

ECOSYSTEM RESTORATION IN INDIA: STATUS QUO AND THE WAY FORWARD TO ACHIEVE LAND DEGRADATION NEUTRALITY

RESEARCH ARTICLE

Canopy cover and ecological restoration increase natural regeneration of rainforest trees in the Western Ghats, India

Anand M. Osuri^{1,2} , Divya Mudappa¹ , Srinivasan Kasinathan¹ , T. R. Shankar Raman¹ 

Restoration of canopy cover through tree planting can assist in overcoming barriers to natural regeneration and catalyze recovery of degraded tropical forests. India has made international pledges to restore millions of hectares of degraded forests by 2030, but lacks empirical research on regeneration under different types of planted and natural overstories to guide this mission. We conducted a field study (65 plots of 25 m²) to examine the influence of overstory type and canopy cover on naturally regenerating tree seedlings across degraded rainforests (DRs), mixed-native species ecological restoration (ER) sites, monoculture eucalypt plantations (MP), and mature “benchmark” rainforests (BR) in the Western Ghats mountains of peninsular India. ER had higher native tree seedling densities and recovered community composition toward BR levels compared to DR, while communities in MP shifted in the opposite direction. Densities of native late-successional species increased with canopy cover (particularly in ER), but greater canopy cover was also associated with increases in alien species, a few of which are shade-tolerant. Further, in a nursery experiment comprising four rainforest species, seed germination and early survival increased with shade, but did not vary across soils originating from DR, ER, and MP. Our findings show that while improving canopy cover is important, doing so by planting diverse native species, and controlling invasive alien species, can benefit rainforest recovery in DR fragments. Conversely, planting non-native monocultures in degraded forests, which is a prevalent practice in India, could prove counterproductive for forest recovery in the long term.

Key words: ecological restoration, forest fragmentation, human-modified landscape, monoculture, native species, seedling

Implications for Practice

- Increasing overstory shade through mixed-native species restoration can promote natural regeneration and recovery in degraded tropical rainforest fragments.
- Planting monocultures in degraded forests can reduce natural regeneration and constrain recovery in the long term.
- Protection of mature forests is important and irreplaceable, particularly for sustaining late-successional tree species and communities.

Introduction

Tropical forest loss and degradation are the main drivers of the global biodiversity crisis and constitute a significant anthropogenic source of carbon dioxide to the atmosphere (Pan et al. 2011; Watson et al. 2018; Maxwell et al. 2019). Efforts to reverse biodiversity declines and mitigate climate change through large-scale reforestation of the tropics have gained global prominence through agreements and missions such as the Bonn Challenge and Paris Climate Accord (Lewis et al. 2019), and the ongoing UN Decade on Ecosystem Restoration (2021–2030;

<https://www.decadeonrestoration.org/>). Nearly 300 Mha of degraded lands have been pledged for reforestation by 2030 by several tropical and subtropical countries, with substantial contributions from India, China, and Brazil (Lewis et al. 2019). India has committed to reforest 26 Mha of deforested and degraded lands and capture an additional 2.5–3.0 billion tons of CO₂ equivalent by 2030 (MoEFCC 2021).

In India and elsewhere, reforestation mostly uses large-scale tree plantations (commercial and noncommercial) characterized by low diversity and non-native species (e.g. *Eucalyptus* spp.), while reforestation through passive or active restoration of bio-diverse natural forests is gaining recognition but practiced at

Author contributions: all authors conceived and designed the study; SK collected the data with assistance of all authors; AMO led data analysis and wrote the manuscript with assistance of all authors; all authors reviewed and revised the manuscript and have approved the final version.

¹Nature Conservation Foundation, Mysore, 570 017, India

²Address correspondence to A. M. Osuri, email aosuri@ncf-india.org

considerably smaller scale (Lewis et al. 2019; Osuri et al. 2019). Given the prominence of the global climate crisis, comparisons between reforestation methods have focused on indicators of carbon sequestration such as initial rates of carbon capture (Bonner et al. 2013), carbon storage potential (Huang et al. 2018; Osuri et al. 2020), and, in case of commercial plantations, additional carbon gains derived from long-lived wood products (Keith et al. 2014). Although the ability to foster next-generation forests by facilitating natural regeneration under reforested canopies is key for sustaining climate and biodiversity benefits over longer periods (Wills et al. 2017), few studies have compared natural regeneration under different reforestation methods, particularly in the south Asian tropics.

Tropical forest recovery on degraded lands is constrained by various factors, including unfavorable abiotic conditions, competition from grasses and invasive species, and disruption of seed dispersal and other animal–plant mutualisms (Holl et al. 2000; Elgar et al. 2014; Gunaratne et al. 2014). Ecological restoration (ER) aims to overcome these barriers using a variety of strategies. Passive or natural restoration focuses on mitigating or managing external agents of degradation (e.g. livestock grazing), while relying on natural succession to overcome recovery barriers (Chazdon & Uriarte 2016; Atkinson & Bonser 2020). This low-cost strategy is believed to hold great potential for large-scale restoration, especially in sites subject to low initial disturbance pressure and in close proximity to existing forests (Chazdon & Guariguata 2016; Crouzeilles et al. 2017). Restoration might also adopt “active” strategies to assist recovery or reconstruct degraded ecosystems, using interventions such as invasive species management and tree planting (Chazdon & Guariguata 2016; Atkinson & Bonser 2020). Studies have shown that an overstory of planted trees can contribute to overcoming recovery barriers by shading out competitors, attracting seed dispersers, and creating favorable microhabitats for regeneration and survival of native species (Ashton et al. 2014).

Previous studies have shown that both mixed-native species plantations and monocultures of native or non-native species can facilitate natural regeneration to different levels (Harikrishnan et al. 2012; Onyekwelu & Olabiwonnu 2016; Nerlekar et al. 2019; Trujillo-Miranda et al. 2021; Wills et al. 2021). However, studies assessing patterns and drivers of natural regeneration across different types of tree plantations are rare (but see Farwig et al. 2009; Jayawardhane & Gunaratne 2020; Wills et al. 2021). If facilitation of natural regeneration is primarily through abiotic changes due to increased shade, then regeneration would be expected to increase with canopy cover both within and across plantation types. If, instead, natural regeneration depends on the identity and composition of planted trees on the basis of, e.g. differences in soil nutrient inputs (Boley et al. 2009; Celentano et al. 2011), allelopathic effects (Reigosa et al. 2000), or visitation by seed dispersers (Parrotta 1995; Mendes et al. 2021) and predators, then restoration type would be expected to have a stronger influence on regeneration relative to shade alone. Moreover, differences in overstory species can also drive variation in the composition of regenerating communities (Farwig et al. 2009; Wills et al. 2017; Jayawardhane & Gunaratne 2020). For example, if planted overstories of mixed-native species attract more wildlife than monocultures (Yahya et al. 2017; Jayawardhane &

Gunaratne 2020), then higher colonization of the former by late-successional animal-dispersed species would be expected, whereas early-successional or abiotically dispersed species may show different patterns.

