1)
Interior	4.3 (3.2)	1.3 (1.2)	5.0 (2.6)	5.6 (1.5)	0.6 (1.2)	2.0 (2.0)	1.7 (0.6)	3.7 (3.5)
BCI								
Exposed	5.0 (3.4)	0.7 (0.6)	4.3 (1.2)	7.3 (1.2)	1.7 (2.9)	0.7 (1.2)	1.3 (1.2)	3.0 (1.0)
Protected	3.7 (2.1)	3.3 (0.6)	4.7 (0.6)	7.3 (1.2)	2.3 (2.5)	1.0 (1.0)	1.3 (1.2)	5.7 (1.2)
Interior	3.0 (3.6)	0.3 (0.6)	5.7 (2.1)	6.3 (2.1)	0.0 (0.0)	2.3 (2.1)	1.0 (1.0)	5.3 (1.2)
Mainland								
Exposed	2.3 (4.0)	1.0 (0.0)	4.5 (0.7)	6.0 (0.0)	3.5 (0.7)	1.0 (1.4)	1.5 (2.1)	3.5 (0.7)
Protected	4.0 (4.0)	1.3 (1.5)	6.0 (1.0)	3.7 (4.0)	5.0 (1.0)	1.7 (2.1)	2.0 (2.0)	6.7 (1.2)
Interior	2.3 (3.2)	0.7 (0.6)	3.3 (3.5)	4.0 (2.8)	5.5 (2.1)	2.5 (0.7)	2.3 (1.5)	5.7 (0.6)

Note: Species codes are: *Om*, *Oenocarpus mapora*; *Pp*, *Protium panamense*; *Ss*, *Swartzia simplex*; *Gs*, *Gustavia superba*; *Cl*, *Calophyllum longifolium*; *As*, *Astrocaryum standleyanum*; *Dp*, *Dipteryx panamensis*; *Pc*, *Prioria copaifera*.

granivores in an intact forest have a chance to germinate on small islands. Although some seeds disappeared on the small islands where we did not record resident mammals, we discovered some of these seeds decomposing, and invertebrates or mammalian visitors may have consumed the others.

Seedling herbivory on *D. panamensis*, *O. mapora*, *G. superba*, and *S. simplex* was minimal on medium islands, BCI, and the mainland forests, and on small islands without rats. Indeed, herbivory was so low in large fragments and on the small islands without rats (and, for *S. simplex*, on islands with rats) that there was no overall difference in seedling survival between caged and uncaged seedlings (treatment effect $F_{1,110} = 0.06$, $P = 0.81$; Appendix E). However, on small islands with rats, 60% of *D. panamensis*, and 100% of *O. mapora* and *G. superba* seedlings were removed from outside the cages (forest type effect $F_{2,110} = 4.65$, $P = 0.01$). *Swartzia simplex* was the exception, suffering virtually no herbivory on small islands with rats. The extremely high levels of herbivory may be a function of the abnormally high densities of rats on Gatun Lake islands (Adler 1996). Post hoc comparisons confirmed that fewer seedlings survived on small islands with rats than in large fragments ($P = 0.025$), but that small islands without rats did not differ from large fragments.

Seed germination and seedling survival

There was no difference in germination rates among medium islands, BCI, and the mainland ($F_{2,136} = 0.08$, $P = 0.9$) (Table 3). The species effect was significant ($F_{7,136} = 13.1$, $P < 0.001$), as was the forest \times species interaction ($F_{14,136} = 2.21$, $P = 0.01$). The exposure effect was also significant ($F_{2,136} = 3.7$, $P = 0.03$): post hoc Bonferroni comparisons showed that germination

at exposed sites was lower than at protected sites ($P < 0.01$), but that neither exposed nor protected sites differed from interior sites. Germination was thus lowest at exposed sites, highest at protected sites, and intermediate at interior sites. Both exposed and protected small islands exhibited very low germination rates. Germination of *Prioria copaifera* was noticeably lower on small islands and at exposed sites than at protected sites, perhaps contributing to the rarity of this species on exposed islands. However, most of the other species, even those that are common on some small islands, also fared worse at exposed sites than at protected sites. Although germination of island-dominating species was low on small islands in comparison to larger forests, of the three species that fared the best at exposed sites, two, *S. simplex* and *O. mapora*, are common trees on small islands.

