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Effects of restoration on tree communities and carbon storage in rainforest fragments of the Western Ghats, India

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Abstract. Ecological restoration is a leading strategy for reversing biodiversity losses and enhancing terrestrial carbon sequestration in degraded tropical forests. There have been few comprehensive assessments of recovery following restoration in fragmented forest landscapes, and the efficacy of active versus passive (i.e., natural regeneration) restoration remains unclear. We examined 11 indicators of forest structure, tree diversity and composition (adult and sapling), and aboveground carbon storage in 25 pairs of actively restored (AR; 7–15 yr after weed removal and mixed-native tree species planting) and naturally regenerating (NR) plots within degraded rainforest fragments, and in 17 less-disturbed benchmark (BM) rainforest plots in the Western Ghats, India. We assessed the effects of active restoration on the 11 indicators and tested the hypothesis that the effects of active restoration increase with isolation from contiguous and relatively intact rainforests. Active restoration significantly increased canopy cover, adult tree and sapling density, adult and sapling species density (overall and late-successional), compositional similarity to benchmarks, and aboveground carbon storage, which recovered 14–82% toward BM targets relative to NR baselines. By contrast, tree height–diameter ratios and the proportion of native saplings did not recover consistently in actively restored forests. The effects of active restoration on canopy cover, species density (adult), late-successional species density (adult and sapling), and species composition, but not carbon storage, increased with isolation across the fragmented landscape. Our findings show that active restoration can promote recovery of forest structure, composition, and carbon storage within 7–15 yr of restoration in degraded tropical rainforest fragments, although the benefits of active over passive restoration across fragmented landscapes would depend on indicator type and may increase with site isolation. These findings on early stages of recovery suggest that active restoration in ubiquitous fragmented landscapes of the tropics could complement passive restoration of degraded forests in less fragmented landscapes, and protection of intact forests, as a key strategy for conserving biodiversity and mitigating climate change.

Key words: carbon storage; climate change mitigation; conservation; ecological restoration; forest recovery; natural regeneration; tree diversity.

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Introduction

Tropical forests harbor over 50% of global biodiversity and constitute among the largest terrestrial reservoirs of carbon (Pimm et al. 1995, Bonan 2008). With ongoing losses amounting to nearly 8 million hectares on average per year (Achard et al. 2014), an increasing majority of remaining tropical forests exist as degraded fragments in human-dominated landscapes (Lewis et al. 2015, Taubert et al. 2018). Restoration offers a potential solution for reversing biodiversity declines and enhancing terrestrial carbon sequestration in such degraded forests (Edwards et al. 2010) and has emerged as a leading strategy for mitigating climate change (Griscom et al. 2017).

Ecological restoration encompasses a range of active (more intensive) and passive (less intensive) interventions aimed at alleviating barriers to natural recovery in degraded forests (Chazdon and Guariguata 2016). While active interventions such as planting trees might be necessary for restoring heavily degraded areas (e.g., abandoned mines), passive interventions such as habitat protection may be as effective as active restoration in areas that are less disturbed and retain some capacity for spontaneous natural regeneration (Crouzeilles et al. 2017, Meli et al. 2017). Previous research on restoration of degraded forests, which has primarily focused on recovery following selective logging, suggests that these forests largely fall into the latter category, wherein passive interventions such as protection from further logging and disturbance can promote recovery of forest structure, diversity, and carbon over time (Berry et al. 2010, Meli et al. 2017).

In fragmented tropical forests, by contrast, multiple abiotic and biotic factors act as barriers to natural recovery and can result in the persistence of species-poor and low-carbon early-successional ecosystems (Tabarelli et al. 2008). For example, abiotic edge effects resulting from increased light, wind, and desiccation favor early- over late-successional species (Laurance et al. 2006) and reduce canopy height (Osuri et al. 2014, Rutishauser et al. 2016), leading to losses of aboveground carbon storage potential (Magnago et al. 2017). Biotic factors include shifts in animal-mediated processes such as seed dispersal; for example, large-seeded, but not small-seeded, tree species decline in isolated fragments because seed dispersers for the former are more susceptible to fragmentation than of the latter (Cramer et al. 2007). Resultant shifts in species composition can reduce carbon storage in fragments, because small-seeded species tend to have smaller adult sizes than large-seeded species (Osuri and Sankaran 2016). Increased competition from disturbance-adapted native (Magnago et al. 2017) and invasive (Joshi et al. 2009) species may further constrain the recovery of late-successional tree communities and carbon storage in fragments. Collectively, these lines of evidence suggest that ecological restoration of degraded tropical forest fragments would require active interventions such as controlling invasive plants and planting native tree species, and that such interventions may be particularly important in isolated fragments that are less likely to recover naturally. However, while previous studies in fragmented tropical forests have examined survival patterns of planted saplings (Alvarez-Aquino et al. 2004, Raman et al. 2009), research into recovery of forest structure, composition, and functions, and the performance of active versus passive interventions remains limited.

This study examines the effects of ecological restoration on 11 indicators of forest structure, diversity and species composition of adult and juvenile (sapling) trees, and aboveground carbon storage in degraded tropical rainforest remnants along a gradient of isolation from large and relatively intact rainforests in the Anamalai Hills, part of the Western Ghats biodiversity hotspot of peninsular India. Since the year 2000, a number of degraded rainforest remnants in this landscape have been ecologically restored using weed removal and mixed-native species plantings (Raman et al. 2009). We assess the effects of active restoration by comparing passively restored (spontaneous natural regeneration) and actively restored (weed removal and mixed species planting) plot pairs established in these remnants. We also assess the extent of recovery of different indicators in actively restored forests by making comparisons to relatively intact benchmark rainforests. Our study evaluates three specific hypotheses. First, that active restoration promotes greater recovery of canopy cover, tree density, tree height–diameter ratio, tree diversity, native tree regeneration, and aboveground carbon storage than spontaneous natural regeneration in degraded tropical rainforest fragments. Second, that restoration effects will vary across indicators (Meli et al. 2017), with active restoration having stronger positive effects on indicators directly manipulated by the restoration intervention (e.g., tree density) than on indicators associated with but not directly manipulated during restoration (e.g., tree height–diameter ratio;

diversity of naturally recruiting saplings). Finally, we test the hypothesis that the effects of active restoration are greater in more ecologically isolated locations, such as in fragments at greater distances from contiguous and relatively undisturbed forests.