Restoration using a mixture of native tree species is generally associated with greater costs and implementation challenges compared to monoculture plantations or passive restoration (Wills et al. 2017), but understanding how these strategies differ in terms of restoration success and natural forest regeneration is vital to develop cost-effective restoration programs. Here, we used a field study and nursery experiment to examine patterns and identify potential drivers of natural regeneration under different overstory types in a human-modified landscape in the Western Ghats mountains, India. In the field study, we sampled seedlings in 65 plots across degraded tropical rainforests left to recover naturally (DR), degraded rainforests with mixed-native species restoration (ER), monoculture eucalypt plantations (MPs), and relatively intact tropical rainforests (benchmark rainforests [BR]). We tested whether ER had more similar seedling density, diversity, and species composition to BR, compared to MP or DR, and examined the role of canopy cover in explaining natural regeneration across plots. Further, we performed a nursery experiment to examine how tree planting in degraded forests, through modifications of shade cover and soil, can affect tree seed germination and early seedling survival. The experiment assessed seed germination and early survival of four rainforest species under low versus high shade cover, in soils that originated from DR, ER, and MP.

Methods

Study Area

The study was conducted on the Valparai Plateau (10.250°–10.367°N, 76.867°–76.983°E), situated within the Anamalai Hills in the southern Western Ghats mountains of India. The area lies within the Western Ghats and Sri Lanka Biodiversity Hotspot (Kumar et al. 2004). The 22,000 ha Valparai Plateau ranges in elevation from 700 to 1,500 m above sea level. Mean annual temperature is 21.0°C (max: 26.3°C; min: 17.7°C), and the area receives around 2,700 mm rainfall annually, over 75% of which falls during the southwest monsoon from June to September (data from weather stations in Iyerpadi and Murugalli—see Fig. 1A).

The predominant land covers of the plateau are tea and shade coffee plantations, remnant natural forests and grasslands, and monoculture forestry plantations (Fig. 1A). Tea and coffee have been cultivated in the region since the 1890s, and seven major private companies own and operate the plantations at present. The companies also raise monocultures of non-native eucalypts (mainly, *Eucalyptus grandis*) for supplying fuelwood to tea factories.

Natural forests of the area are classified as mid-elevation tropical wet evergreen forests, and comprise *Cullenia exarillata*, *Mesua ferrea*, and *Palaquium ellipticum* as the dominant and characteristic tree species (Pascal 1988; Pascal et al. 2004). These rainforests extend over a relatively large >30,000 ha block along and beyond the edge of the plateau within Anamalai Tiger Reserve, Parambikulam Tiger Reserve, and Vazhachal Reserved Forest, and within around 45 forest fragments

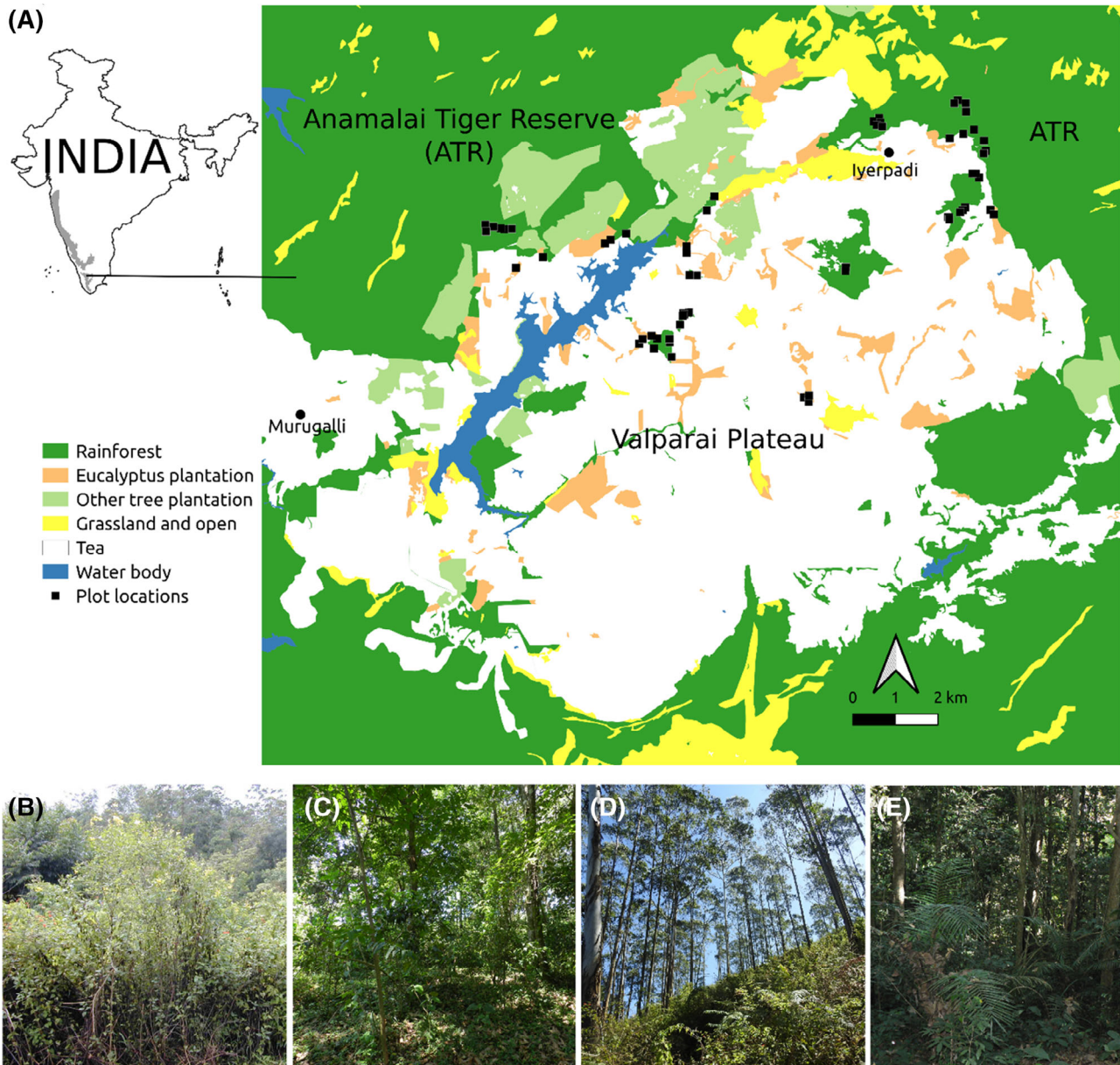


Figure 1. (A) Map of study area situated on the Valparai Plateau in the southern part of the Western Ghats mountain range (shaded gray in the inset). Major land cover types and locations of seedling plots are shown. Map prepared using QGIS (QGIS Development Team 2020). Habitat photos of (B) a degraded rainforest, (C) a (different) degraded rainforest 10 years after ecological restoration, (D) a monoculture eucalypt plantation, and (E) a mature benchmark rainforest.

(1–300 ha) on private lands interspersed among the tea and coffee plantations on the plateau. The large rainforest block within protected areas represents a reference or “benchmark” ecosystem, while many of the fragments harbor primary forests degraded by selective timber felling in the past, fuelwood extraction, and invasion by various alien plant species (Raman et al. 2009). Invasive plants include disturbance-adapted *Lantana camara* L. (woody shrub), *Chromolaena odorata* (L.) R.M.King & H.Rob (nonwoody shrub), and *Mikania micrantha* Kunth (climber), and shade-tolerant woody trees such as *Coffea canephora* Pierre ex A.Froehner, *C. arabica* L., and *Maesopsis eminii* Engl. (Joshi et al. 2009, 2015).

