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Near-Complete Extinction of Native Small Mammal Fauna 25 Years After Forest Fragmentation

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Tropical forests continue to be felled and fragmented around the world. A key question is how rapidly species disappear from forest fragments and how quickly humans must restore forest connectivity to minimize extinctions. We surveyed small mammals on forest islands in Chiew Larn Reservoir in Thailand 5 to 7 and 25 to 26 years after isolation and observed the near-total loss of native small mammals within 5 years from <10-hectare (ha) fragments and within 25 years from 10- to 56-ha fragments. Based on our results, we developed an island biogeographic model and estimated mean extinction half-life (50% of resident species disappearing) to be 13.9 years. These catastrophic extinctions were probably partly driven by an invasive rat species; such biotic invasions are becoming increasingly common in human-modified landscapes. Our results are thus particularly relevant to other fragmented forest landscapes and suggest that small fragments are potentially even more vulnerable to biodiversity loss than previously thought.

Rapid deforestation poses a major threat to one of the planet's greatest bastions of biodiversity, tropical forests (*1*–*4*). Whether by chance or design, small fragments of forest typically persist in the aftermath of deforestation, effectively islands within a sea of agriculture, urbanization, or other modified lands that are unsuitable for most forest species (*5*, *6*). Many of the species that originally occupied the forest will disappear from these isolated fragments, but this loss occurs over a relaxation period until a new, more depauperate equilibrium community is reached (*7*). The number of species that will ultimately disappear from a forest fragment—its "extinction debt" (*8*)—will vary based on the size of the fragment, its surrounding habitat, the vagility of its constituent and neighboring species, and its distance from source populations (*9*).

Extinctions can be averted by reducing deforestation rates and reforesting fragmented forest landscapes (*10*). However, it remains uncertain how quickly such actions must be taken and what minimum fragment size is required to maintain functioning biotic communities. For 1000-ha forest fragments in Kenya, half of the total bird extinctions are projected to occur within 50 years, giving conservationists some time to mitigate conditions in large fragments (*11*). However, for smaller fragments, relaxation times are generally much more rapid (*12*, *13*), and for ≤100-ha fragments, half of their original species can disappear within 15 years (*14*). Most studies of extinctions from forest fragments have focused on birds (*11*–*14*), and little is known about the sensitivity of other taxonomic groups.

We surveyed small mammals on forest islands in a reservoir five separate times after isolation to assess the rate of species loss from forest fragments. Reservoirs can form useful natural laboratories to estimate extinction rates from isolated forest patches (*15*, *16*). Chiew Larn Reservoir in southern Thailand was formed in 1986–1987 when 165 km[2] of forest was flooded, creating over 100 islands in the process (Fig. 1) (*17*). We selected 16 islands in the reservoir ranging from 0.3 to 56.3 ha in area and surveyed small mammal communities 5 to 7 years (for 12 of the 16 islands) and 25 to 26 years after isolation. Chiew Larn Reservoir is surrounded by two protected areas that form part of the largest (>3500 km[2]) contiguous forest area in southern Thailand. All surveyed islands were unoccupied by humans (*18*).

We found that native small mammal communities disappeared rapidly after fragmentation. By 5 to 7 years after fragmentation, three large islands in our sample (10 to 56 ha) sustained 7 to 12 species of small mammals (Table 1), which was similar to diversity found on the nearby mainland (table S3) (*19*). However, on nine small islands (<10 ha), species richness rapidly declined to