Methods

Study area

The study was conducted on the Valparai Plateau (10°15′–10°22′N, 76°52′–76°59′E), a 22,000-ha human-modified landscape in the Anamalai Hills of the Western Ghats biodiversity hotspot (Fig. 1). Annual rainfall across the plateau (elevation 700–1500 m above mean sea level) averages c. 2800 mm, around 70% of which falls during the south-west monsoon between June and September (Rathod and Aruchamy 2010). The natural vegetation of the area is mid-elevation tropical wet evergreen rainforest, with *Cullenia exarillata*, *Mesua ferrea,* and *Palaquium ellipticum*, comprising the dominant and characteristic tree species (Pascal 1988, Pascal et al. 2004).

The rainforests of the Valparai Plateau were extensively deforested between the 1890s and the 1940s for establishing commercial tea, eucalyptus, and shade coffee and cardamom plantations (Mudappa and Raman 2007). At present, rainforests on the plateau are restricted to ~45 forest remnants (1–300 ha in area) mostly on private lands owned by tea and/or coffee plantation companies, or abutting wildlife reserves that surround and extend beyond the plateau. The surrounding wildlife reserves, namely Anamalai Tiger Reserve in Tamil Nadu (95,800 ha), and Parambikulam Tiger Reserve (63,400 ha) and Vazhachal Reserved Forest in Kerala (41,395 ha), retain over 30,000 ha of contiguous and relatively undisturbed rainforests alongside other vegetation types (Osuri et al. 2017).

The rainforest remnants of the Valparai Plateau are former primary forests that have been degraded by the impacts of forest fragmentation, and by resource extraction—mainly selective felling for timber by plantation companies in the past, and firewood collection by local people (Mudappa and Raman 2007, Raman et al. 2009).

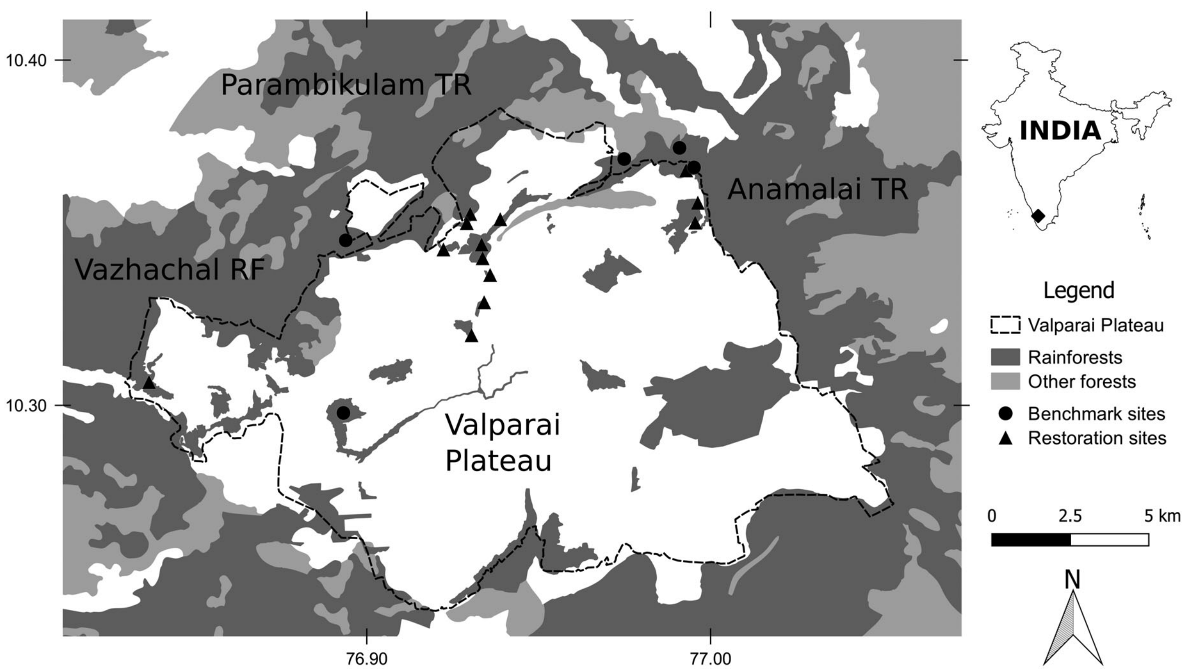

Fig. 1. Map of Valparai Plateau and surrounding areas in the Western Ghats Mountains of India showing forest cover and non-forest areas (white). The general locations of the restoration and benchmark sites sampled in this study are marked.

These remnants also sustain natural regeneration of shade-tolerant non-native plantation species such as *Coffea canephora*, *C. arabica*, and *Maesopsis eminii* that invade from abandoned plantations within the remnants, and from active shade coffee plantations in the surrounding landscape (Muthuramkumar et al. 2006, Joshi et al. 2009). Disturbance-adapted non-native shrubs such as *Lantana camara* and *Chromolaena odorata* are also prolific in some areas (Joshi et al. 2015). Despite the degradation, these remnants nevertheless retain significant conservation value for a range of plant and animal species (Muthuramkumar et al. 2006, Raman 2006, Sridhar et al. 2008, Wordley et al. 2017, Harikrishnan et al. 2018).

Ecological restoration

Three major plantation companies in the Valparai landscape have participated in biodiversity conservation and ecological restoration projects in rainforest remnants on their lands since the year 2000 (Raman et al. 2009). To date, the companies have extended protection to over 1075 ha of forest biodiversity plots across 35 rainforest remnants and taken steps to prevent tree felling, hunting, and fuelwood extraction, that is, passive restoration, in these areas (Mudappa and Raman 2007). Around 100 ha of degraded forests within these protected remnants has been taken up for active restoration since 2000 by removing weeds and planting a diverse mix of nursery-raised native tree saplings. Planting in the 7- to 15-yr-old restored areas surveyed in this study comprised on average 1099 saplings/ha (1 SE = 154 saplings/ha) and 106 species/ha (1 SE = 15 species/ha; Appendix S1: Table S1).