ER of DRs on private lands was initiated in the study area in 2001 as part of a project working on biodiversity conservation and sustainable land use. Over 1,000 ha of forest fragments have been identified and protected (passive or natural restoration) through partnerships with three major plantation companies. Active ER has been attempted in around 100 ha of highly degraded forest patches. Active restoration involved site preparation by removing invasive alien plants (mainly, *L. camara*, *C. odorata*, and *M. micrantha*) and planting a diverse mix of locally sourced and nursery-raised rainforest tree saplings (60–80 species/ha), followed by monitoring and occasional site maintenance to control invasive species and infill gaps (see

Table 1. Sampling effort, forest patch area, distance to continuous forests, and percent canopy cover of plots sampled as part of the field study in the Western Ghats, India. Values in parentheses represent ranges for patch area and distance to continuous forests.

Overstory Type	Sites Sampled	Plots Sampled	Average Area (ha)	Distance from Continuous Forest (m)	Average % Canopy Cover (± 1 SE)
Degraded rainforest	7	17	62.1 (6.8–170.5)	2,416 (309–5,289)	79 \pm 4.3
Ecologically restored rainforest	5	14	14.1 (2.9–41.3)	1,735 (251–3,054)	98 \pm 5.2
Monoculture eucalypt plantation	6	15	22.5 (0.8–78.5)	483 (0–1,305)	87 \pm 4.8
Benchmark rainforest	4	21	>30,000	—	95 \pm 4.2

Mudappa & Raman 2007; Raman et al. 2009; Osuri et al. 2019, for more information about the study area and restoration project).

Eucalypt plantations are typically harvested on an 8–10-year cycle, with trees freshly planted or reemerging from coppiced stems after each cycle. However, many plantations in the landscape (including those sampled in this study) remained unharvested and free of active management over substantially longer periods (based on direct observations and conversations with managers), and are therefore comparable to noncommercial plantations of the type used widely for reforestation in India.

Field Sampling

Naturally regenerating tree seedlings were sampled in four habitats—DR fragments, 10–15-year-old ER sites in degraded fragments, MPs, and mature and relatively intact BRs (Fig. 1B–E). MP plots were located within plantations that were established between 1969 and 1977, and last harvested between 2002 and 2005. Seedling plots were sampled during February to March 2018, February 2019, April 2020, and March 2021.

We identified and counted tree seedlings (10–50 cm height) in 65 square plots of 5 \times 5 m (0.0025 ha) representing DR ($n = 17$), ER ($n = 14$), MP ($n = 15$), and BR ($n = 19$). Plots were situated at least 50 m apart and distributed over seven, five, six, and four fragments/sites in DR, ER, MP, and BR, respectively (Table 1). Species were identified using botanical and field keys (Gamble & Fischer 1935; Pascal & Ramesh 2007), herbarium collections from previous botanical surveys in the study area (Muthuramkumar et al. 2006), and based on familiarity with seedling identification gained through work in a rainforest nursery linked to the ER program. Canopy cover (%) was estimated at the center of each plot using a Spherical Crown Densiometer (Forestry Suppliers, Jackson, MS, U.S.A.).

Species were classified according to habitat affinity and origin as late-successional native, early-successional native, and (invasive) alien species based on literature and previous assessments (Osuri et al. 2017; <http://www.biotik.org/>). Information on seed dispersal modes and seed sizes were recorded from published sources (Ganesh & Davidar 2001; Osuri & Sankaran 2016; Osuri et al. 2017), and direct observations and measurements in the field.

Germination Experiments

The germination experiment aimed to explore the influences of shade and soil (origin) type on natural regeneration associated with different plantation strategies in degraded forests. This *ex situ*

experiment conducted from June to October 2017 examined seed germination and early survival of four native rainforest tree species using a factorial design. Seeds were sown in soils originating from three habitats—ER, MP, and DR—under two shade levels (low: 50% high: 75%; Fig. S1). Shade levels were meant to represent relatively open canopies of degraded areas, and relatively closed canopies under planted understories, and were created in the nursery using a 50% nursery shade net in a single layer (low shade cover) and double layer (high shade cover), respectively (McLaren & McDonald 2003). Topsoil (0–15 cm depth) was collected from five sites each in ER, MP, and DR. A shovel was used over 1 m² to dig up roughly 0.15 m³ soil at one location per site. Collected soils were pooled by habitat type, and passed through a 2.5 mm mesh sieve. Processed soils were distributed over 960 nursery polybags (22.6 cm \times 6.5 cm; 320 per soil type) in five blocks, with 192 polybags per block (32 bags \times 3 soil types \times 2 shade cover levels). The entire experimental set up was enclosed in a chicken-mesh frame to exclude vertebrate seed predators.

Four tree species *Knema attenuata* (Wall. ex Hook.f. & Thomson) Warb., *Actinodaphne wightiana* (Kuntze) Noltie, *Artocarpus heterophyllus* Lam., and *Elaeocarpus tuberculatus* Roxb. were used in the experiment. These species were selected as they are widely distributed in the study area and were fruiting at the start of the experiment. *K. attenuata* is a late-successional species restricted to wet-evergreen forests, and *A. heterophyllus* and *E. tuberculatus* are late-successional species occurring in evergreen and drier semi-evergreen forests, while *A. wightiana* is an early-successional species in wet-evergreen forests in the study area (Osuri et al. 2017; <http://www.biotik.org/>). Mature, fallen, and undamaged fruits were collected from beneath the canopies of five to seven fruiting individuals of each species, 1 or 2 days before initiation of the experiment, and pulp removed with washing in water to extract the seeds. Each block was sown with 48 seeds of each species (one seed per polybag), divided equally among the three soil types and two shade cover levels. As the experiment was conducted during the rainy season, additional watering was only carried out during gaps between rainy days when soils appeared dry.

The experiment was monitored daily, and the status of each seed was recorded under one of five classes: not germinated (N), seed coat cracked (G), main shoot emerged (S), leaves emerged (L), or dead (D). Monitoring of seed germination and seedling emergence was stopped after 128 days once the status of all seeds or seedlings had stabilized and no further transitions were occurring. All seeds that attained a status of S or L by the end of the experiment were considered to have germinated

successfully. Past experience from the restoration nursery suggests that none of the study species exhibit seed dormancy; we therefore considered seeds that remained ungerminated at the end of the experiment as dead, or unlikely to survive.

Statistical Analysis

Data were analyzed and outputs were prepared using the R statistical and programming environment (R Core Team 2020).

Plot Data. Previous studies have calculated species Importance Value Index (IVI) of seedlings as the sum of percent frequency (% plots in which detected), percent relative abundance, and percent dominance (based on height), with values ranging from 0 to 300 (Vargas-Rodriguez et al. 2005). As seedling heights were not recorded in our plots, we report a modified IVI calculated as percent frequency plus percent relative abundance, with a potential range of 0–200 for each species in each overstory type (Table S1).

We used generalized linear models (GLMs) on the plot data to examine regeneration variables in relation to overstory type (DR, ER, MP, and BR) and canopy cover (%). The response variables included overall seedling density (seedlings/plot), overall species density (seedling species/plot), late-successional seedling and species density, early-successional seedling and species density, alien seedling and species density, and species composition (% similarity to benchmark). Community similarity of plots in DR, ER, and MP to benchmarks was estimated as the Bray–Curtis pairwise similarity index (BC_{ij}):

$$BC_{ij} = 1 - \frac{\sum_{k=1}^K |n_{ik} - n_{jk}|}{n_{i+} + n_{j+}}$$

where n_{ik} and n_{jk} are the number of individuals of species k in plots i and j , and n_{i+} and n_{j+} are the total numbers of individuals in i and j .