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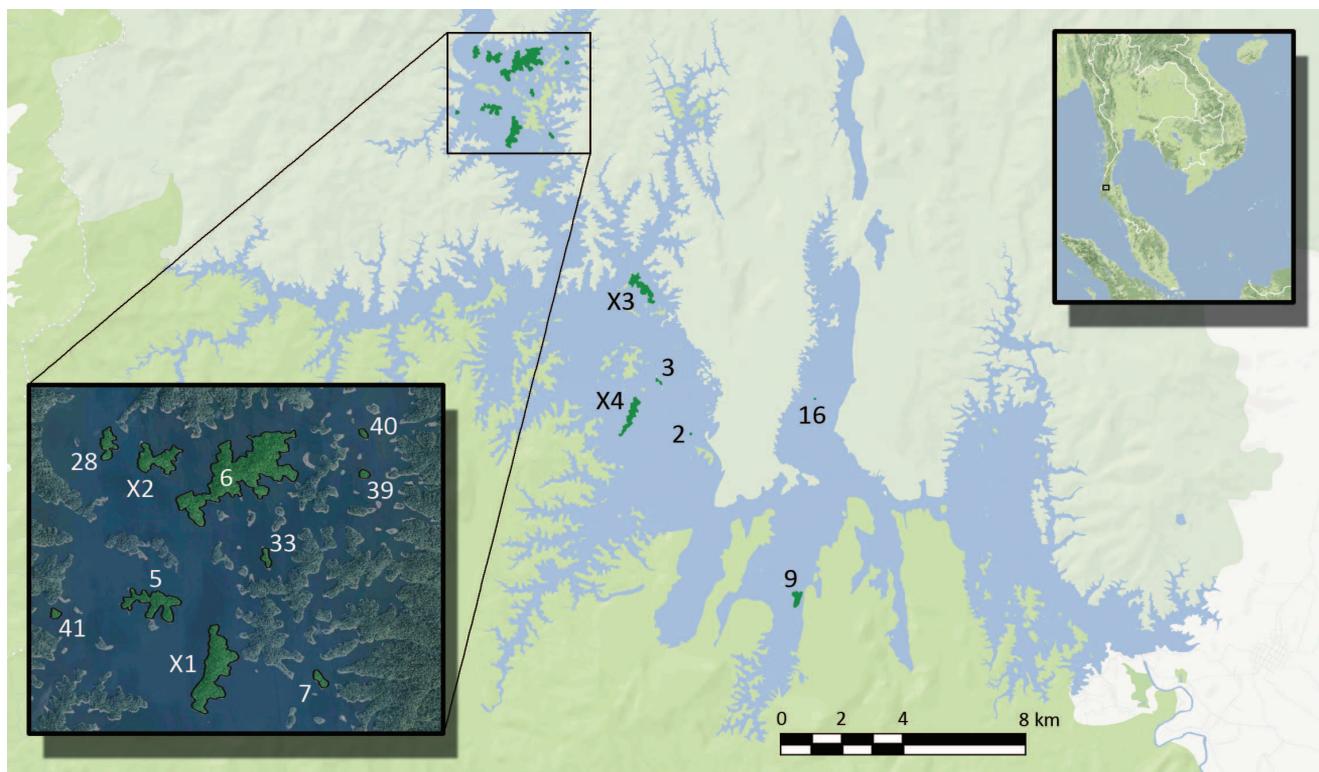
Fig. 1. Islands sampled in Chiew Larn Reservoir, Thailand. The reservoir is surrounded by protected forest areas in Khao Sok National Park to the south and west (shaded dark green) and Khlong Saeng Wildlife Sanctuary to the north and east (shaded light green). The 12 islands sampled during all surveys are labeled by island number [in the sense of (19)], and the additional four islands surveyed in more recent surveys are labeled X1 to X4. The dam is located in the lower right corner of the figure. The location of the reservoir in southern Thailand is shown in the regional map inset.

Table 1. Number of small mammal species found on islands 5 to 7 years and 25 to 26 years after isolation. The maximum number of species observed on each island is reported. Islands X1 to X4 were only surveyed 25 to 26 years after isolation.

Island	Area (ha)	Richness (5 to 7 years)	Richness (25 to 26 years)
6	56.3	12	5
5	12.1	9	3
9	10.4	7	1
28	4.7	2	2
7	1.9	3	2
33	1.7	1	1
3	1.4	2	1
41	1.1	3	1
39	1.0	3	1
40	0.8	2	1
2	0.4	2	1
16	0.3	2	1
X1	23.5		2
X2	10.1		2
X3	24.4		2
X4	21.2		1

Fig. 2. Small mammal species richness per transect in large (10.1 to 56.3 ha, n = 7) and small (0.3 to 4.7 ha, n = 9) islands 5 to 7 years and 25 to 26 years after isolation. Plotted are median values, interquartile ranges, and full ranges (outliers are plotted as open circles). The upper dashed line represents the number of small mammal species found in surrounding mainland forest (table S3).

just one to three species during these initial surveys. After 25 to 26 years, native small mammals had virtually disappeared from all 16 islands (Fig. 2, figs. S1 and S2, Table 1, and table S1).
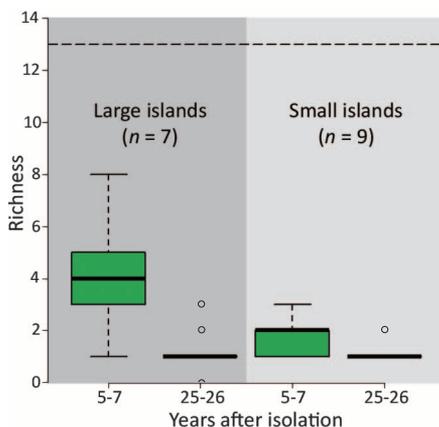
Species richness on islands was most strongly correlated with area, but there was an important contribution of time since isolation, as well as a weak negative interaction between area and time since isolation (table S2). We also surveyed small

mammal communities in the mainland forest surrounding the reservoir and detected no similar decrease in diversity (table S3).

