

UC Santa Cruz

UC Santa Cruz Previously Published Works

Title

Active restoration increases tree species richness and recruitment of large-seeded taxa after 16–18 years

Permalink

<https://escholarship.org/uc/item/2qt6s177>

Authors

Schubert, Spencer C

Zahawi, Rakan A

Oviedo-Brenes, Federico

et al.

Publication Date

2024-11-19

DOI

10.1002/eap.3053

Peer reviewed

1 **Ecological Applications**

2

3 **Article**

4

5 **Active restoration increases tree species richness and recruitment of large-seeded taxa after**
6 **16-18 years**

7

8 Spencer C. Schubert^{1*}

9 Rakan A. Zahawi^{1,2,3}

10 Federico Oviedo-Brenes⁴

11 Juan Abel Rosales⁴

12 Karen D. Holl¹

13

14 ¹ Environmental Studies Department, University of California, Santa Cruz, CA, USA

15 ² Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador

16 ³ School of Life Sciences, University of Hawaii at Mānoa, Honolulu, HI, USA

17 ⁴ Las Cruces Biological Station, Organization for Tropical Studies, San Vito de Coto Brus, Costa
18 Rica

19 *Corresponding Author – scschubert11@gmail.com; <https://orcid.org/0000-0002-5841-8157>

20

21 Open Research Statement: Data and R code needed to reproduce analyses are archived on Dryad
22 platform DOI: 10.5061/dryad.s7h44j1gc

23

24 **Keywords:** applied nucleation, community composition, forest dynamics, late-successional, seed
25 size, succession, tree islands, tropical forest

26 **ABSTRACT**

27 Tropical forest restoration presents a potential lifeline to mitigate climate change and
28 biodiversity crises in the Anthropocene. Yet, the extent to which human interventions, such as
29 tree planting, accelerate the recovery of mature functioning ecosystems or redirect successional
30 trajectories towards novel states remains uncertain due to a lack of long-term experiments. In
31 2004-2006, we established three 0.25-ha plots at ten sites in southern Costa Rica to test three
32 forest restoration approaches: natural regeneration (no planting), applied nucleation (planting in
33 patches), and plantation (full planting). In a comprehensive survey after 16-18 years of recovery,
34 we censused >80,000 seedlings, saplings, and trees from at least 255 species across 26
35 restoration plots (9 natural regeneration, 9 applied nucleation, 8 plantation) and six adjacent
36 reference forests to evaluate treatment effects on recruitment patterns and community
37 composition. Both applied nucleation and plantation treatments resulted in significantly elevated
38 seedling and sapling establishment and more predictable community composition compared to
39 natural regeneration. Similarity of vegetation composition to reference forest tended to scale
40 positively with treatment planting intensity. Later-successional species with seeds ≥ 5 mm had
41 significantly greater seedling and sapling abundance in the two planted treatments, and
42 plantation showed similar recruitment densities of large-seeded (≥ 10 mm) species to reference
43 forest. Plantation tended towards a lower abundance of early-successional recruits than applied
44 nucleation. Trees (≥ 5 cm DBH) in all restoration treatments continued to be dominated by a few
45 early-successional species and originally transplanted individuals. Seedling recruits of planted
46 taxa were more abundant in applied nucleation than the other treatments though few transitioned
47 into the sapling layer. Overall, our findings show that active tree planting accelerates the
48 establishment of later-successional trees compared to natural regeneration after nearly two

49 decades. While the apparent advantages of higher density tree planting on dispersal and
50 understory establishment of larger-seeded, later-successional species recruitment is notable,
51 more time is needed to assess whether these differences will persist and transition to the more
52 rapid development of a mature later-successional canopy. Our results underscore the need for
53 ecological restoration planning and monitoring that targets biodiversity recovery over multiple
54 decades.

55

56 **INTRODUCTION**

57 In recent years, recognition of the regenerative potential of forests in human-modified tropical
58 landscapes (Chazdon and Guariguata 2016, Williams et al. 2023) has contributed to expanding
59 investment in forest restoration as a tool to sequester carbon, preserve biodiversity, and improve
60 human wellbeing (Edwards et al. 2021, Fuss et al. 2021, Koch and Kaplan 2022, Tonetti et al.
61 2022, Aguirre-Gutiérrez et al. 2023). In addition to the ongoing UN Decade on Ecosystem
62 Restoration, numerous global initiatives have emerged to plant vast numbers of trees and restore
63 hundreds of millions of hectares of land (e.g., Trillion Trees Campaign, Bonn Challenge), largely
64 targeting tropical regions (Brancalion and Holl 2020, Martin et al. 2021). Although the goals of
65 restoration vary, efforts targeting recovery of the high species diversity and complex ecological
66 interactions characteristic of tropical forests require management strategies that promote the
67 assembly of rich communities of native species whose composition, structure, and function
68 closely resemble that of reference forests (Gann et al. 2019, Carrick and Forsythe 2020). Despite
69 a large body of research that details how tropical forests recover, well-replicated field
70 experiments directly comparing restoration interventions that are monitored for multidecadal