For DR, ER, and MP, we estimated the average pairwise similarity of each plot to all BM plots, and for each benchmark plot, we estimated average pairwise similarity to all other benchmark plots. Using GLMs, we tested for differences in response variables between the four overstory types, and examined whether variation in responses is best explained by overstory type, canopy cover, or both predictors combined. For each response, we ran four models with different sets of predictors, namely, two single predictor models (Response~Type; Response~Cover), one two-predictor model without an interaction (Response~Type + Cover), and one two-predictor model with a two-way interaction between overstory type and canopy cover (Response~Type × Cover). We ran GLMs with a Poisson error structure for species density responses, GLMs with a negative binomial error structure for seedling density responses (on account of data overdispersion), and beta regression models for % similarity to benchmarks.

For each response, models were ranked in decreasing order of relative likelihood, based on small-sample corrected Akaike Information Criterion (AIC_c), where lower AIC_c scores indicate

greater model relative likelihood (Anderson & Burnham 2004). The model with lowest AIC_c and any other models within four AIC_c units of the lowest AIC_c (i.e. $\Delta AIC_c \leq 4$) were identified as the model(s) that best explained variation for each response. Differences between overstory types were assessed based on 95% confidence intervals (CIs) of model intercepts and slopes, wherein intercept or slope 95% CIs of a given overstory type not overlapping with mean intercepts or slopes of another were interpreted as consistent differences in intercepts or slopes, respectively, between that pair of overstory types (Nakagawa & Cuthill 2007).

Germination Experiments. We used data from the nursery experiment to examine the effects of shade (low vs. high) and soil origin (DR, ER, and MP) on seed germination at the end of the 128-day experiment. Pooling data from 960 seeds across the four species, we modeled germination (1 = germinated, 0 = not germinated) as a function of shade and soil origin (with-out interaction) using a generalized linear mixed-effects model (GLMM) with species ID, and experimental block, included as random factors. The model was specified using a binomial distribution with a logit link function. In addition, to explore variation among species in response to soil and shade, we reran the GLMMs for each species separately, with the experimental block included as a random factor. GLMMs were fit using the lme4 package in R (Bates et al. 2015).

Results

Plot Data

We recorded 2,548 seedlings representing at least 96 species within 65 plots across the four overstory types. The early-successional native species *Clerodendrum infortunatum* L. was among the three most dominant species in DR, ER, and MP. While ER was dominated by native early-successional species, and DR and MP were dominated by both early-successional and alien species (e.g. *Coffea* spp., *L. camara*, and *Gliricidia sepium* [Jacq.] Kunth), the seedling layer of BR was dominated by native late-successional species. See Table S1 for the complete species checklist and modified IVI scores of species in each habitat.

Overall seedling densities were similar, on average, across DR, ER, and BR, ranging from 40 to 53 seedlings per 25 m² plot, while BR had the highest overall species density, followed by ER, DR, and MP (Fig. 2). Late-successional seedling and species densities were highest in BR and lowest in MP, with ER and DR intermediate and statistically indistinguishable from each other, and early-successional seedling and species densities were highest in ER (Fig. 2). Alien seedling densities were highest, on average, in DR but also highly variable, with no statistical differences between overstory types, while alien species densities were lowest in BR, and marginally higher in ER than DR, or MP (Fig. 2). ER had greater community similarity to benchmarks (5.33%; 1 SE = 0.79) than DR (3.44%; 1 SE = 0.58) or MP (1.38%; 1 SE = 0.40), while, as expected, average community similarity of benchmark plots to one another was highest at

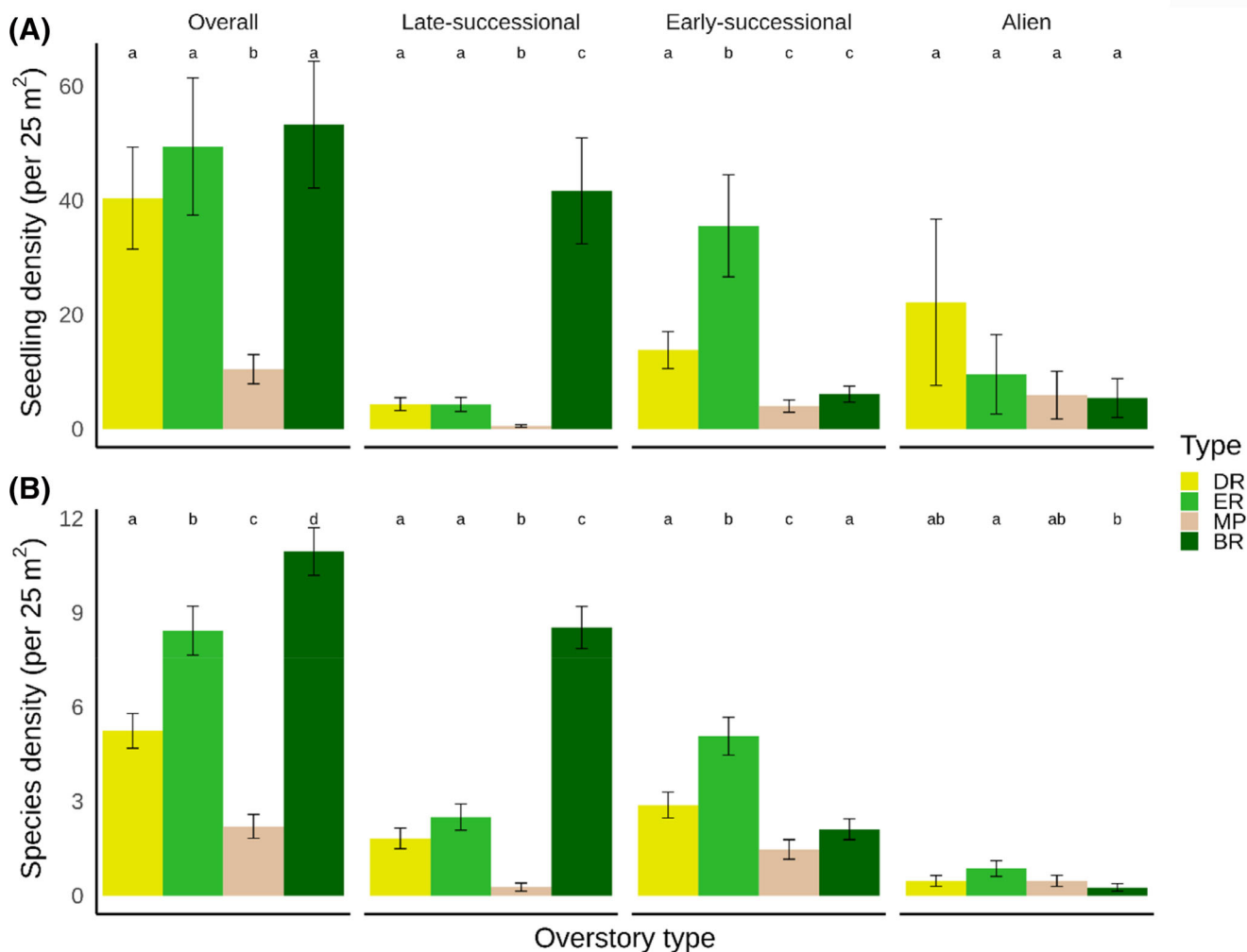


Figure 2. Overall, late-successional-growth, early-successional, and alien seedling densities (A) and species densities (B), in degraded rainforest, ecologically restored rainforest, monoculture eucalypt plantations, and mature benchmark rainforest in the Western Ghats, India. Bars and error bars represent means and \pm SE, respectively. Different characters (a, b, c, d) next to values correspond to statistical differences between overstory types based on interpretation of 95% CIs from the GLMs (also see Tables S2 & S3).