To describe the process of biotic relaxation over time for our islands of different size, we derived an island biogeographic model. The model included both immigration and extinction, which are negatively and positively proportional to the number of species on the islands, respectively (18). The model estimates the number of species occupying forest fragments before isolation and calculates the rate of extinction. The best-fitting model was

$$S_t = 0.751 - (0.751 - 2.223a^{0.482})e^{-0.0732t} \text{ (1)}$$

where S_t is the number of species at time t, a is island area, and t is time since isolation. This model fitted our data well (coefficient of determination = 0.783, fig. S3) and predicted that, before isolation, the largest island (56 ha) had 15.5 species and the smallest island (0.3 ha) had 1.2 species. For all islands, the mean time to extinction of half of the resident species ($t_{1/2}$) was 13.9 ± 3.9 years. Full relaxation to just one species was projected to occur within 40 years, regardless of fragment size (Fig. 3A). To determine the sensitivity of these results to the choice of underlying model, we also constructed a variant of the extinction-immigration component and considered two other species-area relationship models (Kobayashi

Fig. 3. Loss of species from forest fragments of various sizes based on model (1). (A and B) Number of species remaining and number of species lost per year on fragments after time (in years) since isolation. **(C)** Time to extinction of half of the species ($t_{1/2}$) initially present on forest fragments according to fragment area.
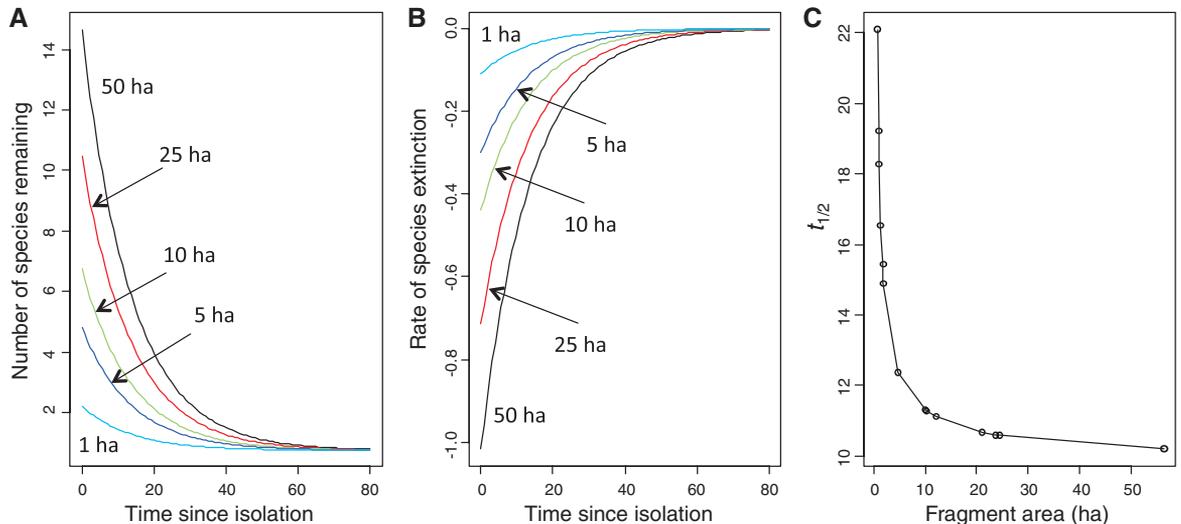
and Gleason) in addition to the Arrhenius power-law model; results differed little from those derived above (18). Our modeled extinction rates are similar to those observed by Ferraz et al. (14), who found that 100-ha forest fragments in the central Amazon lost half of their understory bird species in less than 15 years. However, our results diverge with the unexpected finding that species diversity declined faster on larger than on smaller islands (Fig. 3B), with the former having a shorter extinction half-life (Fig. 3C). This is a consequence of the catastrophic faunal collapse we documented across the entire archipelago of fragments, so that larger islands, which initially sustained the most species and the most forest specialists, exhibited the most rapid rate of species loss.

With few exceptions, only the Malayan field rat *Rattus tiomanicus* remained on islands 25 years after isolation (table S1). Commensal rodents such as *R. tiomanicus* are among the most common invasive species worldwide and often have a devastating effect on native fauna, particularly birds (20–23). *R. tiomanicus* does not occur naturally in undisturbed tropical forests of Southeast Asia, but is common in secondary forests, agricultural areas, and villages (24) and probably spread from such habitats to islands and reservoir fringes after inundation. By the time we had resurveyed islands 25 to 26 years after isolation, few native small mammals remained (just 13 and 9 individuals, respectively, were detected on the 16 sampled islands, not including the invading *R. tiomanicus*; table S1). At that point, all islands were dominated by the invasive rodent and if not already in ecological meltdown (25), were well on their way to becoming *Rattus* monocultures.

Small forest fragments can play important conservation roles in some contexts (26), including enhancing landscape connectivity and sustaining locally endemic species in regions such as Madagascar and the Brazilian Atlantic Forest, where most native vegetation has vanished. In these highly fragmented regions, however, mam-

malian communities can disappear rapidly, as has been observed for medium- and large-sized mammals in the Brazilian Atlantic Forest (27). In fact, regional estimates of extinctions from deforestation are probably worse than previously thought, because studies applying species-area curves have assumed that the persisting forest was contiguous (28). Additionally, exotic species such as *R. tiomanicus* are rapidly expanding into human-transformed and regenerating forest landscapes that increasingly dominate many tropical regions (29) and appear capable of sharply accelerating extinction rates in some fragmented landscapes. Hence, our findings, in which fragments were invaded and evidently profoundly destabilized by an invasive species, have considerable relevance for nature conservation in fragmented habitats globally. The apparent synergism between habitat fragmentation and species invasion underscores a dire need to maintain large intact forest blocks to sustain tropical biodiversity (4, 30).

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