Dry-season survival of seedlings of *S. simplex*, *O. mapora*, and *G. superba* was lower at exposed ($Ss = 69\%$, $Om = 21\%$, $Gs = 68\%$) than at interior ($Ss = 91\%$, $Om = 64\%$, $Gs = 72\%$) sites ($F_{1,55} = 4.4$, $P = 0.04$; Appendix F). *O. mapora* had significantly lower survival than *G. superba* and *S. simplex* (species effect $F_{2,55} = 12.1$, $P < 0.001$, post hoc Bonferroni comparison $P < 0.01$).

Irrigation increased soil moisture content at exposed, protected, and interior sites (Fig. 1). Ambient soil moisture ranged between 23% and 31% at the end of the dry season, whereas irrigation increased moisture to 27–36%. For *G. superba*, *O. mapora*, and *S. simplex*, neither irrigation nor exposure had a significant impact on seedling survival (Table 4). Survival of nonwatered *S. simplex* was virtually identical on islands and at exposed and protected sites, and survival of non-irrigated *Calophyllum longifolium* was actually highest on the small islands. The relatively high survival rates of

TABLE 4. Mean proportion of caged *O. mapora*, *S. simplex*, *G. superba*, and *C. longifolium* seedlings that survived the dry season under irrigated and non-irrigated conditions.

Species and condition	Islands			Exposed sites			Protected/interior sites		
	Mean	1 SE	<i>n</i>	Mean	1 SE	<i>n</i>	Mean	1 SE	<i>n</i>
<i>O. mapora</i>									
Wet	1.00	0.00	36	0.89	0.09	36	0.90	0.09	52
Dry	0.73	0.38	35	0.81	0.38	34	0.63	0.11	50
<i>S. simplex</i>									
Wet	1.00	0.00	47	0.83	0.07	47	0.98	0.04	59
Dry	0.96	0.04	47	0.96	0.05	49	0.95	0.07	60
<i>G. superba</i>									
Wet	0.91	0.12	32	0.83	0.05	29	0.92	0.13	46
Dry	0.84	0.31	30	0.96	0.07	30	0.96	0.07	46
<i>C. longifolium</i>									
Wet	0.93	0.10	15	0.64	0.47	15	0.40	0.35	20
Dry	0.29	0.49	14	0.25	0.05	18	0.22	0.23	27

non-irrigated seedlings in this experiment (as opposed to much lower seedling survival in the previous experiment) may reflect the fact that the irrigation experiment was established earlier, so the transplanted seedlings had longer to establish before the unusually harsh 1997 dry season started. The species \times treatment interaction was significant ($F_{3,80} = 4.6$, $P = 0.005$). Post hoc contrasts (with an adjusted significance level of $P = 0.0125$) within the species \times treatment interaction showed that survival of non-irrigated *O. mapora* did not differ from that of *S. simplex* and *G. superba*, but that *C. longifolium* survival was higher when seedlings were irrigated ($P < 0.001$); survival of *C. longifolium* seedlings was lower than that of the other species in both the irrigated ($P < 0.001$) and the non-irrigated ($P < 0.001$) treatments. Although seedlings of *C. longifolium*, and to a lesser extent, *O. mapora*, suffer from dry-season soil moisture stress, this effect occurs in all forest types, not just on exposed edges and small islands. *Calophyllum longifolium* appears especially susceptible to water stress, so that even when soil moisture was increased through irrigation, dry-season seedling survival remained low.