Table 2. List of models that best explained ($\Delta AIC_c \leq 4$) variation in seedling density, species density, and community similarity to benchmark forests across plots. The ranking of overstory types for each response (model intercepts), and relationships of the response variables to canopy cover (positive, negative, or neutral model slopes) based on interpretation of GLM 95% CIs are reported.

Response	Model	ΔAIC_c	Model Intercept (Overstory Type)	Model Slope (Relationship with Canopy Cover)
Seedling density (seedlings/plot)				
Overall	Type + Cover	0	BR, DR, ER > MP	Positive
Late-successional	Type + Cover	0	BR > DR, ER > MP	Positive
Early-successional	Type	0	ER > DR > BR, MP	—
Alien	Type + Cover	2.2	ER > DR > BR, MP	Neutral
	Cover	0	—	Positive
Species density (species/plot)	Type + Cover	1.7	DR > ER, MP > BR	Positive
	Type	0	BR > ER > DR > MP	Positive
Late-successional	Type + Cover	0	BR > DR, ER > MP	Positive
Early-successional	Type × Cover	3.7	BR > DR, ER > MP	Positive; ER > DR > BR, MP
	Type	0	ER > BR, DR > MP	—
	Type + Cover	0.4	ER > DR > BR > MP	Neutral

Table 2. Continued

Response	Model	ΔAIC_c	Model Intercept (Overstory Type)	Model Slope (Relationship with Canopy Cover)
Alien	Type	4	ER > DR, MP > BR	—
	Cover	0	—	Positive
	Type + Cover	0.6	ER > DR, MP > BR	Positive
Community similarity to benchmark (%)	Type	0	BR > ER > DR > MP	—
	Type + Cover	0.2	BR > ER > DR > MP	Neutral

21.30% (1 SE = 1.23). Parameter estimates based on GLM models are provided in Table S2.

Overstory type and canopy cover both played a role in explaining variation in seedling and species densities, and species composition, across plots. The GLMs and model sorting based on ΔAIC_c identified the two-predictor model with no

interaction (Response~Type + Cover) as among the best at explaining variation in all nine density and composition responses ($\Delta AIC_c \leq 2.2$; Tables 2, S2, & S3). Models with overstory type alone also performed relatively well at explaining variation in early-successional seedling and species densities, and seedling community similarity to benchmarks (Table 2). Overall

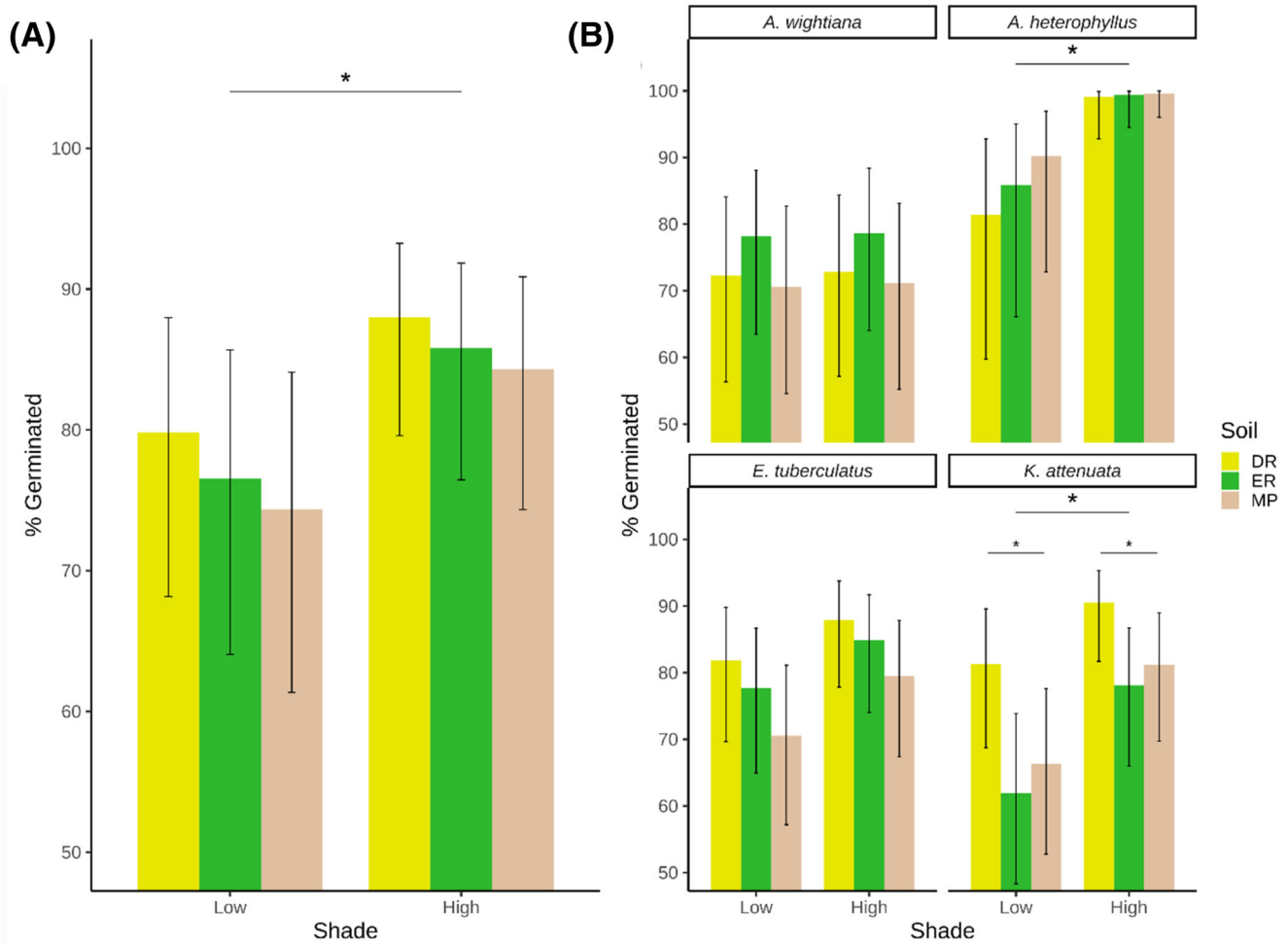


Figure 3. (A) Seed germination increased from low to high shade. (B) This pattern was stronger among late-successional species *A. heterophyllus* and *K. attenuata* than the early-successional species *A. wightiana*. Germination did not differ across soils originating from degraded rainforest (DR), ecologically restored rainforest (ER), and monoculture eucalypt plantations (MP), with the exception of *K. attenuata* that had greater germination in DR soil. Bars represent mean survival and error bars represent $\pm 95\%$ CI. Asterisks represent consistent differences between treatments based on 95% CIs. See Table S4 for model parameters and details.

and late-successional seedling and species densities were positively related to canopy cover across plots (Table 2). For density of late-successional species, the relationship with canopy cover was more positive in ER and DR than MP or BR, based on the two-predictor with interaction model (Response~Type \times Cover), which had substantial empirical support ($\Delta AIC_c = 3.7$; Table 2). Alien seedling and species density were best explained by models comprising canopy cover alone (closely followed by models with Overstory type and Overstory type + Canopy cover as predictors), and increased with canopy cover (Tables 2 & S2). See Table S2 for parameter estimates from all GLM models and Table S3 for detailed summaries of the best-fit models.

