Contributed Paper

Long-Term Dynamics of a Fragmented Rainforest Mammal Assemblage

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Abstract: *Habitat fragmentation is a severe threat to tropical biotas, but its long-term effects are poorly understood. We evaluated longer-term changes in the abundance of larger (>1 kg) mammals in fragmented and intact rainforest and in riparian "corridors" in tropical Queensland, with data from 190 spotlighting surveys conducted in 1986–1987 and 2006–2007. In 1986–1987 when most fragments were already 20–50 years old, mammal assemblages differed markedly between fragmented and intact forest. Most vulnerable were lemuroid ringtail possums (*Hemibelideus lemuroides*), followed by Lumboltz's tree-kangaroos (*Dendrolagus lumholtzi*) and Herbert River ringtail possums (*Pseudocheirus herbertensis*). Further changes were evident 20 years later. Mammal species richness fell significantly in fragments, and the abundances of 4 species, coppery brushtail possums (*Trichosurus vulpecula johnstoni*), green ringtail possums (*Pseudochirops archeri*), red-legged pademelons (*Thylogale stigmatica*), and tree-kangaroos, declined significantly. The most surprising finding was that the lemuroid ringtail, a strict rainforest specialist, apparently recolonized one fragment, despite a 99.98% decrease in abundance in fragments and corridors. A combination of factors, including long-term fragmentation effects, shifts in the surrounding matrix vegetation, and recurring cyclone disturbances, appear to underlie these dynamic changes in mammal assemblages.*

Keywords: Australia, cyclones, forest fragmentation, long-term research, mammal assemblages, marsupials, matrix vegetation, Queensland, tropical rainforests

Dinámica a Largo Plazo de un Ensamble de Mamíferos de un Bosque Lluvioso Fragmentado

Resumen: *La fragmentación del hábitat es una severa amenaza para las biotas tropicales, pero se conoce poco sobre sus efectos a largo plazo. Evaluamos cambios de largo plazo en la abundancia de mamíferos mayores (>1 kg) en bosque lluvioso fragmentado e intacto y en "corredores" ribereños en Queensland, con datos de 190 muestreos con reflector llevados a cabo en 1986–1987 y 2006–2007. En 1986–1987, cuando la mayoría de los fragmentos ya tenían entre 20 y 50 años, los ensambles de mamíferos difirieron significativamente entre bosque intacto y fragmentado. Los más vulnerables fueron zarigüeyas (*Hemibelideus lemuroides*), seguidas por canguros arborícolas (*Dendrolagus lumholtzi*) y zarigüeyas (*Pseudocheirus herbertensis*). Mayores cambios fueron evidentes 20 años después. La riqueza de mamíferos decayó significativamente en los fragmentos, las abundancias de 4 especies,* Trichosurus vulpecula johnstoni, Pseudochirops archeri, Thylogale stigmatica *y* D. lumholtzi, *disminuyó significativamente. El hallazgo más sorprendente fue que* H. lemuroids, *un especialista de bosque estricto, aparentemente recolonizó un fragmento, no obstante un 99.98% de disminución en abundancia en los fragmentos y corredores. Una combinación de factores, incluyendo los efectos de la fragmentación a largo plazo, cambios en la matriz de vegetación circundante y las perturbaciones ciclónicas recurrentes, parece subyacer en estos cambios dinámicos en los ensambles de mamíferos.*

Palabras Clave: Australia, bosques lluviosos tropicales, ciclones, ensambles de mamíferos, fragmentación de bosque, investigación a largo plazo, marsupiales, matriz de vegetación, Queensland

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Introduction

Forest loss and fragmentation are among the most serious of all perils to tropical biodiversity (Laurance & Bierregaard 1997; Lindenmayer & Fischer 2006). Not only are tropical landscapes being rapidly fragmented, but many protected areas are becoming isolated as their surrounding habitats are degraded or destroyed (Curran et al. 2004; DeFries et al. 2005; Mayaux et al. 2005). Tropical forest disruption is expected to continue apace over the next century, driven by continued population growth, rapid industrialization, and agricultural expansion for crops and biofuels (Tilman et al. 2001; Rudel 2005; Laurance 2007). Clearly, the fate of much of tropical biodiversity will depend on our capacity to understand and limit the long-term impacts of forest fragmentation.

Much is unknown about the dynamics of fragmented tropical ecosystems, especially over longer timescales. Some of the clearest insights have come from an experimentally fragmented landscape in Amazonia (Lovejoy et al. 1986; Laurance et al. 2002; Ferraz et al. 2003; Stouffer et al. 2006) and from small islands in a Venezuelan reservoir (Terborgh et al. 2001; Feeley & Terborgh 2006), but fragments in these investigations were just 1–2 decades old. Only in a handful of studies have researchers examined older fragmented systems, such as centuries-old forest remnants in Singapore and Hong Kong (Corlett & Turner 1997; Brook et al. 2003) and Pleistocene land-bridge islands (Terborgh 1975; Wilcox 1978).