To assess whether exposure to winds in the wet season reduced the survival of seedlings that were protected from mammals (Appendix G), we reviewed the ANOVA table that tested prediction 3 for significance of the exposure main effect and the exposure \times treatment interaction. Neither the exposure effect ($F_{1,110} = 0.51$, $P = 0.48$) nor the exposure \times treatment interaction ($F_{1,110} = 0.24$, $P = 0.62$) was significant. Thus, there was no effect of exposure on wet-season survival of any species, suggesting that exposure to the dry-season winds is the critical exposure factor for seedling survival.

DISCUSSION

A restricted subset of tree species dominates small, wind-exposed Gatún Lake islands. As hypothesized by Leigh et al. (1993), the low diversity of these islands

is caused by both an island effect and an exposure effect. Protected and exposed small islands have lower sapling diversity than larger forests, whereas all exposed sites have lower tree diversity than protected sites.

A small number of species (*Protium panamense*, *Oenocarpus mapora*, *Attalea butyracea*, and *Swartzia simplex*) may dominate exposed sites primarily because they are better able to adapt to the unfavorable microclimate. Although germination of *O. mapora* and *S. simplex* was lower on the small islands/exposed sites than at protected sites, these species had higher germination rates than any other species except *Gustavia superba*. Further, reduced dry-season soil moisture, exacerbated by high winds on exposed small islands, had only a minor effect on established *S. simplex*, *G. superba*, and *O. mapora* seedling survival. Species such as *S. simplex* appear to thrive in the dry, exposed, small-island environment.

Large-seeded species may have an advantage over small-seeded species because they have more reserves to survive their first dry season and develop a deep root structure. However, this effect is a function of species' intrinsic susceptibility to water stress, and not just a function of seed size. Drought susceptibility at exposed sites persists at the seedling stage, even for apparently well-adapted species. Even after a two-month establishment phase, survival of *Calophyllum longifolium* was drastically reduced at all sites by a lack of available soil moisture. Dry-season winds on exposed Gatún Lake fragments probably exclude many small-seeded species, and perhaps the large-seeded *C. longifolium* and *Prioria copaifera*.

A second important factor that determines which tree species can survive on small islands is mammal community composition. A lack of mammals favors some tree species over others. More than 85% of *O. mapora*, *S. simplex*, *G. superba*, and *Virola nobilis* seeds had been destroyed after 2–4 months at mainland sites,

whereas only 33% of seeds had disappeared on islands free of small mammals. In contrast, a relatively constant 10–25% of *Astrocaryum standleyanum* seeds disappeared from all sites (many were dispersed and buried). For most species, if an island supports spiny rats, then seed mortality is high. However, rat populations on Gatún Lake islands suffer local extinctions relatively frequently (Adler and Seamon 1991). If a small island is temporarily without rats, seeds of fruiting trees may have a window of opportunity for establishment.

We found no evidence to support the hypothesis that other differences in mammal community composition, specifically the absence of top predators (Terborgh 1992), can have an impact on seed and seedling dynamics and, thus, on forest diversity. Early survival of most tree species was unaffected by differences in mammal community composition among the larger fragments (cf. Terborgh 1992, Dirzo and Miranda 1991, Asquith et al. 1997, Terborgh et al. 2001).

P. panamense had very low germination success at exposed sites in our experiments, so its dominance on small islands cannot be explained simply by a natural propensity for survival in dry conditions. These *Protium* spp. may be particularly resistant to attack by mammals; *P. panamense* seeds are <5 mm, and although they are eaten by rats (Adler 1995), they are not preferred. Perhaps *P. panamense* only dominates some islands because intense seed predation and seedling herbivory by rats excluded other species that are physiologically better able to withstand the small-island microclimate. The two *Protium* species are also dominant whereas *A. butyraceae* is rare in the wind-exposed mainland forests with diverse mammal communities. Small-seeded *Protium* may thus have taken over exposed Gatún Lake islands primarily because spiny rats ate the seeds of *A. butyraceae* and the other large-seeded species that also could dominate.

It appears that the dominant species on small Gatún Lake fragments must pass through a series of selective filters or bottlenecks.