Germination Experiment

Seed germination increased from 77% on average under low shade to 86% under high shade ($p < 0.01$), with no differences in survival across soils from DR, ER, and MP (Table S4; Fig. 3). Seed germination of the early-successional species *A. wightiana* did not increase with shade, while the late-successional species *E. tuberculatus*, showed a weak increase in germination with shade (Table S4; Fig. 3). By contrast, the late-successional species *K. attenuata* and *A. heterophyllus* increased germination with shade (Table S4; Fig. 3). Seed germination was unrelated to soil origin in all species, with the exception of *K. attenuata* having significantly higher germination in DR soil compared to ER and MP soils (Table S4; Fig. 3).

Discussion

Our study from a human-modified landscape in the Western Ghats in India showed greater tree regeneration in mature rainforests and 10–15-year-old ecologically restored rainforests compared to DRs left to recover naturally, and MPs. While active ER increased densities of early-successional species and shifted community composition toward that of mature rainforests, it was less effective in recovering late-successional species. The latter remained substantially lower in restored plots compared to mature forests, although substantially higher compared to eucalypt plantations. Our findings suggest that the positive effects of ER can extend to subsequent tree generations (Wills et al. 2017), and highlight its role in sustaining rainforest revival in human-modified landscapes, while reaffirming the importance and irreplaceability of existing mature forests for sustaining rainforest tree communities (Jones et al. 2018; Sacco et al. 2021).

In contrast to ER which promoted recovery, all indicators of natural regeneration in this study were lower in MPs compared to DRs. However, planting non-native monocultures in degraded forests is widely practiced through reforestation and carbon sequestration programs in India (Seidler & Bawa 2016). While such reforestation strategies could offer short-term benefits such as rapid carbon accrual by certain monocultures (Bonner et al. 2013), our results reiterate that leaving degraded forests to recover naturally, or restoring them with mixed-native species, can sustain multiple benefits (biodiversity, carbon

capture) over longer periods (Chazdon & Guariguata 2016; Osuri et al. 2020).

Our findings support the hypothesis that increasing canopy cover can facilitate rainforest recovery by creating favorable microhabitats for tree regeneration (Holl et al. 2000; Ashton et al. 2014). Canopy cover contributed to explaining patterns of seedling density, diversity, and composition across plots, and was positively associated with regeneration of late-successional species, but not early-successional species. This is corroborated by the nursery experiment, which showed a positive influence of shade on seed germination and early survival, particularly for two late-successional species. Interestingly, seed germination in soil originating from eucalypt plantations was no lower than that in soils from degraded or restored forests, suggesting that allelopathic effects associated with eucalypts that could potentially affect seed and seedling performance (Zhang et al. 2010) are not a major constraint on regeneration in our study. This is consistent with previous research from the study area showing high native seedling and sapling survival under eucalypt overstories (Raman et al. 2009). Collectively, these findings suggest that factors other than germination and survival account for differences in regeneration between overstory types. By providing shade, both mixed-native species restoration and eucalypt plantations can foster germination and survival of rainforest trees, although the former provides better canopy cover and regeneration.

In addition to altering microhabitats to favor seed germination and survival, overstory trees can influence animal-mediated processes such as seed dispersal and predation that shape natural regeneration in tropical forests (Terborgh et al. 2008; Paine et al. 2016). Overstories that attract frugivores can increase seed dispersal into sites (Sansevero et al. 2011; Viani et al. 2015; Osuri et al. 2017), while small mammals, particularly rodents, can increase seed predation risk in degraded areas (Mendes et al. 2016; Gopal et al. 2021). When controlled for canopy cover, we found greater regeneration under native tree overstories than eucalypt monocultures, and that regeneration of late-successional species increased with canopy cover at a greater rate across native overstory plots (restored or degraded) than eucalypt plots. Moreover, we recorded just one native large-seeded (length > 3 cm) animal-dispersed species regenerating in eucalypt plantations, as against two species in DR, six in restored rainforest, and eight large-seeded species in mature rainforest. Thus, although our study did not directly examine animal-mediated processes, our findings suggest that such processes support regeneration better under overstories comprising mixed-native species than under eucalypt monocultures. Our findings also suggest that while early-successional species dominate regeneration in these relatively young restored forests, further development of canopy cover, along with maturation and fruiting of planted overstory trees, could promote rainforest succession over time.

Interestingly, just as regeneration of late-successional species was positively associated with canopy cover across plots in our study, so was regeneration of alien species. This is largely because of two shade-tolerant and animal-dispersed alien species—*Coffea* spp. and *M. eminii*—invading from shade-

coffee plantations that abut some of the study sites (Joshi et al. 2009, 2015). These two species accounted for the majority of seedlings of alien species in degraded, restored, and mature rainforest plots, in contrast to eucalypt monocultures that were dominated by disturbance-adapted *L. camara*. Previous research has shown a negative relationship between densities of invasive *Coffea* and native seedling densities (Joshi et al. 2009), suggesting that control of shade-tolerant alien species, along with additional planting of late-successional species, could play a role in sustaining rainforest succession in restored forests.

Besides shade and overstory composition, factors potentially influencing seedling communities but not examined explicitly in our study include patch size, isolation, and history and management practices of different habitats. The potential for natural regeneration can decrease with increasing isolation from continuous forests (Molin et al. 2018), and this is evident from previous work on saplings in the study landscape (Osuri et al. 2019). It is therefore likely that differences in seedling density, diversity, and composition between eucalypt plantations and degraded or restored forests are mitigated to an extent by the closer proximity of eucalypt plantation plots to continuous forests compared to plots in degraded or restored forests (<500 m vs. >1,500 m).

Patch sizes of ER plots were comparable to *Eucalyptus* plantations, but considerably smaller than DR patches in our dataset, because smaller fragments tend to be more heavily degraded and are therefore prioritized for restoration. This could partly explain the proliferation of early-successional species and occurrence of invasive aliens in restored plots, and the lack of consistent differences in regeneration of late-successional species between restored and degraded plots, given that, when matched for patch size, restored plots sustain greater densities of late-successional saplings and adults than degraded forest plots (Osuri et al. 2019). This also highlights that larger forest fragments, too, should be considered for active restoration, particularly ones that are spatially isolated, because large patch size alone appears inadequate for facilitating recovery from degradation.

In terms of history and management, disturbance-adapted invasive understory shrubs such as *L. camara* were removed initially and have remained suppressed under restored canopies, but dominate the understories of degraded forests and eucalypt plantations. These invasive aliens not only compete directly with native species (Raman et al. 2009), but can also have indirect negative impacts on tree regeneration by exacerbating other disturbances, such as fire (Hiremath & Sundaram 2005). Thus, while invasive shrub control is a consequential additional intervention distinguishing restored forests from degraded forests and plantations in this study, future research on the standalone effects of invasive shrub control on regeneration under different overstories holds promise for developing less expensive and more widely applicable restoration strategies to complement mixed-native species restoration.