Sampling design and site selection

Our study focused on 25 pairs of actively restored (AR; 7–15 yr since restoration) and passively restored or naturally regenerating (NR) sites within biodiversity plots across 11 rainforest fragments and remnants. Individual AR sites were approximately 1.0 ha in area, on average. NR sites were selected in a manner that maximized spatial proximity and similarity to respective AR sites in terms of topography, physiognomy, distance to edge, vegetation, and levels of degradation at the time of restoration. AR–NR site pairs were selected using photographs of the sites pre-restoration (Appendix S1: Fig. S1), and experiences of DM, TRSR, and field assistants who led the restoration efforts across all the 2002–2010 restoration sites. We also sampled vegetation at 17 locations across six areas of relatively intact benchmark (BM) rainforests, two located within the interior of a well-protected 70-ha fragment, and the remaining 15 within contiguous rainforests of the surrounding State-protected wildlife reserves at locations where elevation, climate, and natural vegetation type were similar to the restoration sites (Muthuramkumar et al. 2006).

We estimated isolation of our AR–NR pairs as the distance to the nearest edge of relatively large and undisturbed rainforests (hereafter, distance to contiguous forest) located within the Anamalai Tiger Reserve and adjoining nature reserves. We did not consider other forest remnants in the fragmented landscape in estimating this index of isolation as these forests may be heavily degraded (Muthuramkumar et al. 2006) and thus might not act as seed sources for the restoration sites. Our index of site isolation was strongly and negatively correlated with remnant patch size (Spearman correlation $R_s = -0.70$; $P \leq 0.001$), indicating that remnants close to the nature reserve are larger than more isolated ones.

Vegetation sampling

Square vegetation plots of 20 m side (0.04 ha) were placed in each AR ($N = 25$), NR ($N = 25$), and BM ($N = 17$) location. All trees ≥ 10 cm girth at breast height (gbh) were identified, and measurements of gbh and height were taken using a tape measure and laser range finder, respectively. Naturally recruited saplings ($\geq$10 cm height and < 10 cm gbh) were sampled using 5×5 m square sub-plots located at the center of the tree plots in 15 older ($\geq$10 yr) AR plots, 15 corresponding NR plots, and 15 benchmark forest plots. Tree species were identified using botanical and field keys (Gamble and Fischer 1935, Pascal and Ramesh 1997), and based on the authors' familiarity with the flora, and collections made during an earlier botanical study in the area (Muthuramkumar et al. 2006).

We assessed plot-level percent canopy cover from the center of each plot visually (all plots) and using a spherical canopy densiometer (in 15 AR, NR, and BM plots each). For the former method, an observer looking up from ground level at the plot center visually estimated the fraction of their view covered by canopy vegetation, versus open to sky, over a ~10 m radius. For the latter method, a spherical crown densiometer (Forestry Suppliers) was used to take four canopy cover readings (in each cardinal direction) that were averaged for a single plot-level estimate. Visual and densiometer-based estimates were highly correlated (Pearson correlation $R_P = 0.84$, $P < 0.001$), and the former variable was used in all subsequent analyses of percentage canopy cover, as data were available for all plots.

Aboveground carbon storage

Aboveground biomass of individual trees (AGB_{est}) was estimated using the following allometric equation developed by Chave et al. (2014):

$$\mathrm{AGB}_{\mathrm{est}} = 0.0673 \times \left(\rho D^2 H\right)^{0.976}$$

where ρ is species wood density (g/cm^3), D is tree diameter at breast height (dbh, in cm), and H is tree height (m).

Aboveground biomass at the plot level was calculated as the summation of AGB_{est} across all trees within each plot, and aboveground carbon storage was assumed to constitute 47.1% of aboveground biomass following Thomas and Martin (2012). Wood density data were obtained from the Global Wood Density Database (Chave et al. 2009, Zanne et al. 2009), and from data collected by AMO and colleagues in the Western Ghats (Osuri et al. 2014, Ratnam et al. 2019). Genus-level average wood densities were used in the absence of species-level estimates (Chave et al. 2006), and trees lacking genus-level wood density estimates were assigned a value of 0.54 g/cm^3, which corresponds to the community-weighted average of species with known wood densities across plots in this study. Overall, 53% of species and 61% individuals in the study had species-level wood density data, while data at the genus level were available for 89% of all species and individuals.

Analysis

A total of 11 indicators were assessed as response variables. These include (1) five indicators of forest structure: canopy cover (%), adult and sapling tree density (trees/plot), and adult tree log-height (m) to log-diameter (cm) ratio; (2) six indicators of tree diversity and community composition: adult and sapling species density and late-successional species density (species/plot), the percentage of sapling density comprising native species (%), adult compositional similarity (Bray-Curtis) to less-disturbed rainforests (%), and (3) aboveground carbon storage (Mg/ha). Species' habitat affinity classifications (late-successional vs. early-successional vs. introduced) were obtained from publications describing the tree flora of the study region and/or the Western Ghats, collated by Osuri et al. (2017). We estimated tree height–diameter ratios (tree HD) and aboveground carbon storage at the level of individual trees and aggregated these as averages and totals, respectively, at the plot level.

We examined the effects of active restoration (AR vs. NR) on the 11 indicators and asked whether restoration effects vary with distance from contiguous forests, using generalized linear mixed effects models (GLMMs). Eleven GLMMs were run with each indicator as response variable and restoration strategy (NR or AR), distance to contiguous forest, and a two-way interaction between restoration strategy and distance, included as fixed effect predictor variables. Plot-pair name was included as a random effect grouping term, specifying the pairing of AR and NR plots. Consistent with the statistical distributions of response variables, models for tree density and species density were specified to the Poisson family (counts), canopy cover, and native sapling fraction to the Binomial family (proportions), and others were specified to the Gaussian family of models (log-transformation applied to aboveground carbon storage). Restoration strategy and distance to contiguous forest were inferred as having consistent effects on a given ecological indicator if the model intercept and slope, respectively, had 95% confidence interval ranges that did not intersect zero (Nakagawa and Cuthill 2007). Similarly, the effects of active restoration were inferred as increasing or decreasing with distance to contiguous forests if the two-way interaction term had positive or negative 95% CI ranges, respectively.

We translated active restoration effects on the different indicators in terms of percent recovery, with respective NR forests providing the baseline (0%), and BM forests representing 100% recovery.