71 timeframes relevant to successional processes remain scarce (Chazdon et al. 2017, Brancalion et
72 al. 2019).

73 A suite of well-studied abiotic and biotic barriers limit the recovery of woody plant
74 communities in tropical ecosystems; these frequently include degraded soils, extreme
75 microclimates, competition with invasive vegetation (e.g., grasses), and seed limitation (Holl et
76 al. 2000, Zimmerman et al. 2000, Blackham et al. 2014). Given that most tropical trees are
77 adapted for dispersal by frugivorous animals (Howe and Smallwood 1982), seed dispersal is a
78 dynamic process linked to the abundance and diversity of the disperser assemblage and seed
79 sources (Carlo and Morales 2016, Zahawi et al. 2021). Previous studies from Neotropical forests
80 largely show that wind, bats, and small birds consistently facilitate the dispersal of subsets of
81 early-successional trees and shrubs that are adapted to grow quickly in high-light environments
82 (Ingle 2003, González-Castro et al. 2019, Palma et al. 2021).

83 As secondary forests age, canopy height, contiguity, and habitat complexity are linked to
84 increased animal seed dispersal, greater incidences of large birds and mammals that are
85 responsible for the dispersal of larger-seeded, often later-successional trees (De La Peña-Domene
86 et al. 2016, Bradfer-Lawrence et al. 2018), and understory microclimates that increasingly favor
87 shade-tolerant species adapted to establish and grow under dense mature forest canopies (Dent et
88 al. 2013, Rüger et al. 2023). Research from chronosequence studies consistently show that
89 naturally regenerating secondary tropical forests take a half century or more to recover similar
90 species composition to primary forests (Finegan 1996, Rozendaal et al. 2019). Recovery of
91 maturing forests at these stages is driven by the transition of mid- and late-successional tree
92 species into the canopy and continued colonization of rare and dispersal-limited trees that are
93 most characteristic of old growth forests (Martínez-Garza and Howe 2003, Muscarella et al.

94 2017, Rüger et al. 2023). Therefore, rapid recovery of biomass and initial canopy structure is not
95 necessarily predictive of later-successional processes.

96 Active restoration through tree planting has long been heralded as a key approach to
97 accelerate tropical forest succession (Holl et al. 2000, Chazdon 2008, Brancalion and Holl 2020).
98 Numerous field experiments have shown that tree planting interventions often produce greater
99 tree cover and woody recruitment than in paired natural regeneration sites during the first two
100 decades of recovery (Wilson and Rhemtulla 2016, Li et al. 2018, Trujillo-Miranda et al. 2018,
101 Osuri et al. 2019), although some studies show minimal difference in diversity or compositional
102 measures (Gilman et al. 2016, Meli et al. 2017, Ssekuubwa et al. 2019). Tree planting typically
103 increases the rate of recovery of early-successional (i.e., pioneer) species by enhancing seed
104 dispersal and overcoming barriers to establishment (Parrotta et al. 1997, de la Peña-Domene et
105 al. 2013, Osuri et al. 2019). Nevertheless, conventional tree plantations with fixed spacing in
106 grids (hereafter “plantations”) can create homogeneous habitat conditions, and strong legacy
107 effects from initially planted species can direct succession toward a community composition
108 considerably different to what is found in reference forests (Cusack and Montagnini 2004, Wills
109 et al. 2017, César et al. 2018).