Collectively, our findings suggest that while increasing canopy cover can promote rainforest recovery, canopies restored using diverse native species are more effective at reviving natural regeneration than ones comprising non-native monocultures, although neither achieve recovery to the level of mature

rainforests. They highlight, therefore, the potential benefits of prioritizing restoration of native diversity and composition in massive reforestation efforts pledged by India and other countries over the coming decade, complemented by steps to mitigate further loss and degradation of existing mature forests. These benefits include not just forest regeneration (this study), but also biodiversity, carbon capture, and livelihoods, among others (Bawa et al. 2021). Expanding restoration in India would, however, require substantial expansion of scientific knowledge, technical expertise, and infrastructure (e.g. ethical seed sourcing and establishment of native plant nurseries) for restoring appropriate species in appropriate areas, backed by policies tailored to support ER. At the same time, policies promoting monoculture or species-poor plantations (native or non-native) in degraded forests need to be reexamined in light of negative impacts of this practice on forest regeneration and recovery, as well as on livelihoods and other ecological benefits (Seidler & Bawa 2016). Such species could still play a role in restoration, however, such as fast-growing commercial species planted in polycultures with native species providing shade during initial stages of forest recovery, and partially offsetting restoration costs (Brancalion et al. 2020), or lands currently under monoculture plantations offering conditions conducive to planting and restoration of appropriate native species.

Acknowledgments

The authors are grateful to their entire field team and in particular T. Vanidass, T. Sundarraj, G. Murthi, S. Sumathi, and R. Rajesh for their invaluable contributions to the research and restoration work. The authors thank M. Siddhartha, A. Surendra, A. Gopal, V. Osuri, D. Osuri, and U. Mendiratta for help with setting up the nursery experiment. Discussions with A. Krishnan, K. Bhat, R. Nandakumar, V. Karthick, and V. Kumar, and comments from two anonymous reviewers helped improve our manuscript. The authors thank Tata Coffee Ltd, Hindustan Lever Ltd (and the current owner of these estates, Tea Estates India Ltd), and Parry Agro Industries Ltd for supporting restoration and research activities, and the Tamil Nadu Forest Department for granting research permits. Fieldwork was supported by the Rufford Foundation, SERB National Postdoctoral Fellowship (PDF/2016/000104), Rohini Nilekani Philanthropies, Arvind Datar, and A. M. M. Murugappa Chettiar Research Centre. A.M.O. received a Ramalingaswami Re-entry Fellowship (2018–2019) from the Department of Biotechnology, Government of India, during manuscript preparation. Data and analysis script are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.z34tmpgf9> (Osuri et al. 2021).

LITERATURE CITED

- Anderson D, Burnham K (2004) Model selection and multimodel inference. Second edition. Springer-Verlag, New York
- Ashton MS, Gunatilleke CVS, Gunatilleke IAUN, Singhakumara BMP, Gamage S, Shibayama T, Tomimura C (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

- Atkinson J, Bonser SP (2020) “Active” and “passive” ecological restoration strategies in meta-analysis. *Restoration Ecology* 28:1032–1035
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48
- Bawa KS, Sengupta A, Chavan V, Chellam R, Ganesan R, Krishnaswamy J, et al. (2021) Securing biodiversity, securing our future: a national mission on biodiversity and human well-being for India. *Biological Conservation* 253:108867
- Boley JD, Drew AP, Andrus RE (2009) Effects of active pasture, teak (*Tectona grandis*) and mixed native plantations on soil chemistry in Costa Rica. *Forest Ecology and Management* 257:2254–2261
- Bonner MTL, Schmidt S, Shoo LP (2013) A meta-analytical global comparison of aboveground biomass accumulation between tropical secondary forests and monoculture plantations. *Forest Ecology and Management* 291:73–86
- Brancalion PHS, Amazonas NT, Chazdon RL, van Melis J, Rodrigues RR, Silva CC, Sorriani TB, Holl KD (2020) Exotic eucalypts: from demonized trees to allies of tropical forest restoration? *Journal of Applied Ecology* 57:55–66
- Celentano D, Zahawi RA, Finegan B, Ostertag R, Cole RJ, Holl KD (2011) Litter-fall dynamics under different tropical forest restoration strategies in Costa Rica. *Biotropica* 43:279–287
- Chazdon RL, Guariguata MR (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. *Biotropica* 48:716–730
- Chazdon RL, Uriarte M (2016) Natural regeneration in the context of large-scale forest and landscape restoration in the tropics. *Biotropica* 48:709–715
- Crouzeilles R, Ferreira MS, Chazdon RL, Lindenmayer DB, Sansevero JBB, Monteiro L, Iribarrem A, Latawiec AE, Strassburg BBN (2017) Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances* 3:e1701345
- Elgar AT, Freebody K, Pohlman CL, Shoo LP, Catterall CP (2014) Overcoming barriers to seedling regeneration during forest restoration on tropical pasture land and the potential value of woody weeds. *Frontiers in Plant Science* 5:1–10
- Farwig N, Sajita N, Böhning-Gaese K (2009) High seedling recruitment of indigenous tree species in forest plantations in Kakamega Forest, western Kenya. *Forest Ecology and Management* 257:143–150
- Gamble J, Fischer C (1935) Flora of the presidency of Madras, parts I to XI. Secretary of State for India, London, United Kingdom
- Ganesh T, Davidar P (2001) Dispersal modes of tree species in the wet forests of southern Western Ghats. *Current Science* 80:394–399
- Gopal A, Mudappa D, Raman TRS, Naniwadekar R (2021) Seed fates of four rainforest tree species in the fragmented forests of Anamalais in the southern Western Ghats, India. *Acta Oecologica* 110:103698
- Gunaratne AMTA, Gunatilleke CVS, Gunatilleke IAUN, Madawala HMSP, Burslem DFRP (2014) Overcoming ecological barriers to tropical lower montane forest succession on anthropogenic grasslands: synthesis and future prospects. *Forest Ecology and Management* 329:340–350
- Harikrishnan S, Vasudevan K, Udhayan A, Mathur PK (2012) Biodiversity values of abandoned teak, *Tectona grandis* plantations in southern Western Ghats: is there a need for management intervention? *Basic and Applied Ecology* 13:139–148
- Hiremath AJ, Sundaram B (2005) The fire-lantana cycle hypothesis in Indian forests. *Conservation and Society* 3:26–42
- Holl KD, Loik ME, Lin EHV, Samuels IA (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology* 8:339–349
- Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang A, et al. (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. *Science* 362:80–83
- Jayawardhane J, Gunaratne AMTA (2020) Restoration success evaluation of a thinned and enriched pine plantation in Sri Lanka. *Journal of Tropical Forest Science* 32:402–413
- Jones HP, Jones PC, Barbier EB, Blackburn RC, Rey Benayas JM, Holl KD, McCrackin M, Meli P, Montoya D, Mateos DM (2018) Restoration and repair of Earth’s damaged ecosystems. *Proceedings of the Royal Society B: Biological Sciences* 285:20172577
- Joshi AA, Mudappa D, Raman TRS (2009) Brewing trouble: coffee invasion in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats, India. *Biological Invasions* 11:2387–2400
- Joshi AA, Mudappa D, Raman TRS (2015) Invasive alien species in relation to edges and forest structure in tropical rainforest fragments of the Western Ghats. *Tropical Ecology* 56:233–244
- Keith H, Lindenmayer D, Mackey B, Blair D, Carter L, McBurney L, Okada S, Konishi-Nagano T (2014) Managing temperate forests for carbon storage: impacts of logging versus forest protection on carbon stocks. *Ecosphere* 5:75
- Kumar A, Pethiyagoda R, Mudappa D (2004) Western Ghats and Sri Lanka. Pages 152–157. In: Hotspots revisited—Earth’s biologically richest and most endangered ecoregions. CEMEX, Monterrey
- Lewis SL, Wheeler CE, Mitchard ETA, Koch A (2019) Restoring natural forests is the best way to remove atmospheric carbon. *Nature* 568:25–28
- Maxwell SL, Evans T, Watson JEM, Morel A, Grantham H, Duncan A, et al. (2019) Degradation and forgone removals increase the carbon impact of intact forest loss by 626%. *Science Advances* 5:eaax2546
- McLaren KP, McDonald MA (2003) The effects of moisture and shade on seed germination and seedling survival in a tropical dry forest in Jamaica. *Forest Ecology and Management* 183:61–75
- Mendes CP, Ribeiro MC, Galetti M (2016) Patch size, shape and edge distance influence seed predation on a palm species in the Atlantic Forest. *Ecography* 39:465–475
- Mendes LM, César RG, Uezu A, Beltrame TP, Rodriguez LCE, Gomes HB, Cullen L (2021) Large canopy and animal-dispersed species facilitate natural regeneration in tropical forest restoration. *Restoration Ecology* 29:e13406
- MoEFCC (2021) Annual report 2020–21. Ministry of Environment, Forest and Climate Change, Government of India, New Delhi, India
- Molin PG, Chazdon R, de Barros Ferraz SF, PHS Brancaion (2018) A landscape approach for cost-effective large-scale forest restoration. *Journal of Applied Ecology* 55:2767–2778
- Mudappa D, Raman TRS (2007) Rainforest restoration and wildlife conservation on private lands in the Western Ghats. Pages 210–240. In: Making conservation work. Permanent Black, Ranikhet, India
- Muthuramkumar S, Ayyappan N, Parthasarathy N, Mudappa D, Raman TRS, Selwyn MA, Pragasan LA (2006) Plant community structure in tropical rain forest fragments of the Western Ghats, India. *Biotropica* 38:143–160
- Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* 82:591–605
- Nerlekar AN, Kamath V, Saravanan A, Ganesan R (2019) Successional dynamics of a regenerated forest in a plantation landscape in southern India. *Journal of Tropical Ecology* 35:57–67
- Onyekwelu JC, Olabiwonnu AA (2016) Can forest plantations harbor biodiversity similar to natural forest ecosystems over time? *International Journal of Biodiversity Science, Ecosystem Services & Management* 12:108–115
- Osuri AM, Sankaran M (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
- Osuri AM, Chakravarthy D, Mudappa D, Raman TRS, Ayyappan N, Muthuramkumar S, Parthasarathy N (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 AM, Kasinathan S, Siddhartha MK, Mudappa D, Raman TRS (2019) Effects of restoration on tree communities and carbon storage in rainforest fragments of the Western Ghats, India. *Ecosphere* 10:e02860
- Osuri AM, Gopal A, Raman TRS, DeFries R, Cook-Patton SC, Naeem S (2020) Greater stability of carbon capture in species-rich natural forests compared to species-poor plantations. *Environmental Research Letters* 15:034011
- Osuri AM, Mudappa D, Kasinathan S, Raman TRS (2021) Data from: Canopy cover and ecological restoration increase natural regeneration of rainforest trees in the Western Ghats, India, Dryad, Dataset. <https://doi.org/10.5061/dryad.z34tmpgf9>.