Here we provide a 20-year comparison of the abundances and species richness of tree-kangaroos, wallabies, and larger (>1 kg) possums in fragmented and intact rainforests in tropical Queensland, Australia. Our study area, the southern Atherton Tableland, is a key center of endemism that supports numerous mammal species with highly restricted geographical and elevational ranges (Winter 1988; Williams & Pearson 1997; Kanowski et al. 2001). We initially assessed the impacts of forest fragmentation on this fauna in 1986–1987 (Laurance 1990, 1991*a*, 1994, 1997), when most of the fragments were 2–5 decades old. We returned exactly 20 years later, to evaluate subsequent changes in mammal populations. This comparison provided rare insights into the longer-term dynamics of a fragmented species assemblage.

Methods

Study Area

The Atherton Tableland (600–900 m elevation) in tropical Queensland was formerly dominated by rainfor-

est. This cloudy, wet area (mean rainfall approximately 2800 mm/year on the southern Tableland) is an apparent Pleistocene refugium and is considered the most important center of species endemism in tropical Australia (Winter 1988; Williams & Pearson 1997).

Much of the Tableland and has been deforested, mostly for dairy farming, cattle ranching, and residential development. Clearing began about 1909 and proceeded rapidly for the next 3 decades. By 1983 more than 76,000 ha of forest had been removed (Winter et al. 1987), leaving more than 100 rainforest fragments ranging from 1 to 600 ha in area, scattered over an area of about 900 km². Large (>3600 ha) tracts of intact but selectively logged rainforest, protected since 1988 as a World Heritage area, persist on steeper hillsides that enclose the margins of the Tableland. Fragments are surrounded by mosaics of cattle pastures and narrow (10–50 m wide) strips of forest regrowth along streams (hereafter termed *corridors*).

The southern half of the Atherton Tableland (Fig. 1), where this study was conducted, has experienced only limited change in forest cover over the past 3 decades (determined on the basis of aerial imagery taken in 1986 and 2006). Recent forest clearing has been minimal, and the forest has partially regenerated in certain areas, most notably around a small (12.8-ha) fragment (fragment 5, Fig. 1) 220 m from intact forest. The largest disturbances have been caused by cyclones. The study area was damaged by major cyclones in 1986 and 2006 (Laurance 1991*b*; Laurance & Curran 2008), in each case just 5–7 months before our spotlighting surveys commenced. The region also suffered strong El Niño related droughts in 1982 and 2002 that caused substantial animal and plant mortality (N. I. J. Tucker, personal communication).

Census Methods

In 1986–1987 one of us (W.F.L.) and 2 experienced field assistants used standardized spotlighting methods to repeatedly survey nocturnal mammals in 20 study sites (Fig. 1): 10 forest fragments ranging from 1.4 to 590 ha in area, 7 "controls" in intact but selectively logged rainforest, and 3 corridors along streams (see Laurance 1990, 1991*a*, 1997 for details). All censuses were conducted along forest edges or old logging tracks. The main species encountered were the red-legged pademelon (*Thylogale stigmatica*), a scansorial rainforest wallaby, and 5 arboreal folivorous mammals, the coppery brushtail possum (*Trichosurus vulpecula johnstoni*), lemuroid ringtail (*Hemibelideus lemuroides*), green ringtail (*Pseudochirops archeri*) and Herbert River ringtail possums (*Pseudochirulus herbertensis*), and Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*).

Two of us (W.F.L., S.G.L.) returned to the study area in 2006–2007 to resurvey the same sites. We used
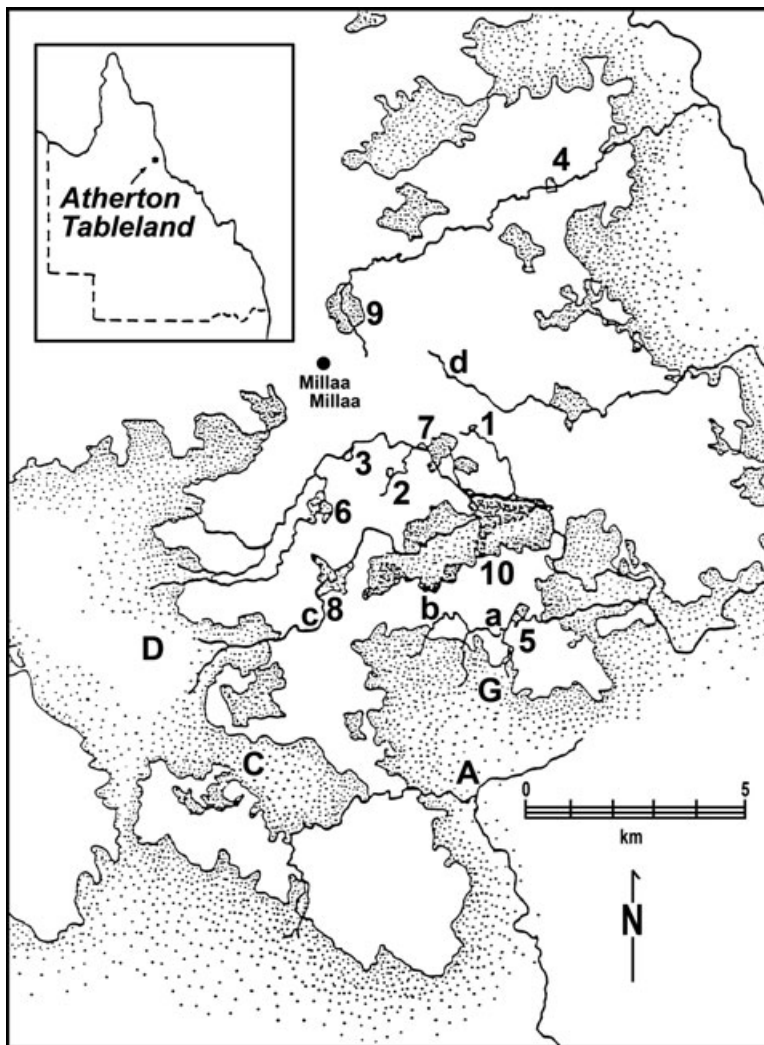
Figure 1. Map of study area in north Queensland in 2006–2007. Four control sites in intact forest are A, C, D, and G; 10 forest fragments ranging from 1.4 to 590 ha in area are numbers 1–10; and 4 regrowth "corridors" along streams are a–d.