110 Spatially-patterned planting methods (sensu Shaw et al. 2020), such as applied nucleation
111 (planting trees in patches), are hypothesized to have similar effects as plantations in overcoming
112 barriers to recovery by enhancing seed dispersal and seedling establishment (Zahawi and
113 Augspurger 2006, Benayas et al. 2008), without redirecting natural successional trajectories to
114 the same extent as plantations. According to nucleation theory, initial patches of recovering
115 vegetation facilitate recruitment of other species via enhanced seed dispersal and improved
116 establishment conditions (e.g. grass suppression, minimizing temperature and moisture

117 extremes), regenerating outward and gradually coalescing with other nuclei (Yarranton and
118 Morrison 1974). Applied nucleation presents an attractive option for restoration managers to
119 accelerate recovery of spatially-heterogenous ecosystems, while also reducing project costs
120 (Robinson and Handel 2000, Benayas et al. 2008, Holl et al. 2011, Corbin and Holl 2012). Prior
121 studies of applied nucleation support its effectiveness in facilitating tropical forest recovery
122 during the early years of restoration through increased bird activity, seed rain, and seedling
123 establishment (Zahawi and Augspurger 2006, Piironen et al. 2015, Ramírez-Soto et al. 2018,
124 Holl et al. 2020). However, the trade-offs between applied nucleation and traditional planting
125 methods have rarely been directly compared (Corbin et al. 2016, Holl et al. 2020), and few field
126 studies have been sustained long enough to observe the effects of differing management
127 interventions on successional processes over multi-decadal timeframes in tropical forests.

128 Here, we report on a comprehensive census of all tree recruits ≥ 20 cm in height from a
129 spatially replicated restoration experiment after almost two decades of recovery, comparing three
130 restoration interventions (natural regeneration, applied nucleation, and plantation-style tree
131 plantings) and nearby reference forests. We examine how species richness, community
132 composition, and relative abundance of tree recruits of different successional stages and seed
133 sizes differ among treatments. Results from the first decade of this experiment previously
134 showed positive effects of both planted treatments compared to natural regeneration on
135 abundance and richness of tree seedlings (Holl et al. 2017, Werden et al. 2022). However,
136 plantations have significantly greater overall canopy cover (Holl et al. 2020) and more frequent
137 incidence of large frugivores (Reid et al. 2021), which could facilitate greater colonization by
138 later-successional larger-seeded trees over time. In contrast, applied nucleation treatments have
139 many fewer planted trees with lower and more heterogenous canopy cover (Zahawi et al. 2015a,

140 Holl et al. 2020) that have previously fostered greater seedling survival and sapling growth rates
141 (Kulikowski et al. 2023). Through an exhaustive census of tree recruits, we sought to evaluate
142 how the differential effects of restoration treatments influence community assembly after nearly
143 two decades.

144

145 **METHODS**

146 **STUDY REGION**

147 We conducted this study at 10 sites spread across a ~100 km² area between the Las Cruces
148 Biological Station (LCBS; 8° 47' 7" N; 82° 57' 32" W) and Agua Buena (8° 44' 42" N; 82° 56'
149 53" W) in southern Costa Rica. The sites are at the boundary between Tropical Premontane Wet
150 and Rain Forest life zones (Holdridge et al. 1971), range in elevation from 1100-1430 m, receive
151 mean annual rainfall of 3500-4000 mm with a dry season from December to March, and have a
152 mean annual temperature of ~21°C. All sites are separated by a minimum of 700 m, and the
153 surrounding landscape is a mosaic of agricultural fields and pasture interspersed with remnant
154 forest patches (Zahawi et al. 2015b). All sites were farmed or grazed by cattle for ≥18 yr and
155 most were dominated by non-native forage grasses prior to the start of the study. Most sites are
156 steeply sloped (15-35°). Soils are volcanic in origin, mildly acidic (pH = 5.3 ± 0.04; mean ± SE),
157 low in P (Mehlich III: 3.9 ± 0.4 mg/kg), and high in organic matter (16.7 ± 0.8%) (Holl and
158 Zahawi 2014).

159

160 **EXPERIMENTAL DESIGN**

161 At each site we established three 0.25-ha plots separated by a ≥5-m buffer. In 2004-2006 each
162 plot received one of three randomized treatments: natural regeneration, applied nucleation, or