Percentage recovery of each indicator was calculated as 100 × (AR–NR)/(BM–NR), where the numerator corresponds to the average effect ± 95% CI of active restoration on that indicator, estimated using the GLMMs described above, and the denominator corresponds to the average difference between BM and NR plots estimated using generalized linear models. Positive values of this metric reflect recovery toward benchmark levels under active restoration, while neutral and negative values reflect no recovery and divergence from benchmarks, respectively, relative to NR baselines.

As the most isolated sites in our study (Injipara and Stanmore) were among the earliest to be restored, and planted with relatively high densities of saplings, the distance to contiguous forest covariate was collinear with age ($R_P = 0.66$; $P < 0.01$) and planted sapling density ($R_P = 0.52$; $P < 0.01$). To disentangle distance effects from those of age and planting density, we additionally ran the GLMMs after excluding data from the two sites (4 AR-NR plot pairs), which effectively removed the collinearity ($P > 0.6$). Only models having qualitatively similar outcomes between the overall and subset datasets were interpreted for restoration strategy-distance effects. All data management, statistical analyses, and graphics were prepared using the R statistical and computing environment (R Core Team 2017).

Results

We recorded 3146 trees belonging to 150 species across all our plots, including 1116 trees and 97 species in benchmark (BM) forests, 1289 trees and 99 species in actively restored (AR) sites, and 741 trees and 79 species in naturally regenerating (NR) sites (Fig. 2a). A total of 3084 individuals and 111 species of saplings were reported in the regeneration plots, with 1467, 1081, and 536 individuals and 81, 62, and 37 species encountered in BM, AR, and NR plots, respectively (Fig. 2b).

Effects of active restoration and recovery relative to benchmarks

Median (and average) canopy cover, tree density, species density of adults and saplings, sapling native fraction, compositional similarity to benchmark forests, tree height–diameter ratios, and aboveground carbon stocks were lowest in passively restored sites, intermediate in actively restored sites, and highest in benchmark forests (Table 1).

Active restoration had positive and consistent (i.e., positive 95% CI range) effects, indicating significant recovery of canopy cover (82%), adult tree density (69%), species density (49%), late-successional species density (42%), and compositional similarity to benchmark forests (14%), relative to difference between benchmark and passively restored sites (BM − NR; Fig. 3). Sapling density, species density, and late-successional species density also recovered consistently by 51%, 52%, and 34%, respectively, while aboveground carbon storage recovered 47% in actively restored forests (Fig. 3, Table 1). By contrast, tree height–diameter ratios and the percentage of native saplings were not consistently related to active restoration (i.e., 95% CI

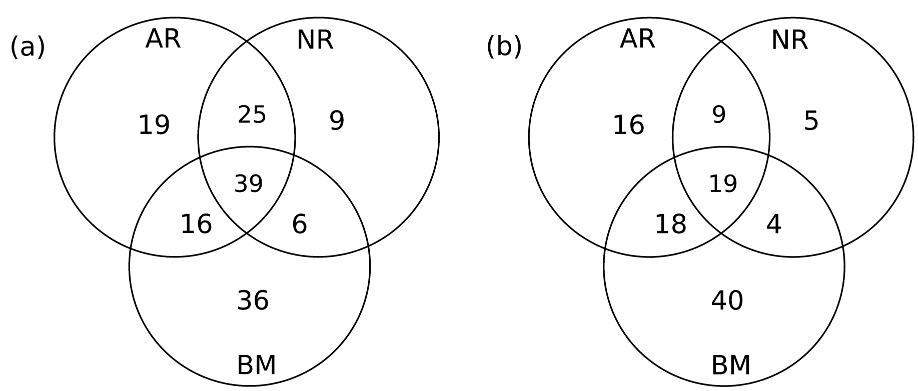

Fig. 2. The number of species of trees (a) and saplings (b) recorded in actively restored (AR), naturally regenerating (NR), and benchmark (BM) rainforest plots in the Western Ghats, India.

Table 1. The medians, averages, and 95% confidence intervals of 11 ecological indicators across plots in naturally regenerating, actively restored, and benchmark rainforests in the Western Ghats, India.

	Naturally regenerating			Actively restored			Benchmark		
Ecological indicator	Median	Mean	CI	Median	Mean	CI	Median	Mean	CI
Canopy cover (%)	20.0	27.8	17.0–38.6	65.0	58	50.9–65.1	75.0	75.0	70.0–80.0
Tree density (no. trees/plot)									
Overall	29.0	29.6	22.2–37.1	49.0	51.6	40.1–62.3	65.0	65.6	58.1–73.2
Small trees (3–15 cm dbh)	24.0	24.7	17.6–31.8	41.0	41.5	31.3–51.8	53.0	53.4	46.1–60.6
Medium-sized trees (15–40 cm dbh)	5.0	3.6	2.4–4.8	7.0	8.4	6.5–10.3	8.0	7.6	5.3–9.9
Large trees (>40 cm dbh)	1.0	1.4	0.6–4.8	1.0	1.6	1.0–2.3	5.0	4.7	3.7–5.7
Tree height–diameter ratio (log–log)	0.90	0.88	0.83–0.94	0.93	0.93	0.89–0.96	1.08	1.05	1.00–1.10
Tree species density (no. species/plot)	8.0	8.6	6.3–10.8	14.0	14.0	11.8–16.2	24.0	24.4	21.8–27.4
Late-successional tree species density (no. species/plot)	1.0	2.5	1.3–3.7	4.0	4.8	3.5–6.0	17.0	18.2	15.9–20.4
Compositional similarity to benchmark (%)	6.0	7.1	4.8–9.4	10.7	9.6	8.0–11.2	25.3	24.8	23.7–25.9
Sapling density (no. saplings/plot)	26.0	35.7	20.9–50.6	54.0	72.1	44.7–99.4	72.0	97.8	69.5–126.1
Sapling native fraction (%)	78.6	76.8	65.7–88.0	86.7	79.8	67.0–92.6	100.0	91.2	83.9–98.6
Sapling tree species density (no. species/plot)	5.0	6.5	4.0–9.1	13.0	13.3	10.8–15.8	21.0	20.2	16.7–23.7
Sapling late-successional tree species richness (no. species/plot)	1.0	1.5	0.3 – 2.6	4.0	4.3	3.1–5.6	18.0	15.9	12.9–18.8
Aboveground carbon storage (Mg/ha)	21.0	49.0	19.3–78.6	89.8	143.9	44.4–243.3	261.1	287.6	215.1–360.1

range includes zero; Fig. 3; see Appendix S1: Table S2 for GLMM parameter estimates).