identical methods and surveyed the same routes as in 1986–1987. All 10 fragments were resurveyed, but only 4 of the 7 control sites were accessible because of heavy cyclone damage. In addition, a landowner refused us access to 1 corridor, so we replaced this with 2 other nearby corridors that we repeatedly surveyed by spotlighting in the early 1990s (Laurance & Laurance 1999). To help standardize comparisons between 1986–1987 and 2006–2007, we included only surveys conducted between the mid-dry season (September–October) and early wet season (January–February). Sampling effort was similar between the 2 intervals. In 1986–1987 each study site was surveyed 4–7 times (104.0 h total), yielding 1035 animal detections, whereas in 2006–2007 each site was surveyed 5 times (124.1 h total), yielding 858 animal detections. Prior work suggests that 4–5 spotlighting surveys are sufficient to obtain stable abundance estimates for most species (Laurance & Laurance 1996).

All surveys were conducted on foot between 2000 and 0100 with hand-held spotlights and binoculars to identify animals. Tree-kangaroos and pademelons were also

identified when heard nearby, because the former has a unique escape behavior (plummeting down from trees and then loudly bounding away) and the latter gives distinctive warning thumps when disturbed. The 2 observers alternated among study sites and habitat types to minimize effects of observer bias, with a minimum 10-day interval between successive surveys of the same site. For each study site we determined the abundance of each species (mean number of individuals detected per hour) in 1986–1987 and 2006–2007. For each animal we recorded species, time of observation, estimated height of the animal, estimated horizontal distance of the animal from the forest or road edge, whether the animal was accompanied by conspecifics, and an age-class estimate for the animal, when possible (see Laurance 1990 for details).

Landscape Predictors

Six quantitative predictors were recorded for each habitat fragment on the basis of 1986 aerial imagery and other data summarized in Laurance (1990), updated with

recent (August 2006) aerial imagery. These variables were $\log_{10}$ fragment area; a continuous index of fragment shape; a simple index of topographic diversity (1, flat or nearly flat terrain; 2, gentle or rolling slopes; 3, moderately steep slopes; 4, steep slopes or sharply dissected terrain); a composite index of fragment isolation (integrating 3 intercorrelated measurements of distance to nearby intact forest and large fragments); a "corridor-gap code" that described the largest gap in tree-cover along stream-corridors linking each fragment to nearby intact forest (1, no gap in the corridor; 2, 10- to 50-m gap; 3, 50- to 100-m gap; 4, 100- to 200-m gap; 5, 200- to 500-m gap; and 6, >500-m gap); and an index of fragment age in 2006 (1, <30 years since isolation; 2, 30–40 years; 3, 40–55 years; 4, >55 years). Detailed descriptions of these predictors are provided in Laurance (1990).

Data Analysis

We evaluated changes in mammal abundances and species richness in 2 ways. First, we used repeated-measures analysis of variance (ANOVA) to test for changes in each response variable between the 2 time intervals (1986–1987 vs. 2006–2007) and among 4 habitat types (4 controls, 5 small [<20-ha] fragments, 5 large [>20-ha] fragments, and 4 corridors). Second, within each habitat type, we used paired t tests to contrast each variable between the 1986–1987 and 2006–2007 periods. Most response variables were $\log(x+1)$ transformed to improve data normality and reduce heteroscedasticity, with Wilk-Shapiro tests used to assess data normality.

We used best subsets and multiple regressions to assess the influence of landscape predictors on mammal species richness. None of the predictors was intercorrelated strongly enough ($R^2 < 50\%$) to produce significant colinearity effects in the multiple-regression models. Performance of the final regression model was assessed by comparing the standardized residuals to fitted values and to each significant predictor.

Raw data on foraging heights of the 5 arboreal species could not be located for 1986–1987, so comparisons among habitat types and time periods were conducted by comparing their means and 95% CIs ($\bar{x} \pm 1.96$ SE), with the 1986–1987 data generated from descriptive statistics in Laurance (1990). Although such comparisons assume a normal data distribution, foraging heights of the arboreal species in 2006–2007 exhibited only modest departures from normality (Wilk-Shapiro statistic = 0.88–0.96), suggesting this assumption is not unreasonable. Raw data on animal detectability (horizontal distance of each individual from the forest edge or logging track) also were lost for 1986–1987, but key inferences were possible with summary statistics in Laurance (1990).

