Tropical secondary forest regeneration conserves high levels of avian phylogenetic diversity

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ABSTRACT

Secondary forests are promoted as having pivotal roles in reversing the tropical extinction crisis. While secondary forests recover carbon and species over time, a key question is whether phylogenetic diversity—the total evolutionary history across all species within a community—also recovers. Conserving phylogenetic diversity protects unique phenotypic and ecological traits, and benefits ecosystem functioning and stability. We examined the extent to which avian phylogenetic diversity recovers in secondary forests in the Colombian Chocó-Andes. sesPD, a measure of phylogenetic richness corrected for species richness, recovered to old-growth forest levels after ~30 years, while sesMPD, a measure of the phylogenetic distance between individuals in a community, recovered to old-growth levels even within young secondary forest. Mean evolutionary distinctiveness also recovered rapidly in secondary forest communities. Our results suggest that secondary forests can play a vital role in conserving distinct evolutionary lineages and high levels of evolutionary history. Focusing conservation and carbon-based payments for ecosystem services on secondary forest recovery and their subsequent protection thus represent a good use of scarce conservation resources.

1. Introduction

More than 150,000,000 ha of tropical forest were converted for farming between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013). The conversion of tropical forest to farmland is the major driver of the global extinction crisis (Laurance et al., 2014), causing dramatic species loss (Gibson et al., 2011) as forest specialists are replaced by widespread habitat generalists (Socolar et al., 2016). There is also a reduction in the diversity of ecological functions (e.g., pollination or nutrient cycling) fulfilled by communities (Edwards et al., 2013; Edwards et al., 2014b; Flynn et al., 2009) and a loss of the phylogenetic diversity (or total evolutionary history) within communities (Edwards et al., 2015; Frishkoff et al., 2014; Prescott et al., 2016) when forest is converted to farmland.

Given that the loss of primary tropical forests is likely to continue, particularly in productive tropical ecosystems, there is increasing interest in the potential for secondary forests that regenerate naturally on abandoned farmland to mitigate some of the forest and biodiversity losses (Chazdon, 2014). This is particularly so in more marginal agricultural areas—such as those that are too dry or steep for modern agriculture—where conservation gains could be made at minimal financial cost to conservation funds or to carbon-based payments for ecosystem service schemes (e.g., carbon enhancements under REDD+) (Gilroy et al., 2014b). In some regions that have already undergone substantial loss of primary forest, including Central America, the Tropical Andes, and the Philippines, there is already a phase of farm abandonment, equating to >360,000 km^2 of new woody vegetation in Latin America and the Caribbean between 2001 and 2010 (Aide et al., 2013).

Over time, there are major benefits of secondary forest recovery in terms of carbon sequestration and carbon stocks (Chazdon, 2008). The rate of carbon absorption in 20-year secondary forests of the lowland Neotropics is 11-fold the rate in old-growth forests and above-ground biomass stocks take a median of 66 years to recover 90% of old-growth above-ground biomass levels (Poorter et al., 2016). In the Tropical Andes (>1000 m a.s.l.), approximately half of old-growth above-ground biomass was restored in ~30 years (Gilroy et al., 2014b). In turn, there is a significant recovery of biodiversity within secondary forests (Barlow et al., 2007; Gilroy et al., 2014b; Queiroz et al., 2014), including a host of threatened forest-dwelling species (Basham et al., 2016; Gilroy et al., 2014b).

A key knowledge gap in determining whether secondary forest regrowth can play a significant role in reversing biodiversity losses is whether phylogenetic diversity also recovers over time. Phylogenetic diversity—the total evolutionary history and the way in which

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evolutionary relationships are patterned in a site or community (Faith, 1992)—provides insights into patterns of community assembly (Webb et al., 2002; Pavoine and Bonsall, 2011) and has intrinsic conservation value (Winter et al., 2013). Focusing on the conservation of phylogenetic diversity means that a greater proportion of evolutionary history is preserved, decreasing the chance of unique phenotypic and ecological traits being lost forever (Jetz et al., 2014).

In this study, we use field data from the Chocó-Andes of Colombia, a zone straddling two of the most highly threatened hotspots of global biodiversity (Myers et al., 2000), to examine the extent to which phylogenetic diversity recovers in secondary forests. We use birds as model communities, because they have a preliminary global phylogeny (derived from genetic data for 6663 species, and thus lacking genetic data for approximately a third of known species; Jetz et al., 2012), are functionally important (Sekercioglu, 2006), cost-effective to sample rigorously (Gardner et al., 2008) and are a good predictor of the impacts of land-use change on other taxa (Barlow et al., 2007; Edwards et al., 2014a). We do so by quantifying bird community dynamics across sample sites in farmland, secondary forest of different ages, and primary forest, to predict whether phylogenetic diversity can recover to primary forest levels.

