Review

Dynamics of avian species and functional diversity in secondary tropical forests

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ARTICLE INFO

ABSTRACT

Deforestation for agriculture in the tropics, followed by abandonment, has resulted in large areas of secondary forest. Some authors have suggested that this secondary regrowth could help prevent mass extinction in the tropics by providing habitat for forest species. However, there is little generalised understanding of the biodiversity value of secondary forest. To address this knowledge gap, we conducted an analysis of avian responses to secondary forest succession, comparing data from 44 tropical secondary forest sites with nearby primary forest sites and investigating both species and functional diversity based metrics. Total species richness in secondary forests was 12% lower than in primary forests and was not related to secondary forest age. In contrast, forest specialist species richness increased with time since disturbance, reaching 99% of primary forest values after 100 years. In terms of functional diversity, functional dispersion (FDis) and functional divergence (FDiv) were similar in primary and secondary forests. However, functional evenness (FEve) was 5% higher in secondary than in primary forests. The standardized effect size of functional diversity (sesFD) was higher in young secondary forests than primary forests and declined with time since disturbance. Overall, these results suggest that secondary tropical forests can support provision of ecosystem services but that these services may be less stable in young forests. Therefore, secondary tropical forests, particularly older regrowth, have biodiversity value and can support important ecosystem functions. These secondary forests should be protected from further disturbance but preserving primary forest is vital for supporting overall and forest specialist species richness.

1. Introduction

Agricultural expansion in the tropics has led to large-scale deforestation (Gibbs et al., 2010), causing loss of forest species. Traditionally, protected areas have been seen as the best way to reduce deforestation and limit the resulting loss of biodiversity. These protected areas generally consist of natural or near-natural ecosystems, such as primary forest (Dudley, 2008). In the tropics such primary forests are generally considered to be irreplaceable for their biodiversity value (Gibson et al., 2011), as well as providing numerous ecosystem services. However, biodiversity declines continue in many tropical forest protected areas (Curran, 2004; Laurance et al., 2012). Additionally, it is not always feasible to designate sufficient land to adequately represent the range of communities found in specific biomes (Cox and Underwood, 2011) or support viable populations of all species (Struhsaker et al., 2005). Thus, it is clear that we cannot rely solely on protected areas of primary forest to conserve tropical forest biodiversity.

Forests that have been altered as a result of unsustainable use or natural disasters are considered degraded, and this includes secondary forests, which have undergone forest clearance (ITTO, 2002). While degraded tropical forests may be of lower biodiversity value than primary forests, given that over half of all tropical forests are now considered to be degraded (ITTO, 2002), they may provide a valuable opportunity for conservation. Wright and Muller-Landau (2006) suggested that expansion of secondary forests could play an important role in preventing extinctions by providing alternative habitat for forest species. Previous reviews suggest that secondary forests may provide habitat for forest specialists, but also that these forests differ in their conservation value depending on connectivity, disturbance history and, in particular, site age (Bowen et al., 2007; Chazdon et al., 2009; Gardner et al., 2007). Recently, the increasing recognition of the importance of degraded forests has led to ambitious restoration targets such as the Aichi Targets and the New York Declaration on Forests, which aim to restore more than 15% of degraded forests (Convention on Biological Diversity, 2010) and 200 million hectares of degraded

forests (United Nations, 2014) worldwide, respectively. However, although there are numerous site and landscape level studies, there are a lack of syntheses on the benefits of secondary forests for biodiversity and ecosystem services, and those published are largely limited to impacts on plant communities and carbon storage (Derroire et al., 2016; Martin et al., 2013) or to a limited number of biodiversity metrics, such as species richness (Dent and Wright, 2009; Dunn, 2004a).

Measures of the conservation value of an ecosystem commonly use species-based metrics (Myers et al., 2000), with the value of an area measured by the community species richness or the presence of particular species of interest. A complementary approach to species-based metrics is to assess changes in functional diversity, which describes the range of functional roles played by species within a community (Petchey and Gaston, 2006). Ecosystem functioning in general tends to be correlated with both species richness and functional diversity, with indices based on traits (e.g. feeding behaviour) performing better than those based solely on species richness and abundance (Griffin et al., 2009; Petchey and Gaston, 2006). Both the identity and distribution of functional traits have been shown to be important in predicting function (Gagic et al., 2015).

In this study we focus on birds as they provide key functions, such as pollination, seed predation and dispersal, removal of carrion, and predation of other animals, in tropical forests, and as the roles of individual species can be characterized in terms of their feeding behaviour (Sekercioglu et al., 2004). We conducted a systematic review and analysis to assess: i) how avian species richness and species richness of forest specialists in secondary tropical forests compares with that of primary tropical forests; ii) the functional diversity of avian communities in secondary tropical forests compared with that of primary tropical forests; and iii) how both metrics change, and possibly recover, with secondary forest age.

