Commentary

Theory meets reality in fragmented forests

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For those of us who study fragmented ecosystems, island biogeographic theory (MacArthur & Wilson, 1967) is still in many ways the conceptual Mecca towards which we face when thinking about imperiled biodiversity. The theory posits that species richness results from a dynamic equilibrium between the opposing forces of colonization and extinction, which are governed respectively by island isolation and size. Small islands lose species faster than big islands, the theory suggests, because they contain small populations of species that are inherently likely to disappear from random demographic fluctuations.

But reality is both more complicated and more interesting than theory suggests (see Laurance, 2008 for a recent synthesis). In the real world, species in fragmented landscapes are beset by more than just a contraction of their habitat; they also face a daunting array of external challenges. Edge effects – physical and biotic changes associated with abrupt fragment boundaries – can alter many aspects of fragment ecology. Pollutants and invasive species can penetrate into fragments from surrounding modified lands, further altering fragment ecology. In the tropics, many fragments are selectively logged, harvested for fuel wood and other products, and heavily hunted. In provinces suffering major changes in land cover, shifts in evapotranspiration, rainfall, albedo, subsurface water tables and fire regimes can dramatically alter the physical environment in which fragments occur.

The net effect of such alterations is that the biotic and abiotic attributes of fragments are changing in many ways all at once. For instance, large, dominating predators tend to be killed off by hunters in fragmented landscapes, sometimes allowing smaller-bodied omnivores such as raccoons, coatis and opossums to proliferate; and these in turn may have serious impacts on nesting birds and small vertebrates. Many such ecological changes tend to co-vary with fragment size, because smaller fragments are inherently more vulnerable to external vicissitudes and threats. This, then, raises an important question: to what extent have earlier investigators wrongly presumed that species losses in fragments are caused by random demographic fluctuations, as posited by island biogeographic theory, when in fact they were largely driven by other environmental insults that also occur in fragments?

In this issue of Animal Conservation, Ken Feeley and John Terborgh step into the fray with an analysis of species extinctions and trophic distortions on small islands in a Venezuelan hydroelectric reservoir named Lago Guri, which was created in 1986. Supporting tropical dry forest, the Lago Guri islands have become famous as Terborgh and his students have insightfully revealed just how quickly these ecosystems unravel when fragmented. As a model system, such islands have certain advantages over mainland fragments, as they are surrounded by a matrix – water – that is homogeneous and serves as a virtually complete barrier to many species.

Over the past decade Feeley and Terborgh have studied the extinctions of forest birds on 11 Lago Guri islands, most of which are small (10 of the 11 islands are under 12 ha in area; the last spans 211 ha). Earlier studies by Terborgh’s group have shown that the trophic structures of these islands are severely distorted, especially on the smallest islands (e.g. Terborgh et al., 2001). Large predators such as jaguars, pumas and harpy eagles have essentially vanished from all the islands. Medium-sized islands (9–12 ha) generally support mid-sized mammals such as howler monkeys, capuchin monkeys, agoutis and armadillos. The smallest islands (<3.5 ha) are ecologically depauperate but often have hyperabundant generalist herbivores, particularly howler monkeys and leaf-cutter ants.

Such trophic distortions could potentially affect the survival of wildlife such as forest birds. Feeley and Terborgh use path analysis to contrast the importance of island area versus three kinds of prominent trophic distortions – elevated nest predation, hyperabundant howler monkeys and hyperabundant leafcutter ants – in driving bird extinctions. The three trophic distortions are themselves at least partially a consequence of fragment size, and thus Feeley and Terborgh frame their study as a comparison of the direct versus indirect effects of fragment area on species extinctions.

Using two estimates of avian extinction rates for each island (one that measures only species extinctions and a second that incorporates both extinctions and colonization), the authors conclude that the indirect effects of fragmentation were 1.5–7.3 times as important as direct effects in causing species extinctions. This is an intriguing result, for it implies that local extinctions of species may be driven more
strongly by ecological distortions in fragments than by fragment size per se. In other words, ecological wackiness on islands is evidently trumping demographic randomness as a driver of extinction.

But is this really a compelling explanation? I see two potential weaknesses of the Lago Guri story as presented by Feeley and Terborgh. Firstly, it is not strikingly apparent how some of the ecological distortions they describe could affect bird diversity. For instance, they found no evidence that elevated nest predation — to me, the most plausible driver — caused bird extinctions (though initial bird losses on some islands, before the study began, might have obscured such effects, according to Terborgh). They did, however, find that bird extinctions were lower on islands with lots of howler monkeys, and they suggest that howlers could be promoting primary productivity — and thereby indirectly helping birds to survive — by consuming and defecating lots of foliage. However, howlers tend to poop in one spot (they have actually created giant poop piles on some of the islands) and so they seem rather better at concentrating nutrients in one place than distributing them around democratically. In fact, islands with many howlers actually have lower nutrient availability but, surprisingly, faster tree growth (Feeley & Terborgh, 2005, 2006), so we are left scratching our heads about this one. The final ecological linkage that Feeley and Terborgh surmise — that islands with hyperabundant leafcutter ants lose bird species more rapidly — does seem more plausible, given the fact that the rapacious ants have virtually defoliated the understory vegetation on smaller islands.

A second concern is that the Feeley and Terborgh study is entirely correlative in nature. They have only 11 islands in this study, limiting their statistical power, and their smallest islands also tend to be the most isolated. This does not necessarily obviate their findings, but one would feel more comfortable if at least some of the intriguing ecological effects they postulate — such as the putatively positive effect of howler monkeys on bird diversity — were backed up with some experimental evidence. It can be tempting, with small sample sizes, to invoke compelling post hoc explanations and then explain away inconsistencies as mere artifacts or outliers.

At the end of the day we are left with Feeley and Terborgh’s contentions that the effects of island area were ‘primarily indirect and mediated through altered trophic interactions’ and that such events are likely to be ‘a typical consequence of habitat fragmentation, even in mainland systems’. Hmm. I want to believe these assertions — I really do — as they have all kinds of sexy implications, such as the notion that we must maintain intact predator assemblages in our nature reserves. But I suspect that small islands embedded in a big lake — which sharply arrests dispersal for many animal species — are simply more prone to dramatic ecological warping than are mainland fragments. Feeley and Terborgh have attacked an important research topic with vision and verve, but I will remain less than fully swayed until someone shows me comparably dramatic effects in ‘real’ habitat fragments.

References