Restoration effects in relation to distance from contiguous forest

The interactive effects of restoration type and distance from contiguous forests varied across different indicators. The interaction between restoration type and distance was consistently positive (i.e., positive 95% CI range) for canopy cover, adult species density, adult late-successional species density, and compositional similarity to benchmarks, and for sapling late-successional species density (Fig. 4, Table 2). For each of the above indicators, recovery in actively restored forests, relative to passively restored baselines, was greater in more isolated fragments than in those closer to or abutting continuous forests. The exclusion of four plot pairs to reduce collinearity between distance, age, and planting strategy did not alter the above pattern (Table 2). The interactive effects of restoration type and distance on tree height–diameter ratio and overall sapling species density were also positive, on average, but less consistent (Table 2). By contrast, the restoration–distance interaction did not have significant effects on aboveground carbon storage, adult tree and sapling density, and proportion of native saplings (Table 2). See Appendix S1: Table S2 for a summary of the restoration type-distance parameter estimates based on the overall and trimmed datasets.

Discussion

Our study from the Western Ghats shows that active restoration can promote varying levels of recovery of forest structure, composition, and carbon storage in degraded tropical rainforest fragments. Actively restored (weeds/invasive removal + mixed-native species planting) plots in our study had greater tree diversity, higher densities of late-successional species among adults and saplings, and stored more carbon, than comparable passively restored (naturally regenerating) plots 7–15 yr after restoration. Our results suggest that active restoration could mitigate some of the effects of unfavorable abiotic conditions, competition from invasive or weed species, and reductions in seed dispersal, which are known to constrain natural recovery of late-successional tree species in fragmented tropical forest landscapes (Laurance et al. 2002, Tabarelli et al. 2008). Active restoration might therefore

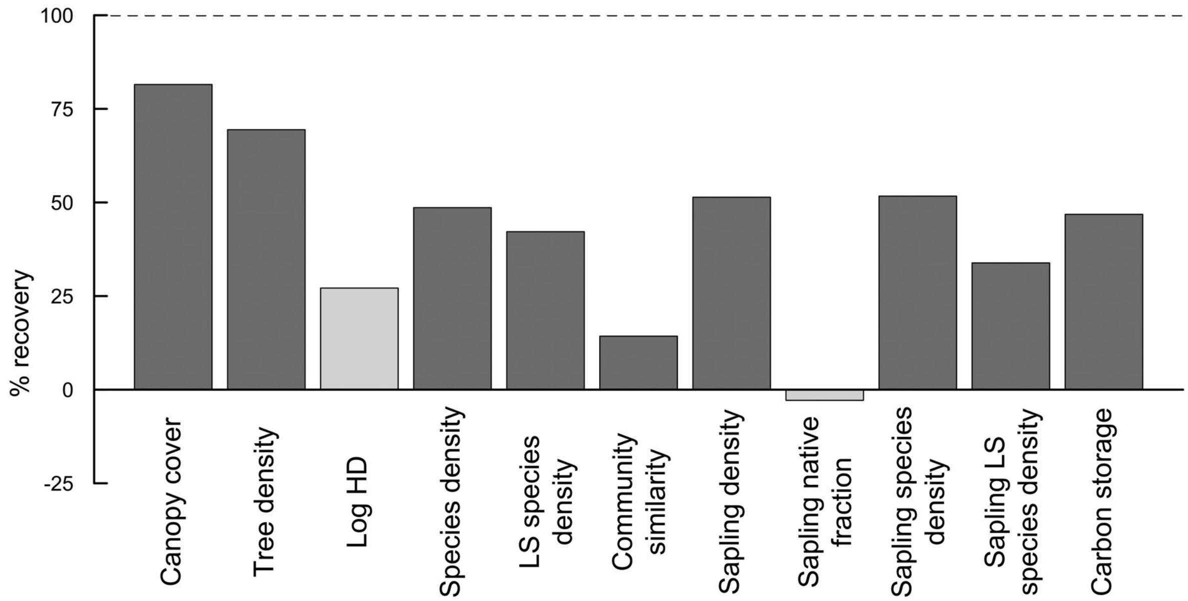

Fig. 3. Percentage of recovery in actively restored forests (AR–NR)/(BM–NR) across different ecological indicators. Bars represent average recovery, with dark and light coloring representing the presence or absence of consistent recovery in AR relative to NR based on 95% CIs, respectively.

generate larger conservation and climate change mitigation gains relative to passive restoration in fragmented tropical forests, compared to degraded forests in less fragmented landscapes (e.g., selectively logged or secondary forests), which are known to recover naturally over time without active interventions (Letcher and Chazdon 2009, Martin et al. 2013, Meli et al. 2017).

Our findings highlight that the nature of restoration targets, and degree of isolation in fragmented landscapes, can alter the balance of (recognized) benefits to costs of active versus passive restoration. First, our results suggest that while active restoration could drive consistent recovery of indicators directly related to specific interventions, the recovery of indicators not directly related to the interventions may be weaker and more variable. For example, planting native trees in AR plots had a strong direct effect on tree density (69% recovery toward BM targets), but indirect effects on indicators that might be influenced by changes in tree density and diversity, such as height–diameter ratios (Osuri et al. 2014) and regeneration of late-successional species (Wills et al. 2017), were weaker and more variable. Estimates of recovery in restored forests, and of the efficacy of active versus passive restoration interventions, can therefore vary markedly depending on what types of indicators are prioritized in assessments of restoration success.

