

Dispatches

Conservation Biology: Predicting Birds' Responses to Forest Fragmentation

Understanding species' ecological responses to habitat fragmentation is critical for biodiversity conservation, especially in tropical forests. A detailed recent study has shown that changes in the abundances of bird species following fragmentation may be dramatic and unpredictable.

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Because of unprecedented rates of deforestation and forest degradation, habitat fragmentation has become a major issue in conservation biology. Forest fragments are often scattered among human-dominated urban and agricultural areas. Forest fragmentation results in three prominent changes: reduced forest area, increased isolation among fragments, and creation of edges where forests abut non-forested habitats. Because of factors such as the loss of microhabitats and the influx of invasive competitors and predators, fragments significantly decline, over time, in their conservation value for many forest species [1,2] (Figure 1). Which species flourish or perish as a result of fragmentation is a critical question. Ecological traits such as body size, diet, mobility and specialization often correlate strongly with fragmentation sensitivity [3–5]. In some ecosystems, however, it may be impossible to predict species' responses to fragmentation [6]. This is illustrated by a recent study [7] which has shown that, in southeast Australia, bird species' abundances changed very unpredictably after the fragmentation of *Eucalyptus* woodlands and even some species in the same genus differed greatly in their responses.

Area has been reported as the strongest predictor of species richness in forest fragments [8–10]. However, isolation can also affect species richness and abundance in fragments [11]. The species–area relationship (Figure 2) has been

widely used to estimate and predict biotic losses from human-modified landscapes [12,13]. The rule-of-thumb is that a 90% loss of habitat area leads to a ~25–50% loss of species [14]. The predictive power of this relationship may be weak, because it does not account for either habitat heterogeneity or fragmentation, but it is the only such existing model [15]. Although the identities of disappearing species are as important as their number, how the abundances of species change because of habitat degradation has been conceptually and empirically little developed. This is a critical lacuna as the disappearance of functionally important and irreplaceable groups such as specialists, scavengers or seed dispersers can affect the entire community [16].

Fragmentation frequently results in the 'cutting' of the long tail of the rank-abundance curve, as rare species, particularly diverse in tropical forests, often disappear first (see Figure 1 in [7]). Such 'nested' distributions where "species present at species-poor sites are subsets of those present

at species-rich sites" [17] mean that species that will disappear from fragments can be predicted. Species that are rare, sedentary or specialized in their habitat requirements are expected to have lower persistence [6].

Mac Nally [7] examined whether the relative abundances of woodland bird species can be predicted following fragmentation. He surveyed birds in 73 remnants ranging from 15 ha to 2900 ha in size in south-eastern Australia. Because of the absence of pre-fragmentation data, three large remnants (16,000–41,000 ha) were used as reference sites. Although relative-abundance distributions changed little, suggesting reorganization of abundances at ecological time frames, the changes in the abundances of individual species were not predictable. Fragmentation did not necessarily favor species common at reference sites. The bird communities in smaller fragments were also not nested subsets of the reference ones, contrary to what some studies have shown elsewhere [4,9,17–19]. Mac Nally [7] suggests that our knowledge of how bird communities organize themselves in fragmented landscapes is shallow and that more research should be



Figure 1. An example of a fragmentation-sensitive Southeast Asian forest specialist, the Black-browed Barbet (*Megalaima oorti*). Photo by Malcolm Soh.

conducted in this direction. We agree with Mac Nally that we must look beyond predicting species richness in human-altered habitats and focus on the factors that change species abundances, which he originally depicted with the 'abundance spectrum'.

We suggest that nestedness analysis be more widely (albeit judiciously [17]) employed in fragmentation studies, and that existing fragmentation data be meta-analyzed to understand regional and ecological differences in nestedness. Bird communities are often comprised of distinctive groups of species with similar responses to fragmentation [9]. In nestedness analyses, pooling all species can obscure important patterns [17] as a result of the idiosyncratic responses of more mobile and less specialized species [4]. Specialized and sedentary species, typical of tropical humid forests, are more likely to show nested distributions [18], and these species are also the ones that are more extinction-prone [9,10,20]. Other examples of more nested groups are forest understory species, large-bodied species and species of conservation concern [4,9]. Comparing the nestedness of ecologically distinct groups will reveal those that are more nested and hence more vulnerable to fragmentation [4,9]. Species-by-species examination of the nestedness matrix (a graphic representation of species' distributions, see Figure 1 in [17]) is also valuable, as some species, including sensitive ones, may be affected by factors other than fragmentation [17]. Used in this manner, nestedness analysis becomes an important conservation tool.

Highly nested distributions imply that a few large patches can conserve most or all species. However, statistically significant nestedness does not mean perfect nestedness [17], and many species can exhibit idiosyncratic patch occupancies [7]. Differences in species extinction or colonization rates are the two main causes of nestedness in fragments. Species richness patterns become less nested and more unpredictable if

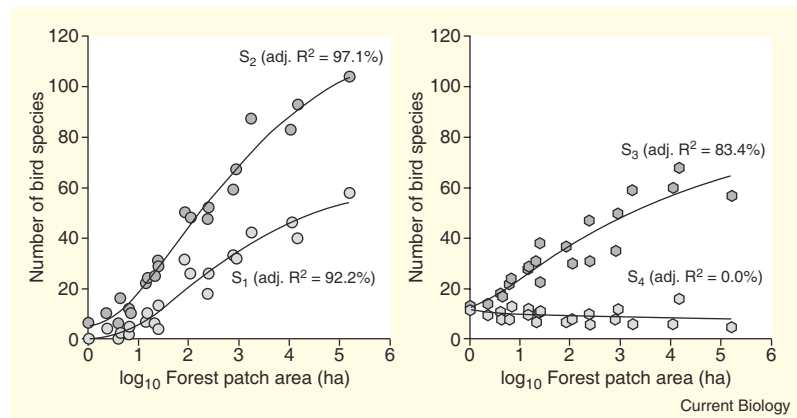


Figure 2. Species–area relationships for four avian functional groups that vary in their habitat requirements.