163 plantation. By the time of this census three sites were missing one or two treatments due to major
164 human disturbances over the nearly two decades of the study: natural regeneration n = 9 plots,
165 applied nucleation n = 9, plantation n = 8. Plantations were uniformly planted with tree
166 seedlings, while the applied nucleation treatment was planted with six tree islands of three sizes:
167 two each of 4×4, 8×8 and 12×12 m. Planted seedling spacing was kept constant (~2.8 m) in
168 plantation and applied nucleation treatments; 313 trees were planted in plantation, 86 in applied
169 nucleation, and none in natural regeneration plots (Holl et al. 2011). All plots (including natural
170 regeneration) were cleared to ground level by machete at ~3-mo intervals for the first 2.5 yr to
171 allow planted tree seedlings to grow above existing vegetation. We planted seedlings (20-30 cm
172 tall) of four tree species; these included two native late-successional species, *Terminalia*
173 *amazonia* (J.F. Gmel.) Exell (Combretaceae) and *Vochysia guatemalensis* Donn. Sm.
174 (Vochysiaceae), and two naturalized early-successional species, *Erythrina poeppigiana* (Walp.)
175 Skeels and *Inga edulis* Mart. (both Fabaceae) that are used widely in intercropping systems in
176 Central America. By the time of the surveys presented here, a majority of the planted softwoods
177 had died (mean survival and standard deviation: *E. poeppigiana* 34.5 ± 28.5%; *I. edulis* 22.9 ±
178 18.5%). Survival of the other two species remained high (*V. guatemalensis* 82.8 ± 18.4%; *T.*
179 *amazonia* 82.1% ± 17.8%). At six sites, we also sampled adjacent remnant forests to serve as
180 references. These reference forests ranged in size from 2-320 ha and showed no evidence of
181 clearing in the last 75 years since aerial photographs have been available (Zahawi et al. 2015b).
182 All have all been impacted to some extent by human disturbance, as “pristine” forests are not
183 present in our study area (Clement and Horn 2001).

184

185 DATA COLLECTION

186 During June and July 2022, 16-18 years after establishing plots, we censused all naturally
187 recruiting trees ≥ 20 cm height (hereafter “recruits”) throughout each restoration treatment plot.
188 We mapped individual recruits to a grid of 3×3 m quadrats and counted the number of seedlings
189 ≥ 20 cm but < 1 cm diameter at breast height (DBH) of each species within each quadrat. We
190 measured DBH for all recruits ≥ 1 cm and categorized each into sapling (1- < 5 cm DBH) or tree
191 (≥ 5 cm DBH) size classes. If an individual had multiple stems, we based our size classification
192 on the largest stem. Individual restoration plots were mostly 48×48 m (256 3×3 m quadrats), but
193 in some cases plots were 42×54 m (252 quadrats) due to constraints in the landscape at initial
194 plot set up. In a few cases, a smaller plot area was sampled primarily due to extensive
195 anthropogenic damage to a section of the plot (Table S1). The layout of the reference forest plots
196 was slightly different and consisted of four 21×21 m plots (196 quadrats) at five sites and three
197 21×21 m plots (147 quadrats) at one site. Tree recruits were identified to the lowest operational
198 taxonomic unit (hereafter referred to as “species”) following the nomenclature of Tropicos
199 (<https://www.tropicos.org>).

200

201 DATA ANALYSIS

202 We categorized recruits of all species that were not planted as part of restoration treatments as
203 either early-, mid- or late-successional (Table S2), based on the extensive observations and
204 botanical expertise of two of the authors (RAZ and FOB) who have sampled vegetation
205 composition in many sites in the region for over two decades. We considered early-successional
206 taxa (37 spp.) as pioneer trees which are commonly found in disturbed environments and young
207 secondary forests but typically are not found in mature forests; nearly all early-successional
208 recruits have animal-dispersed seeds < 5 mm in width or wind-dispersed seeds. Mid-successional

209 taxa (referred to as “both” in Werden et al. 2021) include tree species that colonize at any stage
210 of forest succession but are well represented in old growth forests. We considered late-
211 successional species as taxa typically observed in mature forests only. Both mid- and late-
212 successional taxa had a range of seed sizes, so we further categorized the latter two successional
213 groups based on seed width: <5 mm, $5-<10$ mm, and ≥ 10 mm, referred to as small, medium, and
214 large, respectively. Successional groups and seed size are not independent, with most (64%) mid-
215 successional species having small seeds whereas 71% of late-successional species had seeds ≥ 5
216 mm (i.e., medium and large). We use the term “later-successional” when referring to these two
217 groups collectively. A few distinct taxa (i.e., *Citrus* spp., *Heliocarpus* spp.) were not consistently
218 identified to species level and, therefore, grouped together in analyses of diversity and species
219 composition. A small number of individuals (0.04%) in the census were not identified and were
220 excluded from analyses.