2. Materials and methods

2.1. Data collation

Using a standard methodology (Pullin and Stewart, 2006), a systematic review of the literature was conducted in May 2013 by searching Thomson Reuters Web of Knowledge with the terms bird* AND (secondary or disturb*) AND forest AND tropic*. Additional studies were found in the reviews by Barlow et al. (2007), Bowen et al. (2007), Gardner et al. (2007), Dent and Wright (2009) and Chazdon et al. (2009). Gilroy et al. (2014) and the PREDICTS database (Hudson et al., 2017), were searched for additional relevant data.

Studies were selected if they included details of avian community composition in at least one secondary forest site and a reference undisturbed primary forest site. A primary forest was defined as a naturally forested area where there was no evidence of previous deforestation or degradation. A secondary forest was defined as a previously forested area undergoing secondary succession following total or near-total removal of trees (Corlett, 1994). This definition allowed inclusion of forests that had previously been clear-cut or cleared for agriculture or villages, but not those undergoing succession after fires. Additionally, forests that had been selectively logged were excluded as these recover differently (Corlett, 1994; Dunn, 2004b). Only studies from the tropics and sub-tropics between the latitudes of 40°N and 40°S were included.

Data on the abundances of bird species present in forest sites were extracted from the articles. Additionally, for each secondary forest site, the age, land use history and whether the site was continuous or discontinuous with primary forest were noted. Article authors were contacted to request these data when articles suggested that they had been collected but were not presented. The median age of the secondary forest was recorded when a range of values was given. Methodologies used to sample bird communities, including sampling effort, were consistent within studies, but differed among studies. Methodologies used were recorded for use in statistical analyses to control for differences among studies. Data were recorded from only one study when multiple studies used the same dataset.

Data on the traits of bird species were obtained from Wilman et al. (2014), the Handbook of the Birds of the World (del Hoyo et al., 2016) and BirdLife International (BirdLife International, 2013). For this study we selected traits with importance for ecological functions: (i) foraging strata (ground, understory, mid-high levels in trees, canopy, or well above vegetation); (ii) diet (invertebrates, mammals/birds, reptiles/amphibians, fish, scavenger, fruit, nectar, seeds, or other plant material); (iii) body mass in grams; (iv) body length in cm; and (v) movement pattern (migrant/not migrant). We selected these traits because they can be directly linked to ecosystem processes such as seed dispersal and pollination. Where no match was found for the Latin binomial name of a species in the trait database of Wilman et al. (2014) a web search was carried out to find synonymous names and the correct trait values assigned using these (10 species). Forest dependency data for all bird species were provided by BirdLife International, with each species categorised as having high, medium or low forest dependency, or being a non-forest species (BirdLife International, 2013). Species with high forest dependency were then classed as forest specialists and forest specialist species richness was calculated for each site.

We then calculated total species richness and six functional diversity metrics: functional diversity (FD), the standardized effect size of FD (sesFD), functional richness (FRic), functional evenness (FEve), func-

Table 1
Descriptions of functional diversity metrics used in this study.

Metric name	Abbreviation used in this study	Metric description	Relevant references
Functional diversity	FD	A distance based metric of functional diversity that is not influenced by species abundances.	Petchey and Gaston (2006)
Functional richness	FRic	The volume multidimensional trait space occupied by a community. High FRic indicates that many traits are present within a community.	Laliberté and Legendre (2010); Villéger et al. (2008)
Functional evenness	FEve	The evenness of species abundances in multidimensional trait space. High FEve values suggest a relatively equal abundance of species in trait space, and in theory this means that resources within an ecosystem are being used in an efficient manner (Prescott et al., 2016)	Laliberté and Legendre (2010); Villéger et al. (2008)
Functional divergence	FDiv	The distribution of species abundance along multidimensional trait axes. FDiv is low when abundant species have trait values that are close to the centre of functional trait space, but high when abundant species have extreme trait values (Villéger et al., 2008). This can be seen as a measure of the niche differentiation within a community, such that if FDiv is high, then there are high levels of niche differentiation (Prescott et al., 2016).	Laliberté and Legendre (2010); Villéger et al. (2008)
Functional dispersion	FDis	The distance from the centroid of multidimensional trait space, weighted by species abundances. This metric has been suggested as a unified metric for functional diversity (Laliberté and Legendre, 2010).	Laliberté and Legendre (2010); Villéger et al. (2008)