Filter 1: Avoid seed consumption by rats.—This filter will allow passage of many small-seeded species (Adler 1995), but large-seeded species can also pass through, as long as they fruit when island rat populations are low or absent.

Filter 2: Survive the first dry season.—Although the roots of adult trees on small islands can reach lake water, the seedlings of many species cannot tolerate the physiological stress on islands with soil moisture lower than 25%. The species that can tolerate such water stress tend to be large seeded (e.g., *S. simplex*). The few large-seeded species that passed propagules through the first filter are probably at a distinct advantage when it comes to the second. However, if the first dry season is relatively wet, many more species will survive this filter.

Filter 3: Avoid seedling herbivory by rats.—This is again dependent on external factors for many species:

successful recruitment will probably occur only if rats are temporarily absent or at low density. If rats are present, seedling herbivory can be as high as 100% for some species. Although most species on small islands can only avoid high rat herbivory when rat populations disappear, species such as *S. simplex* do not appear to be susceptible.

There are undoubtedly other important filters, including invertebrate seed attack (Hammond and Brown 1998) and herbivory (Arnold and Asquith 2002). However, these three filters are likely to play the most critical role in determining a fragment's tree species composition. Given the apparent susceptibility of all species' seedlings to water stress, the species that eventually come to dominate a particular small island are probably those that had a bumper seed crop and then faced a relatively wet dry season in the first year after the island's spiny rat population disappeared.

What would have happened to tree species diversity on Gatún Lake islands if exposure had not been such an important factor? On the two small, protected islands, adult tree diversity is still high. This belies an important pattern in the understory: sapling diversity on protected small islands is significantly lower than at mainland sites, and similar to the low sapling and tree diversity on exposed small islands. Thus, although the loss will take longer, protected small islands may ultimately lose as much tree species diversity as exposed islands.

The significant forest type \times exposure interaction effect in the tree diversity ANOVA indicates that the effects of island size (a proxy for mammal community composition) and exposure (indicator of a changed abiotic environment) have acted synergistically. On exposed small islands in Gatún Lake, it thus appears that the presence or absence of spiny rats and exposure to dry-season winds are synergistic filters through which tree species must pass to persist.

If one of these filters is removed, as occurs on non-exposed islands, more tree species will pass through this bottleneck and diversity will remain higher for longer periods. However, the strong selective filter of 100% seedling herbivory for some species when rats are present suggests that even in fragments that have not experienced major changes in their abiotic environment, species recruitment across the community will eventually be affected. Diversity will be lost, but at a slower rate than if the exposure filter were also operating simultaneously.

It is clear that biotic and abiotic factors are important determinants of seed and seedling survival in central Panamanian forests, and that changes in either the biotic or abiotic environment can profoundly alter forest composition. Synergistic interactions between changes in mammal community composition and exposure to winds, as has occurred on small Gatún Lake islands, can lead to an even more dramatic loss of tree species diversity.

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APPENDIX A

A table of the terrestrial mammal community at sites around Gatún Lake, Panama is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A1.

APPENDIX B

A list of the dominant tree species on islands at exposed and protected sites around Gatún Lake is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A2.

APPENDIX C

A table of modal midday wind velocity at 1 m above ground at Gatún Lake sites in the 1997 dry season is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A3.

APPENDIX D

A table showing the proportion of unprotected seeds dispersed after two weeks is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A4.

APPENDIX E

A table showing the proportion of protected *Oenocarpus mapora*, *Swartzia simplex*, *Gustavia superba*, and *Dipteryx panamensis* seedlings surviving after six months is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A5.

APPENDIX F

A table showing the proportion of protected *Oenocarpus mapora*, *Swartzia simplex*, and *Gustavia superba* seedlings that survived the 1997 dry season at exposed and interior forest sites is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A6.

APPENDIX G

A table showing the mean proportion (SE) and original *n* of mammal-protected seedlings that survived the wet season at exposed and interior sites is available in ESA's Electronic Data Archive: *Ecological Archives* E086-020-A7.