Results

Animal Detectability

In 1986–1987, 93.7% of all animals were detected within 15 m of forest or logging-track edges. Mean and maximum detection distances were 5.7 and 40 m, respectively. Detectability increased slightly in 2006–2007. Of all animals detected, 85.5% were within 15 m of edges, and the mean and maximum detection distances were 7.2 and 70 m, respectively. Thus, approximately 8% more individuals were detected in 2006–2007 relative to 1986–1987, mostly >15 m from transects. We did not attempt to correct for this difference (see Discussion).

Animal detectability did not differ between intact forest versus forest fragments and corridors ($F_{1,828} = 0.01$, $p = 0.91$), despite large differences in mean detection distances among species ($F_{5,828} = 7.65, p < 0.001$; 2-way ANOVA with log-transformed distance data for 2006–2007). In pairwise comparisons following a one-way ANOVA ($F_{5,834} = 18.81$, $p < 0.0001$), tree-kangaroos, pademelons, and lemuroid ringtails were detected at larger distances than coppery brushtails, green ringtails, and Herbert River ringtails ($p \leq 0.002$). Tree-kangaroos and pademelons were often identified by sound, which increased their detection distances, whereas lemuroid ringtails have an especially bright eyeshine. In addition, Herbert River ringtails had a larger detection distance than green ringtails ($p = 0.04$) (Tukey's tests), which have a dim eyeshine and cryptic coloration.

Species Abundances

Repeated measures ANOVAs revealed strong effects of both habitat type and time on mammal community composition (Table 1). Lemuroid ringtail possums, Lumholtz's tree-kangaroos, and red-legged pademelons varied significantly in abundance among the 4 habitat types (controls, large fragments, small fragments, and corridors), as did overall mammal species richness. Effects of time were significant for coppery brushtail possums, green ringtail possums, tree-kangaroos, and pademelons, and Herbert River ringtails exhibited a significant time-habitat interaction.

Results of paired t tests comparing mammal assemblages in each habitat type and time (Table 2) showed that, relative to 1986–1987, tree-kangaroo abundance declined significantly in intact forest in 2006–2007. Herbert River ringtails declined in abundance in large fragments, whereas coppery brushtails, green ringtails, and red-legged pademelons all declined in small fragments. In addition, tree-kangaroos and pademelons exhibited marginally nonsignificant ($p \leq 0.08$) declines in large fragments. No species changed in abundance in corridors, although 2 species (lemuroid ringtails and pademelons) were never detected in corridors. A tendency for many species to decline in abundance over time,

Table 1. A comparison with repeated-measures analyses of variance of mammal abundances and species richness between 2 time intervals (1986–1987 and 2006–2007) and among 4 habitat categories[a].

Response variable	Time		Habitat		Time*habitat interaction	
	$F_{1,14}$	p	$F_{3,14}$	p	$F_{3,14}$	p
Coppery brushtail possum	7.87	0.014	0.25	0.86	0.32	0.81
Green ringtail possum[b]	9.41	0.008	0.21	0.89	0.36	0.78
Herbert River ringtail possum[b]	0.18	0.68	1.07	0.39	5.53	0.010
Lemuroid ringtail possum[b]	0.95	0.35	144.51	< 0.001	2.73	0.084
Lumholtz's tree-kangaroo[b]	11.32	0.005	4.12	0.027	1.90	0.18
Red-legged pademelon[b]	15.63	0.001	5.36	0.011	2.21	0.13
Species richness	3.94	0.067	13.59	< 0.001	1.35	0.30

[a]*Intact forest; small (<20-ha) forest fragments; large (>20-ha) fragments; riparian corridors.*
[b]*Data log(x+1) transformed.*

especially in forest fragments, was apparent in the comparison of species distributions between 1986–1987 and 2006–2007 (Fig. 2).

The most vulnerable species we studied was the lemuroid ringtail possum (Fig. 2). In 1986–1987 it was detected in only a single, 27-ha forest fragment (fragment 7, Fig. 1), and its overall abundance in fragments and corridors declined by 98.2% relative to intact forest. In 2006–2007 it was never observed in the 27-ha fragment, but a single individual was detected in a 12.8-ha fragment (fragment 5, Fig. 1) located just 220 m from intact forest. Compared to intact forest, its abundance in fragments and corridors decreased by 99.98%.

Species Richness

Mammal species richness declined significantly over time in forest fragments. Effects were not significant when small ($p = 0.099$) and large ($p = 0.18$) fragments were evaluated separately (Table 2), but were significant when data from all fragments were pooled ($t = 2.86$, df = 9, $p = 0.019$; paired t test). Forest fragments averaged 4.4 species (SD 1.0) in 1986–1987, but just 3.5 (1.4) species

in 2006–2007. Regressions of species richness against fragment area were significant, or nearly so, for both 1986–1987 ($F_{1,8} = 4.21$, $R^2 = 34.5\%$, $p = 0.074$) and 2006–2007 ($F_{1,8} = 7.01$, $R^2 = 46.7\%$, $p = 0.029$), but slopes of the species–area relationship became much steeper over time (Fig. 3; linear regressions with log-transformed axes). Unlike forest fragments, species richness was constant over time in intact forest (5.8 [0.5] species) and varied little over time in corridors (2.5 [1.0] vs. 2.5 [0.6] species in 1986–1987 and 2006–2007, respectively).