221 For analyses of taxonomic richness among experimental treatments, we separated recruit
222 data by size class: seedling (<1 cm DBH), sapling ($1-<5$ cm DBH), or tree (≥ 5 cm DBH). All
223 statistical analyses were performed in R 4.3.3 (R Core Team 2024). We summarized species
224 richness of experimental treatments using species-accumulation models from the ‘iNEXT’
225 package (Hsieh et al. 2016), in which rarefied, observed, and extrapolated richness were
226 calculated from incidence data across sampling quadrats. Estimated sampling completeness was
227 high across all size classes and successional groups (85-99%). We made statistical inferences
228 from sample-sized-based calculations of bootstrapped ($n = 1,000$) 95% confidence intervals for
229 accumulated richness at 1.01 ha, which was the minimum area sampled for all four treatments.

230 To compare the composition of communities, we used non-metric multidimensional
231 scaling (NMDS) of the species abundance matrices of each experimental plot with distances

232 calculated from the Chao dissimilarity index and 95% confidence intervals calculated from
233 within-treatment variability in the ‘vegan’ package (Chao et al. 2005, Oksanen et al. 2022). We
234 compared groups using pairwise permutational analysis of variance (PERMANOVA) between
235 centroids and adjusted p-values using the Bonferroni method for multiple tests.

236 We drew further inferences on community composition differences through variation in
237 densities of successional groups and recruit size classes among treatments. For each grouping
238 (e.g., early-successional saplings), we used generalized linear mixed models with a negative
239 binomial distribution to analyze the effect of restoration treatment using the ‘glmmTMB’
240 package (Magnusson et al. 2017). Site was included as a random factor and an offset term was
241 used to account for differing sampling areas. We interpreted pairwise comparisons of estimated
242 marginal means of treatment groups with a Bonferroni correction to resulting p-values using the
243 ‘emmeans’ package (Lenth 2021).

244

245 **RESULTS**

246 *Species richness*

247 We censused a total of 66,446 seedling, 14,038 sapling, and 3,842 tree recruits representing 255
248 operational taxonomic units from 65 families, as well as 1,941 survivors of the originally-planted
249 trees. Of the naturally recruited taxa (hereafter, species) we identified 94.2% of individuals to
250 species, 4.6% to genus, and 1.1% to family levels. Overall observed species richness among the
251 treatments increased across the planting gradient with natural regeneration lowest (156), and
252 applied nucleation (185) and plantation (196) intermediate; species richness of reference forest
253 (205) highest, despite the fact that total reference forest sampling area was approximately half

254 that of the three restoration treatments. All but 10.5% of tree species recorded in reference forest
255 were found to have colonized at least one restoration plot.

256 Early-successional seedling and sapling richness were consistently higher across
257 restoration treatments than in reference forest (Fig. 1A&D, Table S3), and while seedling
258 richness was similar among the restoration treatments, sapling richness was notably higher in
259 applied nucleation than plantation. Species richness of early-successional trees (≥ 5 cm DBH)
260 was greater in natural regeneration and applied nucleation than in plantations and was
261 intermediate in reference forest (Fig. 1G, Table S3). We observed higher richness of mid-
262 successional seedlings in plantation than the other restoration treatments (Fig. 1B, Table S3).
263 Mid-successional saplings and late-successional seedlings and saplings showed a similar trend of
264 the highest richness in reference forest, intermediate richness in both planted treatments, and the
265 lowest in natural regeneration (Fig. 1C,E,F, Table S3). This pattern was strongest for late-
266 successional saplings with both planted treatments having $>50\%$ more species than natural
267 regeneration, but only approximately half the number of late-successional species that were
268 censused in reference forest (Fig. 1F). Later-successional tree communities showed similarly low
269 richness across all restoration treatments (Fig. 1H&I), with only approximately 50% of mid- and
270 15% of late-successional species recorded in the tree size class of any restoration treatment
271 compared to that in reference forest.

272

273 *Community composition*

274 Seedling and sapling community composition tended to increase in similarity to reference forest
275 with the extent of the planting treatment (Fig. 2A-B), although for seedlings the differences
276 among restoration treatments were not significant but all restoration treatments differed from

277 reference forest. For saplings, all treatments differed significantly except applied nucleation and
278 plantation (Table S4). The compositional differences among restoration treatments in the sapling
279 layer were partly driven by the relative abundance of early-successional species (e.g.,
280 *Koanophyllon pittieri*, *Myrsine coriacea*, *Conostegia xalapensis*, *Psidium guajava*, *Viburnum*
281 *costaricanum*); early-successional taxa made up 54.0% and 43.3% of saplings in natural
282 regeneration and applied nucleation, but only 18.6% in plantations. Species commonly found in
283 reference forest that were rarely recorded as saplings in restored sites included *Drypetes brownii*,
284 *Guarea montana*, *Inga punctata*, *Garcinia intermedia*, *Desmopsis oerstedii*, and *Posoqueria*
285 *costaricensis*, among others. Both seedling and sapling communities showed greater variability
286 in species composition under natural regeneration than in either planting intervention.

