

COMMENTARY

Defining the conservation value of secondary tropical forests

D. H. Dent

Smithsonian Tropical Research Institute, Apartado, Balboa, Panama

CorrespondenceDaisy H. Dent, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panama.
Email: daisy.h.dent@gmail.com

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Over the last 50 years, tropical forests have been exploited for timber extraction, cleared for agriculture, pasture and roads and degraded by wildfires and overhunting (Laurance & Peres, 2006; Sodhi *et al.*, 2007). The result of these processes is that human-modified landscapes, composed of a mosaic of old-growth (OG) forest fragments, degraded forest, regenerating forest and agricultural land, now cover large areas of the tropics (Gardner *et al.*, 2009). Although large expanses of OG forest remain and 9.8% of the tropical forest biome is protected within strict reserves, recent estimates suggest that there is now a larger area of secondary and degraded tropical forest than there is undisturbed OG (FAO, 2006; Schmitt *et al.*, 2008; Brooks *et al.*, 2009). Therefore, the long-term conservation of tropical forest biodiversity is dependent on the capacity of human-modified landscapes to maintain viable populations of tropical forest species.

Secondary forests (SF) are increasingly important habitats within fragmented tropical landscapes (FAO, 2006), and the extent to which regenerating SF can prevent extinctions of tropical forest species due to loss of OG has been the focus of a highly publicized debate (Brook *et al.*, 2006; Wright & Muller-Landau, 2006a,b; Gardner *et al.*, 2007; Laurance, 2007). Three recent meta-analyses have shown that the proportion of tropical forest species present in SF is high (Dunn, 2004; Chazdon *et al.*, 2009; Dent & Wright, 2009). In the studies reviewed by Dent & Wright (2009), the mean proportion of OG species present in SF < 10 years old was 0.51 (± 0.02), with similarity to OG increasing with SF age. For example, in SF > 50 years old, the mean proportion of OG species present was 0.80 (± 0.06), supporting the argument that SF can play a vital role in the conservation of OG species. Sberze *et al.*'s (2010) study also corroborates this argument, demonstrating that the nocturnal bird communities in 30-year-old SF and neighboring OG in the Brazilian Amazon were indistinguishable.

All recent reviews of SF biodiversity have highlighted the methodological deficiencies in studies of SF faunal communities (Dunn, 2004; Bowen *et al.*, 2007; Gardner *et al.*, 2007; Chazdon *et al.*, 2009; Dent & Wright, 2009). Low replication of sampling sites, insufficient or uneven sampling and inconsistencies in sampling methods severely limit our capacity to

draw conclusions about comparisons of faunal communities in SF and OG (Gardner *et al.*, 2007; Dent & Wright, 2009). The study by Sberze *et al.* (2010) sets new methodological standards; the authors use a uniquely rigorous sampling methodology, sample repeatedly throughout the year and have exceptionally large numbers of replicate sample sites in both SF and OG. To evaluate SF–OG similarity, it is critical that we have an understanding of background variation within each of these forest types, and yet just 11 of the 65 studies reviewed by Dent & Wright (2009) included replicate sites in both SF and OG. In contrast, Sberze *et al.* (2010) sampled 30 replicate OG sites and 24 replicate SF sites, and maintained a minimum distance of 400 m between sampling sites to reduce the detection of individuals at more than one site. This uniquely robust dataset, combined with statistical analyses, which accounted for detection failure and spatial autocorrelation, allowed them to make strong inferences about differences in occupancy between forest types and among species. This rigor sets a much-needed standard for faunal comparisons between SF and OG, and further studies that sample broader taxonomic groups with similarly rigorous methods and replication are urgently required.

Determining the proportion of OG species that can persist in SF remains the key research focus, but we must also begin to determine the limits of species conservation in SF. We need to identify which OG species are consistently absent from SF and the defining traits of these species. The faunal communities of many SF sites have a high representation of OG species (> 70% of OG species), and yet still lack local endemics and species with specialized dietary or habitat requirements (e.g. Spitzer *et al.*, 1993; Veddeler *et al.*, 2005; Renner *et al.*, 2006). Therefore, it is possible that the species that are consistently absent from SF also tend to be the most vulnerable species in undisturbed habitats. Using life-history traits to describe species may enable us to make more general statements about which species are most at risk from loss of OG habitat. Vagility is an important trait because it determines a species' ability to disperse and colonize regenerating forest. Volant invertebrates and vertebrates (butterflies, birds and bats) accumulate more rapidly in SF than less vagile taxa (Chazdon *et al.*, 2009).

There are many more specific traits related to species dietary and behavioral requirements that can help to tease apart differences in species occupancy across different habitats. For example, the diet and foraging behavior of the nocturnal bird species that Sberze *et al.* (2010) surveyed may explain why many species had higher occupancy in SF than OG sites. Owls predate small mammals, which Sberze *et al.* (2010) postulate may be more abundant in SF. Nightjars and potoos forage from perches, making short flights into the open air to catch flying insects, and suitable open areas may be more abundant in SF than OG. Nocturnal birds, therefore, have dietary requirements and foraging behavior that may be met more easily in SF than in OG. Lees & Peres (2008, 2009) have shown that morpho-ecological traits and foraging guilds of bird species can be linked to persistence in highly fragmented forests. They found that medium- and large-sized, non-flocking, canopy frugivores and omnivores were most tolerant of fragmentation, whereas small, flock-following, terrestrial insectivores were most vulnerable to fragmentation (Lees & Peres, 2008). Nevertheless, the traits that allow persistence of species in forest fragments may be very different from those related to presence in SF and will surely depend on the site and landscape characteristics of the SF.

Future SF research will need to couple studies of SF occupancy with the collection of species life-history data. The challenge, therefore, is to collect and report suitable species trait data, such as body mass, range size, abundance in OG, dietary preferences and habitat requirements for foraging and breeding. Because the rate at which secondary forests accumulate species is strongly affected by the initial site conditions and the surrounding landscape (Chazdon *et al.*, 2009), it is essential that these studies also present metrics and maps that clearly describe SF such as, forest age, previous land use, area of SF, habitats surrounding SF and distance to OG. These data can then be used in meta-analyses to assess whether broad patterns exist that link species presence in SF with species traits and SF characteristics.

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