On the basis of 1986–1987 data, 3 of the 6 landscape variables were selected as predictors of mammal species richness in fragments, with best-subsets and multiple regressions. Log species richness increased with log fragment area and declined with larger corridor gaps and greater fragment isolation ($F_{3,9} = 18.08$, $R^2 = 90.0\%$, $p = 0.002$). These same 6 landscape variables were used to predict species richness in 2006–2007, but the corridor-gap variable was modified for 4 fragments (numbers 3, 5, 7, and 8; Fig. 1) to reflect changes in the surrounding matrix vegetation. As before, log species

Table 2. Paired t tests contrasting species abundances and species richness of rainforest mammals in 4 habitat categories[a] between 1986–1987 and 2006–2007[b].

Response variable	Controls[c]		Large fragments[d]		Small fragments[d]		Corridors[c]	
	t	p	t	p	t	p	t	p
Coppery brushtail possum	−2.88	0.064	−0.69	0.53	−2.77	0.050	−1.02	0.38
Green ringtail possum[e]	−1.60	0.21	−0.88	0.43	−2.84	0.047	−1.63	0.20
Herbert River ringtail possum[e]	0.61	0.58	−4.73	0.009	0.79	0.48	2.25	0.11
Lemuroid ringtail possum[e]	1.64	0.20	−1.00	0.37	1.00	0.37	—	—
Lumholtz's tree-kangaroo[e]	−8.70	0.003	−2.34	0.080	0.32	0.77	−1.22	0.31
Red-legged pademelon[e]	−2.11	0.13	−2.59	0.061	−3.11	0.036	—	—
Species richness	0.00	1.00	−1.63	0.18	−2.14	0.099	0.00	1.00

[a]*Intact forest; small (<20-ha) forest fragments; large (>20-ha) fragments; riparian corridors.*
[b]*A negative* t *statistic indicates the parameter declined over time.*
[c]n = 4 sites.
[d]n = 5 sites.
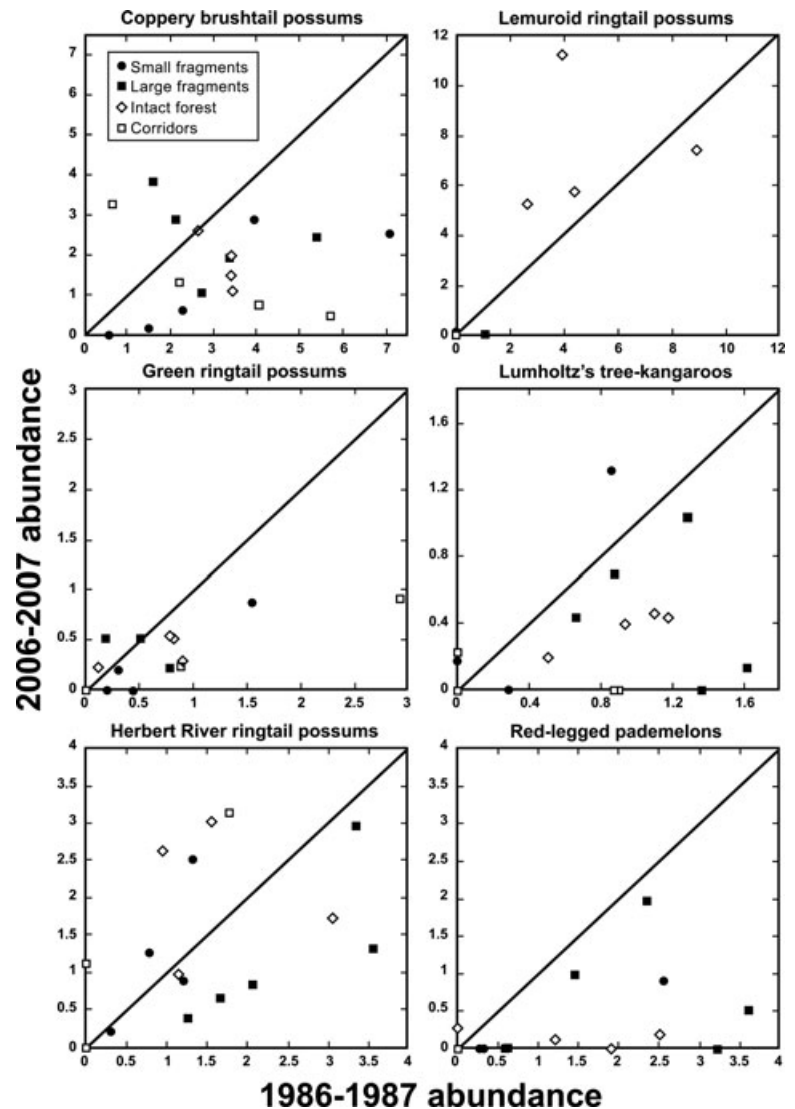[e]*Data log(x+1) transformed.*

Figure 2. Contrasting abundances (mean no. individuals/h) of 6 mammal species across 18 study sites in tropical Queensland, between 1986–1987 and 2006–2007. The diagonal lines show y = x.

richness rose with log fragment area, declined with greater corridor gaps and fragment isolation, and declined with topographic variability ($F_{3,9} = 13.45$, $R^2 = 91.5\%$, $p = 0.007$). In these models, fragment area accounted for less than half (35–47%) of the total variability in species richness, with measures of fragment connectivity (corridor gaps, fragment isolation) accounting for another 27–56% of the total variability.