Second, patterns of spatial variation in the benefits of active restoration over natural regeneration are likely to differ by indicator type across fragmented landscapes. In our study, adult and sapling densities of late-successional species decreased with isolation in naturally regenerating forest plots, possibly as a result of seed dispersal limitation (Cramer et al. 2007, Osuri et al. 2017), but either did not vary or increased with isolation in actively restored forest plots. This result suggests that actively restoring degraded forests in isolated sites, combined with securing natural regeneration in areas closer to intact forests, could prove an effective strategy for restoring late-successional tree species and communities in landscapes of forest fragments. By contrast, the absence of a relationship between the effects of active restoration on carbon storage and isolation suggests that active restoration could provide benefits for climate change mitigation in isolated and in well-connected fragments, at least over the relatively short timeframes (e.g., 10–15 yr) targeted by major climate change

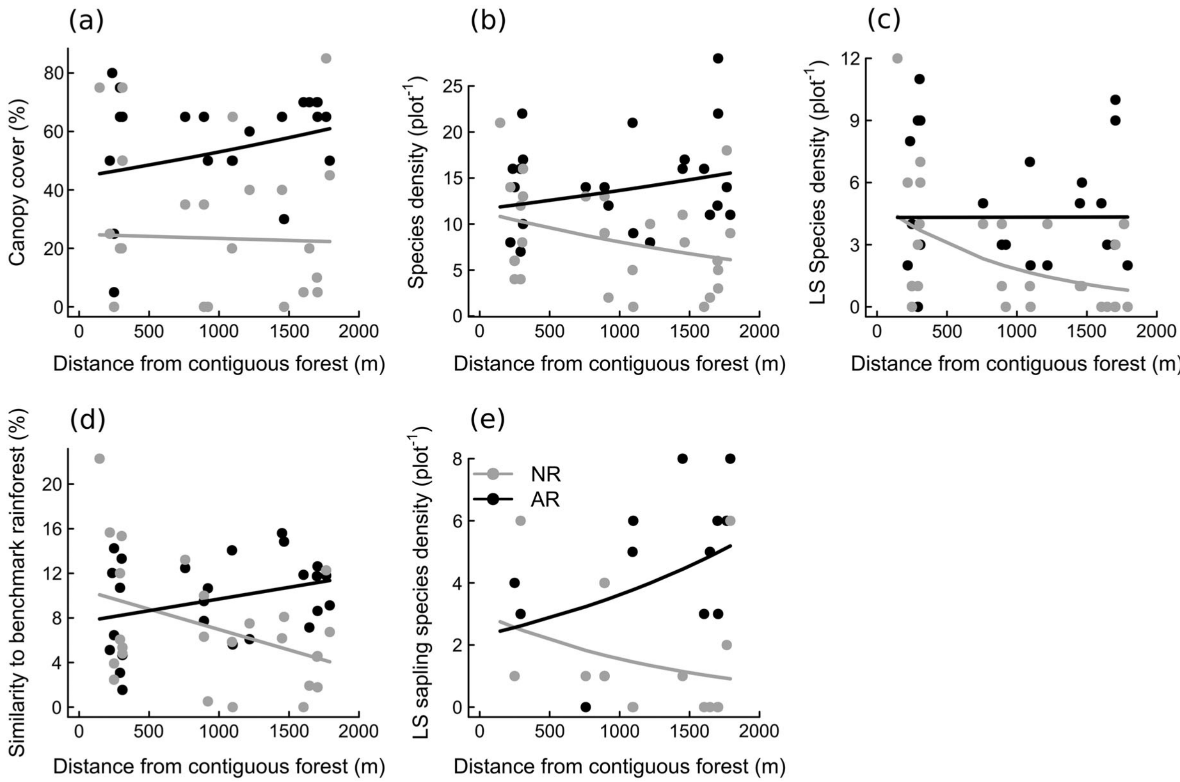

Fig. 4. Canopy cover (a), adult species density (b), late-successional (LS) species density (c), compositional similarity to benchmark rainforests (d), and LS sapling species density (e) in relation to geographical distance from contiguous rainforests across AR and NR plots. Lines represent fitted generalized linear models which included a two-way interaction between restoration strategy (AR vs NR) and distance. GLMM slopes were statistically different between AR and NR for all five responses.

policies (United Nations 2015). Collectively, these findings underscore the importance of considering multiple components of recovery (Gatica-Saavedra et al. 2017), and accounting for spatial heterogeneity in natural regeneration (Molin et al. 2018), in prioritizing active and passive interventions within restoration strategies for degraded forests.

While increases in the magnitude of active restoration effects with distance from contiguous forests are consistent with our hypothesis, higher absolute values of some indicators in AR plots in more isolated sites (e.g., late-successional sapling density: Fig. 4e) were unexpected. These patterns remained qualitatively unchanged even after accounting for covariation between isolation, age, and planting density among our study sites (Table 2) and point to the possible influence of other factors affecting tree and sapling densities that vary along the isolation gradient, such as potentially higher levels of herbivory close to contiguous forests (Benitez-Malvido 1998).

Although our restoration sites are comparable in age (7–15 yr) to the majority of empirical studies on the effects of ecological restoration (Wortley et al. 2013, Meli et al. 2017), they are young relative to the timescales of tropical forest succession and recovery, which typically span decades to centuries (Chazdon 2003, Marín-Spiotta et al. 2007). Compared to degraded forests in less fragmented landscapes that may attain mature forest levels of tree diversity and carbon storage over 20–30 yr of natural recovery (Letcher and Chazdon 2009), restored fragmented forests in our study appear on a trajectory of relatively low and/or slow recovery (species richness, 49%; carbon storage, 47%). Longer-term recovery in the restored areas may be facilitated by the sealing of fragment edges by

Table 2. Model-derived estimates of the interactive effects of restoration type (passive vs. active) and distance to contiguous forest on the 11 ecological indicators.

Indicator	Restoration type-distance interactive effect Mean (95% CI range)	
	All sites	All sites excluding Injipara and Stanmore
Canopy cover (%)†	0.15 (0.04–0.26)	0.15 (0.02–0.29)
Adult tree density (no. trees/plot)‡	0.10 (0.01–0.19)	0.03 (−0.08–0.14)
Adult species density (no. species/plot)‡	0.31 (0.14–0.48)	0.21 (0.01–0.41)
Adult late-successional species density (no. species/plot)‡	0.62 (0.29–0.95)	0.44 (0.06–0.83)
Compositional similarity to benchmarks (%)	3.43 (1.25–5.66)	3.58 (0.77–6.40)
Sapling density (no. saplings/plot)‡	0.41 (0.29–0.53)	0.14 (−0.03–0.32)
Sapling native fraction (%)†	−0.12 (−0.3–0.06)	0.16 (−0.10–0.42)
Sapling species density (no. species/plot)‡	0.26 (−0.02–0.53)	0.37 (−0.02–0.77)
Sapling late-successional species density (no. species/plot)‡	0.68 (0.13–1.22)	1.09 (0.32–1.86)
Tree height:diameter ratio (log:log)	0.05 (−0.01–0.10)	0.04 (−0.02–0.11)
Aboveground carbon storage (Mg/ha) (log-transformed)	−0.19 (−0.88–0.51)	−0.15 (−0.98–0.68)

Notes: Positive values reflect increased slope of the indicator–distance (scaled) relationship in actively restored relative to naturally regenerating forests. Estimates from models based on all sites and based on a subset of sites (with and without distance–age–planting strategy collinearity, respectively; see *Analysis*) are presented.