2. Materials and methods

2.1. Study areas

We sampled three study areas at the agricultural frontier in the departments of Antioquia, Risaralda and Chocó, Colombia (Fig. A1; (Gilroy et al., 2014b)). We focus on cattle farming as the dominant land-use in the region, accounting for >95% of farmed land at each site, mirroring wider land-use patterns throughout the Colombian Andes (Etter et al., 2006). The study areas span an altitudinal range of 1290–2680 m above sea level, a range typified by subtropical and submontane cloud forest (Gilroy et al., 2014b). Each site straddles the interface between farmland and large contiguous tracts of forest (>1,000,000 ha; Fig. A1), dominated by primary forests with some secondary forest cover regrowing on abandoned cattle farmlands (age range 6 to 35 years) (Gilroy et al., 2014b).

We sampled bird communities at points arrayed within 400 m × 400 m squares located randomly across the landscape in proportion to habitat cover: 20 squares in pasture, 9 in young secondary forest (<15 year), 6 in well-established secondary forest (>15 year), and 23 in primary forest (Fig. A1; also see (Gilroy et al., 2014b) for further details). Squares were spaced ≥300 m apart between habitats and ≥400 m within habitats. All young secondary forests were owned by conservation NGOs, who provided detailed records of stand ages. Ages of older secondary forests (15–35 years) were estimated through informal interviews with locals and reserve managers, taking the mean when reported ages differed. Beyond the exclusion of cattle, all secondary forests were unmanaged, and all had some degree of connectivity to primary forest, which is typical of the majority of secondary regeneration in the tropics (Crk et al., 2009; Endress and Chinea, 2001; Helmer, 2000; Sloan et al., 2016).

2.2. Bird surveys

Bird sampling used repeat-visit point counts at three sampling points within each square (174 points in total; (Gilroy et al., 2014a)), with 200 m spacing between points to allow community independence (Hill and Hamer, 2004). We visited each point on four consecutive mornings for counts of 10-minute duration (06:00 to 12:00), avoiding conditions of rain or high winds. We varied the routes taken by observers each day to ensure that each point was visited both early and late in the sampling window. We recorded unknown vocalizations using Sennheiser ME66 microphones and Olympus LS11 recording devices, allowing subsequent identification using online reference material (www.xeno-canto.org, recordings deposited in the Colección de Sonidos Ambientales, Instituto Alexander von Humboldt, Colombia). We restricted our analyses to detections within an estimated 100 m radius, excluding records of highly mobile or transient species (e.g. non-breeding trans-continental migrants, large raptors, and swifts). All point counts were conducted by experienced observers familiar with the regional avifauna (JJG and DPE) from January to March and June to July 2012, corresponding with the relatively dry period in the region.

2.3. Measures of phylogenetic diversity

We calculated six abundance-weighted measures of phylogenetic diversity and two measures of evolutionary uniqueness for each sampling point. For each metric, we used 500 trees downloaded from http://birdtree.org/ (Jetz et al., 2012) based on the Hackett backbone (used to constrain deep-level relationships among major clades; (Hackett et al., 2008)). Having checked that the 500 values were normally distributed for each metric, we took the mean value (see below) at each sample point to ensure that our results were robust to phylogenetic uncertainty.

PD (phylogenetic diversity) – the sum of evolutionary history in a community (Faith, 1992), given in millions of years.

sesPD (the standard effect size (ses) of PD) – PD is positively related with species richness (Swenson, 2014). Thus, sesPD was calculated by comparing observed PD with that of null communities of equal species richness drawn randomly from the regional species pool (Swenson, 2014). Positive values of sesPD indicate higher PD than expected by chance for a given species richness, while negative values indicate lower PD than expected by chance.

MPD (mean pairwise distance) – the average phylogenetic distance between all combinations of pairs of individuals (including conspecifics) in a community.

sesMPD (the standard effect size (ses) of MPD) – mean phylogenetic distance between all combinations of pairs of individuals, corrected for species richness (as MPD can be positively correlated with richness). Higher values indicate that communities contain species that are distributed across clades that diverged from each other a long time ago (more phylogenetically even), whereas lower values indicate communities consisting of species that are distributed within clades with relatively recent common ancestors (more phylogenetically clustered) (Webb et al., 2002).

MNTD (mean nearest taxon distance) – the average distance between an individual and the most closely related (non-conspecific) individual. MNTD is thus affected by phylogenetic distance in terminal branches.

sesMNTD (the standard effect size (ses) of MNTD) – mean nearest taxon distance corrected for species richness, as MNTD and richness may be positively correlated. Communities with greater MNTD than expected for a given species richness have positive values, suggesting that closely related individuals do not co-occur in the community (more phylogenetically even), and those with lower MNTD than expected have negative values suggesting the co-occurrence of closely related individuals (more phylogenetically clustered).

ED (evolutionary distinctiveness) – a measure of how much unique evolutionary history a species contributes to a phylogenetic tree. Species with no extant close relatives have high values of ED, whereas species with closely related extant species have low values. A community with high ED thus has more evolutionarily unique species.

EDR (evolutionary distinctiveness rarity) – ED adjusted for species rarity measured by range size. Species with highest EDR thus implies both high importance for the conservation of evolutionary diversity and an elevated risk of extinction associated with a small global range size.

We calculated these six metrics of phylogenetic diversity using the picante package (Kembel et al., 2010) in R version 3.3.1 (R Core Team