Foraging Heights

In 1986–1987 significant differences in mean foraging heights were evident among the 5 arboreal species (Fig. 4). In intact forest, lemuroid ringtails and green ringtails foraged at greater heights than did coppery brushtails and Herbert River ringtails, which in turn foraged at greater heights than the larger-bodied tree-kangaroos. In addition, foraging heights of coppery brushtails, green ringtails, and Herbert River ringtails all shifted downward in fragments and corridors, relative to intact forest (Laurance 1990).

Despite modest differences between 1986–1987 and 2006–2007, overall patterns were similar between the 2 intervals. No species significantly altered their foraging heights over time in either fragmented or intact forest, on the basis of comparisons of 95% CIs (Fig. 4). In 2006–2007 foraging heights varied among arboreal species in intact forest ($F_{4,449} = 15.57$, $p < 0.0001$; one-way ANOVA), with lemuroid ringtails foraging higher than all species except green ringtails ($p < 0.05$, Tukey's test). In addition, coppery brushtails foraged at lower heights in fragments and corridors than in intact forest ($t = 2.21$, df = 230, $p = 0.028$), but differences for the other species were not significant (all 2-sample t tests).

Discussion

Animal Detectability

The spotlighting surveys we conducted in 1986–1987 and 2006–2007 were both preceded by major cyclones that caused considerable forest disturbance in our study area
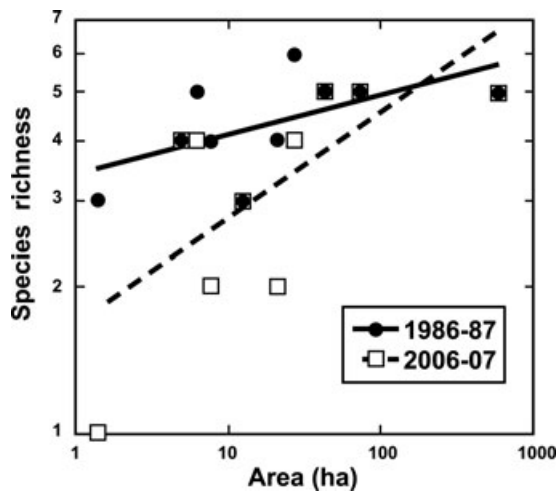
Figure 3. Species–area relationships for mammals in rainforest fragments in tropical Queensland; contrasting patterns in 1986–1987 (species = 3.40 area$^{0.08}$) and 2006–2007 (species = 1.67area$^{0.22}$).

(Laurance 1991*b*; Laurance & Curran 2008; Turton 2008). Did these storms affect animal detectability? It has been suggested that, at least for arboreal possums and tree-kangaroos in intact forest, the principal effect of the 2006 cyclone was to increase animal detectability because the damaged forest was more open than undisturbed forest (Kanowski et al. 2008). The 2006 cyclone caused greater forest damage than the one in 1986, and we estimate this damage enhanced animal detectability by approximately 8% in 2006–2007 relative to 1986–1987. Correcting for this difference had minimal effects on our statistical analyses, and we elected to use uncorrected data because of a general concern about potentially creating artificial structure in our data set. One caveat is that the estimated abundance declines in several species (Table 2) may be conservative, because animal detectability was somewhat higher in 2006–2007 than in 1986–1987.

Dynamics of Mammal Assemblages

During our initial survey in 1986–1987, most forest fragments in our study area were already 20–50 years old.

Over the following 20 years, we documented 5 general changes in mammal assemblages.

First, species richness of mammals in fragments, which was already depressed relative to intact forest, declined even further over time (Fig. 3). This decline was greater in small than large fragments (Table 2), resulting in a steeper slope of the species–area relationship in 2006–2007 ($z = 0.22$) than in 1986–1987 ($z = 0.08$). This erosion of species richness mainly resulted from an absence of green ringtail possums and Lumholtz's tree-kangaroos in several smaller (<20-ha) fragments during our latter survey (Fig. 2). Hence, even in a fragmented landscape that had experienced almost no additional deforestation, species richness of larger mammals continued to decline over time. This decline is consistent with most models of extinction kinetics, which predict a relatively rapid loss of forest-dependent species in recently isolated fragments (Terborgh 1975; Brooks et al. 1999; Watson 2002). Eventually, the pace of species loss is expected to decrease as fragments approach an "equilibrium" species richness. In simple island-biogeographic models (MacArthur & Wilson 1967), this equilibrium is determined solely by the size and isolation of the fragment, which are assumed to govern the rates of species colonization and extinction in fragments. In reality, however, species losses and gains in fragments can be strongly influenced by additional factors such as edge effects (Laurance et al. 2002); human activities, such as logging and hunting (Laurance & Cochrane 2001); and the dynamics of the surrounding matrix vegetation (Gascon et al. 1999; Laurance & Laurance 1999).