† Denote indicators assessed using Poisson GLMMs.

‡ Denote indicators assessed using Binomial GLMMs. The rest were run assuming Gaussian error distribution.

regrowth (Nascimento et al. 2006), increasing overstorey shade (Ashton et al. 2014), and the recovery of biotic processes such as pollination and seed dispersal (Kormann et al. 2016, de la Peña-Domene et al. 2016), but the impacts of these processes remain poorly understood. Forest recovery would also depend on the extent to which human disturbances such as pole cutting and fuelwood removal, which were recorded in a few of our restored sites (active and naturally regenerating) and are a common feature of tropical forests in human-dominated landscapes, can be effectively mitigated in the restored forest fragments. Research into the ecological and anthropogenic factors governing the magnitude and rate of longer-term recovery in fragmented tropical forest landscapes is therefore needed for better understanding the role of restoration in strategies for conserving biodiversity and mitigating climate change.

Collectively, our findings highlight the potential of restoration as a strategy for enhancing recovery of forest structure, tree diversity and community composition, and carbon sequestration in degraded tropical forest fragments. Restoration programs in fragmented landscapes could employ a combination of active interventions such as planting trees and passive interventions such as promoting natural regeneration, guided by clearly defined restoration targets that consider multiple dimensions of ecosystem recovery, and by the extent and spatial configuration of forest remnants. However, our ability to predict the true conservation and carbon sequestering potential of restoration is constrained by gaps in current knowledge regarding magnitudes and rates of recovery in restored forests over longer timescales. It is important that conservation and climate policies recognize this uncertainty, to prevent the inappropriate promotion of restoration as an alternative to protecting the irreplaceable ecological and climate-regulating values of relatively large and undisturbed tropical forest landscapes.

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Literature Cited

Achard, F., et al. 2014. Determination of tropical deforestation rates and related carbon losses from 1990 to 2010. Global Change Biology 20:2540–2554.

Alvarez-Aquino, C., G. Williams-Linera, and A. C. Newton. 2004. Experimental native tree seedling establishment for the restoration of a Mexican cloud forest. Restoration Ecology 12:412–418.

Ashton, M. S., C. V. S. Gunatilleke, I. A. U. N. Gunatilleke, B. M. P. Singhakumara, S. Gamage, T. Shibayama, and C. Tomimura. 2014. Restoration of rain forest beneath pine plantations: A relay floristic model with special application to tropical South Asia. Forest Ecology and Management 329:351–359.

Benitez-Malvido, J. 1998. Impact of forest fragmentation on seedling abundance in a tropical rain forest. Conservation Biology 12:380–389.

Berry, N. J., et al. 2010. The high value of logged tropical forests: lessons from northern Borneo. Biodiversity and Conservation 19:985–997.

Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. Science 320:1444–1449.

Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. Ecology Letters 12:351–366.

Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. T. Steege, and C. O. Webb. 2006. Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. Ecological Applications 16:2356–2367.

Chave, J., et al. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Global Change Biology 20:3177–3190.

Chazdon, R. L. 2003. Tropical forest recovery: legacies of human impact and natural disturbances. Perspectives in Plant Ecology, Evolution and Systematics 6:51–71.

Chazdon, R. L., and M. R. Guariguata. 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48:716–730.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Cramer, J. M., R. C. G. Mesquita, and G. B. Williamson. 2007. Forest fragmentation differentially affects seed dispersal of large and small-seeded tropical trees. Biological Conservation 137: 415–423.

Crouzeilles, R., M. S. Ferreira, R. L. Chazdon, D. B. Lindenmayer, J. B. B. Sansevero, L. Monteiro, A. Iribarrem, A. E. Latawiec, and B. B. N. Strassburg. 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. Science Advances 3:e1701345.

de la Peña-Domene, M., E. S. Minor, and H. F. Howe. 2016. Restored connectivity facilitates recruitment by an endemic large-seeded tree in a fragmented tropical landscape. Ecology 97:2511–2517.

Edwards, D. P., B. Fisher, and E. Boyd. 2010. Protecting degraded rainforests: enhancement of forest carbon stocks under REDD+. Conservation Letters 3:313–316.

Gamble, J., and C. Fischer. 1935. Flora of the Presidency of Madras, Parts I to XI. Secretary of State for India, London, UK.

Gatica-Saavedra, P., C. Echeverría, and C. R. Nelson. 2017. Ecological indicators for assessing ecological success of forest restoration: a world review. Restoration Ecology 25:850–857.

Griscom, B. W., et al. 2017. Natural climate solutions. Proceedings of the National Academy of Sciences 114:11645–11650.

Harikrishnan, S., D. Mudappa, and T. R. S. Raman. 2018. Herpetofaunal survey in rainforest remnants of the Western Ghats, India. Herpetological Bulletin 146:8–17.

Joshi, A. A., D. Mudappa, and T. R. S. Raman. 2009. Brewing trouble: coffee invasion in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats, India. Biological Invasions 11:2387.

Joshi, A. A., D. Mudappa, and T. R. S. Raman. 2015. Invasive alien species in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats. Tropical Ecology 56:233–244.

Kormann, U., C. Scherber, T. Tscharntke, N. Klein, M. Larbig, J. J. Valente, A. S. Hadley, and M. G. Betts. 2016. Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. Proceedings of the Royal Society B: Biological Sciences 283:20152347.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology 16:605–618.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. C. Andrade, P. M. Fearnside, J. E. L. Ribeiro, and R. L. Capretz. 2006. Rain forest fragmentation and the proliferation of successional trees. Ecology 87:469–482.