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species vary little in their vulnerability to extinction or in their ability to colonize fragments [4,18]. Birds that are less specialized and/or have small home ranges are less vulnerable to extinction. Colonization likelihood is higher if birds are more mobile (e.g. long-distance migrants, nomadic species) [18] or if fragments are less isolated.

Because mobile and generalist bird species reduce nestedness, temperate, more seasonal, and more open ecosystems, which harbor higher proportions of migrant species and habitat generalists (Figure 3), should be less nested than tropical humid forests [4,9,19]. But global comparisons are lacking.

Mac Nally's [7] study took place in a temperate, dry habitat (300–700 mm of rain per year) and open *Eucalyptus* woodlands. As expected, the bird community is relatively mobile and generalized, helping explain the reduced nestedness and high idiosyncrasy observed. The study species, on average, resemble other temperate woodland birds in their mobility and habitat specialization, and are more mobile and more flexible in their habitat use than most tropical forest birds (Figure 3).

Increased habitat similarity between fragments and the surrounding matrix also reduces isolation and nestedness. A more 'permeable' matrix can increase the presence of some common, generalist species in small

fragments, but reduced isolation can also hamper the persistence of some rare, specialized species in larger fragments if these birds leave and do not come back [19]. Matrix–remnant similarity contributes to the idiosyncrasy of species distributions in the Mac Nally study [7]. Compared to closed, humid tropical forests, open, dry, temperate woodlands are more similar to surrounding farmlands. Interestingly, the study fragments do not exhibit a species–area relationship — $S = 75.6 \cdot A^{-0.0027}$, $r^2 = 0.0033$, based on species lists provided by Mac Nally [7] — further suggesting that the fragments in this landscape are less isolated than the surrounding matrix than is typical of tropical forest remnants.

The presence of an unusual 'despotic' species, the colonial and aggressive Noisy Miner (*Manorina melanocephala*), is another factor that contributes to the difficulty of predicting post-fragmentation abundances in this system. This species dominates forest fragments and drives out most native forest species, regardless of their ecological differences [6]. Such a native species is hardly equaled in other forest fragmentation studies, especially in the tropics. As open, dry woodland habitats that are frequented by relatively generalized and mobile bird species and where fragments are dominated by the unique Noisy Miners, Australian

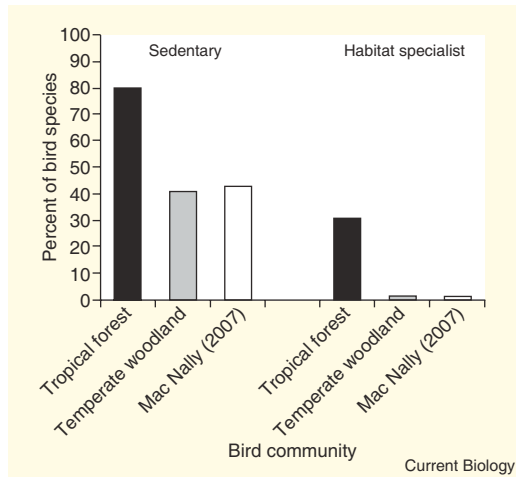


Figure 3. Comparison of world's tropical forest (5086 species) and temperate woodland birds (472 species), with the 123 study species.

Sedentary species do not make any long-distance movements (for example, migration, altitudinal migration, nomadic movements). 'Habitat specialist' indicates a species that is confined to only one main habitat (for example, forest only or woodland only). The list of study species was provided by MacNally. For a description of the bird ecology database that was used for this analysis, see [20].

ironbark woodlands are not representative of most forests, underlining the need for global syntheses of avian responses to fragmentation.

The difference between a species' abundance rank in the reference plots and its rank in fragments is a key measure of its response to fragmentation. Ecological correlates of rank differences can illuminate the causes of fragmentation sensitivity. Based on the fragments' species lists we obtained from Mac Nally [7], we compared the basic ecological characteristics of species that declined versus increased in the smallest (A2) study fragments in relation to the reference areas. Forest specialists, insectivores, nectarivores, and species with lower clutch sizes were fragmentation-sensitive whereas open habitat species, granivores, and raptors increased in small fragments. Interestingly, so did the large-bodied species (median body mass 142 g versus 21 g), contrary to most tropical forest findings [4].

Even when species responses to fragmentation are highly idiosyncratic, analyses of rank differences can reveal interesting ecological patterns and highlight potentially vulnerable species. There is a major need for global meta-analyses of fragmentation responses, combining standardized measures [17,18] with existing

data. These analyses will help formulate the drivers of fragmentation sensitivity and nestedness, explain regional differences, and contribute to the development of ecological theory [7]. For example, the same characteristics that make fragments less nested (more permeable matrix, high proportion of generalist, mobile, and fragmentation-tolerant species) can also make them more vulnerable to invasive species, but this has been little-studied. We hope that Mac Nally [7] will inspire similar studies worldwide, particularly in the tropics where an improved understanding of species' responses to fragmentation is critical to the conservation of biodiversity.

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