Second, 4 mammal species, the coppery brushtail possum, green ringtail possum, Herbert River ringtail possum, and red-legged pademelon, declined significantly in abundance in small (<20-ha) or large (>20-ha) forest fragments, and the Lumholtz's tree-kangaroo exhibited a nearly significant decline ($p = 0.08$) in large fragments (Table 2). Among these species, the tree-kangaroo and Herbert River ringtail are considered the most vulnerable to fragmentation (Pahl et al. 1988; Laurance 1990), the former because of its low population density, vulnerability to roadkill, and predation by domestic dogs and dingos
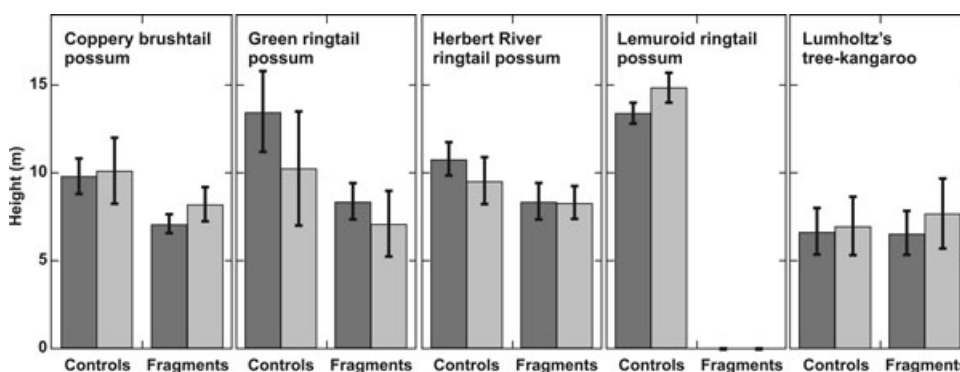

Figure 4. Mean foraging heights of arboreal mammals in intact forest (controls) and in fragments and stream corridors (fragments) in 1986–1987 (dark-gray columns) and 2006–2007 (light-gray columns). Error bars show 95% CIs.

(Newell 1999), and the latter because it is almost strictly arboreal and highly reticent to cross open habitat (Laurance 1990). In 1986–1987 coppery brushtails and green ringtails were at least as abundant in fragments as in intact forest, evidently as a result of their ability to cross relatively small expanses of open ground and dietary requirements that include a mix of secondary- and primary-forest plant species (Procter-Gray 1984; Laurance 1990; Jones et al. 2006). Similarly, pademelons are often abundant in forest fragments and are considered an edge-favoring species (Vernes et al. 1995). It is unknown why abundances of these species declined in 2006–2007, although many fragments were heavily disturbed by the 2006 cyclone (Laurance & Curran 2008). We suggest that this cyclone had a negative effect on mammal communities, at least in forest fragments where damage was intense and where resident mammal populations are small, despite a lack of evidence for such an effect in intact forest (Kanowski et al. 2008).

Third, Lumholtz's tree-kangaroos declined significantly in our 4 intact-forest sites (Table 2). The most likely explanation, we believe, is that the spotlighting routes we used in intact forest had previously been selectively logged, promoting a temporary flush of pioneer plant species, some of which are favored by tree-kangaroos (Procter-Gray 1984; Newell 1999). Except for control D (which partly encompassed private land), logging operations in our intact-forest sites were halted in 1988 when the region was protected as a World Heritage area, and young pioneer plants declined in these areas. It is also not inconceivable that sampling variation contributed to the apparent decline of tree-kangaroos, given their relative rarity, but this seems a less likely cause than successional changes in intact forest.

Fourth, the lemuroid ringtail possum has nearly vanished from fragmented and regrowth forest in our study area, with its abundance being just a tiny fraction (0.02%) of that in nearby intact forest. The lemuroid ringtail exhibits a suite of traits, such as being strictly arboreal, feeding almost entirely on the leaves of primary-forest trees, and requiring a hollow tree-cavity for daytime denning that makes it particularly vulnerable to forest fragmentation (Pahl et al. 1988; Laurance 1990). A key factor that predisposes lemuroids to local extinction is their strong reliance on primary forest, which means that populations in fragments are entirely isolated and therefore highly vulnerable to random demographic and genetic effects (Laurance 1990, 1991a). In a survey of 36 potential faunal corridors on the Atherton Tableland, the lemuroid ringtail was only ever detected in wide (100–300 m), primary-forest corridors that were directly linked to nearby intact forest (Laurance & Laurance 1999).

Finally, our most surprising finding was the detection of a lone lemuroid ringtail in a small (12.8-ha) fragment located just 220 m from intact forest (fragment 5, Fig. 1). It

seems inconceivable that a relict population of lemuroids persisted in this small fragment, which was isolated since at least 1951 (Pahl 1979). With its brilliant eyeshine, the lemuroid is the most easily detected of all the mammal species we encountered, yet it was never previously detected in the fragment despite repeated spotlighting surveys in 1979 (Pahl et al. 1988), 1986–1987 (Laurance 1990) and 1991–1992 (Vernes 1994). In 1986 only a narrow (generally <20 m wide), discontinuous band of regrowth linked the fragment with nearby intact forest. By 2006, however, this band had coalesced into a much wider (100–200 m wide) regrowth mosaic with a core of tall (>25 m) secondary-forest trees. Although lemuroids have never been detected in regrowth forest (Laurance 1990, 1991a; Laurance & Laurance 1999), the most plausible explanation, we believe, is that one or perhaps a few individuals recolonized the fragment from nearby intact forest. Heavy cyclone damage might have contributed to this by prompting some unusual animal-dispersal movements (J. W. Winter, personal communication).