Letcher, S. G., and R. L. Chazdon. 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica 41:608–617.

Lewis, S. L., D. P. Edwards, and D. Galbraith. 2015. Increasing human dominance of tropical forests. Science 349:827–832.

Magnago, L. F. S., A. Magrach, J. Barlow, C. E. G. R. Schaefer, W. F. Laurance, S. V. Martins, and D. P. Edwards. 2017. Do fragment size and edge effects predict carbon stocks in trees and lianas in tropical forests? Functional Ecology 31: 542–552.

Marín-Spiotta, E., W. L. Silver, and R. Ostertag. 2007. Long-term patterns in tropical reforestation: plant community composition and aboveground biomass accumulation. Ecological Applications 17:828–839.

Martin, P. A., A. C. Newton, and J. M. Bullock. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proceedings of the Royal Society B: Biological Sciences 280:20132236.

Meli, P., K. D. Holl, J. M. Rey Benayas, H. P. Jones, P. C. Jones, D. Montoya, and D. M. Mateos. 2017. A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. PLOS ONE 12:e0171368.

Molin, P. G., R. Chazdon, S. F. de Barros Ferraz, and P. H. S. Brancalion. 2018. A landscape approach for cost-effective large-scale forest restoration. Journal of Applied Ecology 55:2767–2778.

Mudappa, D., and T. R. S. Raman. 2007. Rainforest restoration and wildlife conservation on private lands in the Western Ghats. Pages 210–240 *in* Making conservation work. Permanent Black, Ranikhet, Uttaranchal, India.

Muthuramkumar, S., N. Ayyappan, N. Parthasarathy, D. Mudappa, T. R. S. Raman, M. A. Selwyn, and L. A. Pragasan. 2006. Plant community structure in tropical rain forest fragments of the Western Ghats, India. Biotropica 38:143–160.

Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews 82:591–605.

Nascimento, H. E. M., A. C. S. Andrade, J. L. C. Camargo, W. F. Laurance, S. G. Laurance, and J. E. L. Ribeiro. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. Conservation Biology 20:853–860.

Osuri, A. M., D. Chakravarthy, D. Mudappa, T. R. S. Raman, N. Ayyappan, S. Muthuramkumar, and N. Parthasarathy. 2017. Successional status, seed dispersal mode and overstorey species influence tree regeneration in tropical rain-forest fragments in Western Ghats, India. Journal of Tropical Ecology 33:270–284.

Osuri, A. M., V. S. Kumar, and M. Sankaran. 2014. Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India's Western Ghats. Forest Ecology and Management 329:375–383.

Osuri, A. M., and M. Sankaran. 2016. Seed size predicts community composition and carbon storage potential of tree communities in rain forest fragments in India's Western Ghats. Journal of Applied Ecology 53:837–845.

Pascal, J.-P. 1988. Wet evergreen forests of the Western Ghats of India. Institut Français de Pondichéry, Pondicherry, India.

Pascal, J.-P., and B. R. Ramesh. 1997. Field key to the trees and lianas of the evergreen forests of the Western Ghats. Institut Français De Pondichéry, Pondicherry, India.

Pascal, J.-P., B. Ramesh, and D. D. Franceschi. 2004. Wet evergreen forest types of the southern Western Ghats, India. Tropical Ecology 45:281–292.

Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. Science 269:347–350.

Raman, T. R. S. 2006. Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. Biodiversity and Conservation 15:1577–1607.

Raman, T. R. S., D. Mudappa, and V. Kapoor. 2009. Restoring rainforest fragments: survival of mixed-native species seedlings under contrasting site conditions in the Western Ghats, India. Restoration Ecology 17:137–147.

Rathod, I. M., and S. Aruchamy. 2010. Spatial analysis of rainfall variation in Coimbatore district Tamilnadu using GIS. International Journal of Geomatics and Geosciences 1:106–118.

Ratnam, J., S. K. Chengappa, S. J. Machado, N. Nataraj, A. M. Osuri, and M. Sankaran. 2019. Functional traits of trees from dry deciduous "forests" of southern India suggest seasonal drought and fire are important drivers. Frontiers in Ecology and Evolution 7. https://doi.org/10.3389/fevo.2019.00008

Rutishauser, E., B. Hérault, P. Petronelli, and P. Sist. 2016. Tree height reduction after selective logging in a tropical forest. Biotropica 48:285–289.

Sridhar, H., T. R. S. Raman, and D. Mudappa. 2008. Mammal persistence and abundance in tropical rainforest remnants in the southern Western Ghats, India. Current Science 94:748.

Tabarelli, M., A. V. Lopes, and C. A. Peres. 2008. Edge-effects drive tropical forest fragments towards an early-successional system. Biotropica 40:657–661.

Taubert, F., R. Fischer, J. Groeneveld, S. Lehmann, M. S. Müller, E. Rödig, T. Wiegand, and A. Huth. 2018. Global patterns of tropical forest fragmentation. Nature 554:519–522.

Thomas, S. C., and A. R. Martin. 2012. Carbon content of tree tissues: a synthesis. Forests 3:332–352.

United Nations. 2015. Paris agreement. United Nations, Paris, France. https://unfccc.int/process-and-meetings/the-paris-agreement/the-paris-agreement

Wills, J., J. Herbohn, M. O. M. Moreno, M. S. Avela, and J. Firn. 2017. Next-generation tropical forests: Reforestation type affects recruitment of species and functional diversity in a human-dominated landscape. Journal of Applied Ecology 54:772–783.

Wordley, C. F., M. Sankaran, D. Mudappa, and J. D. Altringham. 2017. Bats in the Ghats: Agricultural intensification reduces functional diversity and increases trait filtering in a biodiversity hotspot in India. Biological conservation 210:48–55.

Wortley, L., J.-M. Hero, and M. Howes. 2013. Evaluating ecological restoration success: a review of the literature. Restoration Ecology 21:537–543.

Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Ilic, S. Jansen, S. L. Lewis, R. B. Miller, N. G. Swenson, M. C. Wiemann, and J. Chave. 2009. Global wood density database. Dryad Digital Repository. https://doi.org/10.5061/dryad.234

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2860/full