- Paine CET, Beck H, Terborgh J (2016) How mammalian predation contributes to tropical tree community structure. *Ecology* 97:3326–3336
- Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, et al. (2011) A large and persistent carbon sink in the world's forests. *Science* 333:988–993
- Parrotta JA (1995) Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science* 6:627–636
- Pascal JP (1988) Wet evergreen forests of the Western Ghats of India. Institut Français de Pondichéry, Pondicherry, India
- Pascal JP, Ramesh BR (2007) Field key to the trees and lianas of the evergreen forests of the Western Ghats. Institut Français De Pondichéry, Pondicherry, India
- Pascal JP, Ramesh BR, Franceschi DD (2004) Wet evergreen forest types of the southern Western Ghats, India. *Tropical Ecology* 45:281–292
- QGIS Development Team (2020) QGIS geographic information system. Open Source Geospatial Foundation Project
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Raman TRS, Mudappa D, Kapoor V (2009) Restoring rainforest fragments: survival of mixed-native species seedlings under contrasting site conditions in the Western Ghats, India. *Restoration Ecology* 17:137–147
- Reigosa MS, Gonzalez L, Souto XC, Pastoriza JE (2000) Allelopathy in forest ecosystems. Pages 183–193. In: Narwal SS, Hoagland RE, Dilday RH, Reigosa MJ (eds) Allelopathy in ecological agriculture and forestry: proceedings of the III international congress on allelopathy in ecological agriculture and forestry, Dharwad, India. Springer Netherlands, Dordrecht
- Sacco AD, Hardwick KA, Blakesley D, Brancalion PHS, Breman E, Rebola LC, et al. (2021) Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global Change Biology* 27:1328–1348
- Sansevero JBB, Prieto PV, de Moraes LFD, Rodrigues PJP (2011) Natural regeneration in plantations of native trees in lowland Brazilian Atlantic Forest: community structure, diversity, and dispersal syndromes. *Restoration Ecology* 19:379–389
- Seidler R, Bawa KS (2016) India faces a long and winding path to green climate solutions. *Proceedings of the National Academy of Sciences* 113:12337–12340
- Terborgh J, Nuñez-Iturri G, Pitman NCA, Valverde FHC, Alvarez P, Swamy V, Pringle EG, Paine CET (2008) Tree recruitment in an empty forest. *Ecology* 89:1757–1768
- Trujillo-Miranda AL, Toledo-Aceves T, López-Barrera F, Günter S (2021) Tree diversity and timber productivity in planted forests: *Pinus patula* versus mixed cloud forest species. *New Forests* 52:177–195
- Vargas-Rodríguez YL, Vázquez-García JA, Williamson GB (2005) Environmental correlates of tree and seedling–sapling distributions in a Mexican tropical dry forest. *Plant Ecology* 180:117–134
- Viani RAG, Vidas NB, Pardi MM, Castro DCV, Gusson E, Brancalion PHS (2015) Animal-dispersed pioneer trees enhance the early regeneration in Atlantic Forest restoration plantations. *Natureza & Conservação* 13:41–46
- Watson JEM, Evans T, Venter O, Williams B, Tulloch A, Stewart C, et al. (2018) The exceptional value of intact forest ecosystems. *Nature Ecology and Evolution* 2:599–610
- Wills J, Herbohn J, Moreno MOM, Avela MS, Firn J (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
- Wills J, Herbohn J, Wells J, Moreno MOM, Ferraren A, Firn J (2021) Seedling diversity in actively and passively restored tropical forest understories. *Ecological Applications* 31:e02286
- Yahya MS, Syafiq M, Ashton-Butt A, Ghazali A, Asmah S, Azhar B (2017) Switching from monoculture to polyculture farming benefits birds in oil palm production landscapes: evidence from mist netting data. *Ecology and Evolution* 7:6314–6325
- Zhang D, Zhang J, Yang W, Wu F (2010) Potential allelopathic effect of *Eucalyptus grandis* across a range of plantation ages. *Ecological Research* 25: 13–23

Supporting Information

The following information may be found in the online version of this article:

- Figure S1.** Germination experiment factorial design comprising seeds of four species.
- Table S1.** Tree species, traits, and the modified Importance Values Index.
- Table S2.** Intercepts, slopes, and ΔAIC_c estimated from GLMs.
- Table S3.** Summaries of generalized linear models comprising overstory type and/or canopy cover.
- Table S4.** Summaries of generalized linear mixed-effects models of seed germination and early survival in relation to shade and soil origin.

Guest Coordinating Editor: Kripal Singh

Received: 16 June, 2021; First decision: 20 July, 2021; Revised: 12 September, 2021; Accepted: 12 September, 2021