Conservation Implications

Our results have 2 implications of general importance. The first is that fragment connectivity appears to play a key role in the maintenance of mammal species richness. In multiple-regression models, 2 landscape variables describing the size of discontinuities in stream corridors and the distance of fragments from other forest areas explained from 27% (1986–1987) to 56% (2006–2007) of the total variation in species richness. Moreover, among these mammal species there is a strong association between matrix tolerance and survival in fragmented forests, with corridor-using species persisting in many fragments and corridor-avoiding species tending to decline or disappear (Laurance 1990, 1991a, 1994, 1997).

These trends highlight the importance of faunal corridors for partially mitigating the effects of habitat fragmentation, a conclusion that accords with other studies of arboreal-mammal assemblages in Australia (Lindenmayer et al. 1994; Lindenmayer & Possingham 1996; Downes et al. 1997). We believe corridor effectiveness is likely to interact strongly with fragment isolation and that the most strongly forest-dependent species, such as the lemuroid ringtail possum, are more likely to use corridors to traverse short rather than long distances (Laurance & Laurance 2003). For vulnerable mammal species in tropical Queensland, the best corridors will be wide (>200 m) and continuous; composed of primary forest (or at least mature, species-rich secondary forest); and occur at higher (>750 m) elevations (Laurance & Laurance 1999). Targeted reforestation efforts are increasingly being used to accelerate the establishment of faunal corridors in fragmented landscapes (Goosem & Tucker 1995; Tucker & Murphy 1997; Lamb et al. 2005).
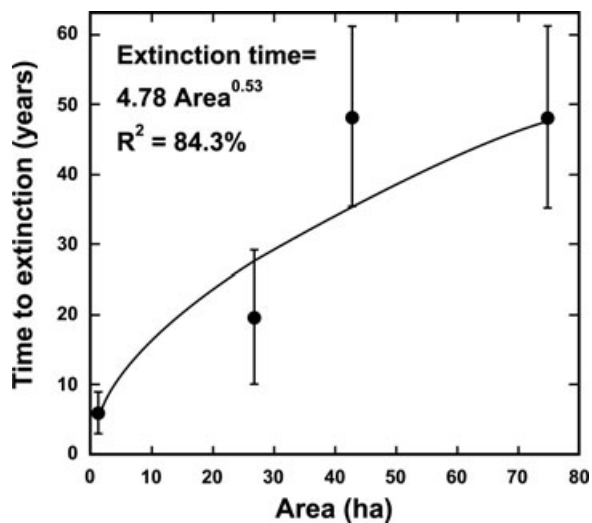
*Figure 5. Estimated time to local extinction for the lemuroid ringtail possum (*Hemibelideus lemuroides*) in tropical Queensland as a function of fragment area. Error bars indicate the possible range of fragment ages.*

The second key implication is that the most vulnerable species in this region, such as the lemuroid ringtail possum, musky rat-kangaroo (*Hypsiprimnodon moschatus*), spotted-tailed quoll (*Dasyurus maculatus*), Atherton antechinus (*Antechinus godmani*), and Southern Cassowary (*Casuarius casuarius*), have disappeared or declined in forest fragments (<600 ha in area) with surprising rapidity (Laurance 1997). The kinetics of local extinction are especially well documented for lemuroid ringtails because of their high detectability; the well-known history of forest fragments in our study area (see Pahl 1979; Laurance 1990, and references therein); and because arboreal mammals in our fragments were repeatedly surveyed by spotlighting in 1979 (Pahl et al. 1988), 1986–1987 (Laurance 1990, 1991*a*), and 2006–2007 (this study). These observations reveal that lemuroids disappeared from a small (1.4-ha) fragment in 3–9 years (Laurance 1990), from a medium-sized (27-ha) fragment in 10–29 years (this study), and from 2 larger (43–75 ha) fragments in 35–61 years (Laurance 1990). This pattern suggests a strong effect of fragment area on time to extinction (Fig. 5), which is in agreement with other studies (Brooks et al. 1999; Ferraz et al. 2003). The curvilinear relationship in Fig. 5 is best fitted by a power function ($R^2 = 84\%$); linear, logarithmic, and exponential models provided weaker ($R^2 < 81\%$) fits.

Extrapolating from this curve (Fig. 5) implies that an isolated forest fragment of approximately 300 ha would be required to increase persistence time of lemuroids to a century, whereas a far larger fragment (approximately 24,000 ha) is needed to increase persistence time to a millennium. Obviously this is very rough reckoning, but

it suggests that large, intact forest tracts are required to ensure the long-term persistence of lemuroid ringtails and other vulnerable wildlife. Moreover, such models do not consider the strong likelihood that global warming and atmospheric changes will diminish habitat quality for cool-adapted, upland-endemic species, such as the lemuroid ringtail (Hilbert et al. 2001, 2004; Kanowski 2001; Williams et al. 2003), in which case minimum critical areas for population survival might well be much larger.

Acknowledgments

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