287 The community composition of recruited trees in restoration treatments had no overlap
288 with reference forest (Fig. 2C), and differences among restoration treatments resulted primarily
289 from higher densities of the originally planted trees (Fig. 3C), as the difference disappeared when
290 planted trees were removed from the analysis (Fig. S1). Naturally-recruited trees in restored plots
291 were largely comprised of a handful of early-successional taxa – *Cecropia obtusifolia*, *Hampea*
292 *appendiculata*, *Koanophyllon pittieri*, *Myrsine coriacea*, *Viburnum costaricanum*, *Heliocarpus*
293 spp., and several Melastomataceae that accounted for >75% censused individuals.

294

295 *Abundance of naturally-recruiting trees*

296 Seedlings from planted tree species formed a small percentage of the total number of
297 recruiting seedlings across all treatments, but their abundance, particularly of *I. edulis* and *V.*
298 *guatemalensis*, was significantly greater in applied nucleation (13.0%) than plantation (4.7%),
299 despite the difference in original planting intensity (Fig. 3A). There were relatively few saplings

300 of planted species in any treatment (1.8% of all saplings), and 60% of these stems in the two
301 planted treatments were originally-planted individuals that never grew into the tree size class. All
302 trees (≥ 5 cm DBH) of these species in applied nucleation and plantation were planted as part of
303 the initial restoration (Fig 3C). The few saplings and trees of planted species in natural
304 regeneration were largely *E. poeppigiana* that had resprouted from individuals present prior to
305 the start of the study.

306 Early-successional seedling and sapling abundance did not differ significantly across
307 restoration treatments, but there was a trend toward a larger number of individuals in applied
308 nucleation plots (Fig. 3A&B). The abundance of early-successional trees was greater in both
309 natural regeneration and applied nucleation than plantation and reference forest treatments (Fig.
310 3C).

311 Density of later-successional individuals in the tree size class across all restoration
312 treatments was a small fraction (8%) of that in reference forest, although applied nucleation
313 showed marginally higher densities of small- and medium-seeded recruits than did the other
314 restoration treatments (Fig. 3C; Fig. S2). Differences in abundance of later-successional
315 seedlings and saplings across treatments varied by seed size. Small-seeded, later-successional
316 seedlings showed similar abundance across all treatments (Fig. 3A), whereas sapling densities
317 were lower in natural regeneration (Fig. 3B). *Miconia* spp. and *Palicourea padifolia* were
318 particularly common mid-successional taxa across all restoration treatments, though *P. padifolia*
319 was rarely observed in reference forest (Fig. S3-4). Small-seeded, late-successional saplings
320 were more abundant in reference forest (Fig. S2B) largely driven by *Trophis mexicana* and
321 *Lacistema aggregatum* (Fig. S4D).

322 Seedlings and sapling density of later-successional species with medium and large seeds
323 generally were lowest in natural regeneration, intermediate in applied nucleation, and highest in
324 plantation and reference forest with the pattern being strongest for large-seeded late-successional
325 taxa (Fig. 3A-B, Fig. S2A-B). Medium-seeded, mid-successional saplings (e.g., *Ocotea*
326 *puberula*, *Allophylus psilospermus*; Fig. S3) had the lowest densities in natural regeneration
327 while both planted treatments had densities at least equal to those observed in reference forest
328 (Fig. S2A-B).

329

330 **DISCUSSION**

331 After nearly two decades, our comprehensive census of experimental restoration plots showed
332 that the naturally recruiting tree communities are still limited to planted and early-successional
333 taxa, but understory communities show high potential for future forest recovery. Natural
334 regeneration plots had more than twice the expected number of species (corrected for differences
335 in sampling area) as recorded in surveys 7 years prior (Holl et al. 2017). In turn, both planted
336 treatments produced similarly elevated richness of recruiting seedling and sapling communities
337 as compared to natural regeneration, but the relative abundance of late-successional recruits,
338 particularly those with large seeds, was greatest in plantation plots. Any positive effects of either
339 tree-planting strategy on later-successional species recruitment, however, were not yet detectable
340 among the largest stem sizes, and the overall composition of all restoration treatments still
341 differed substantially from reference forest. These demographic and compositional patterns
342 signal that differing restoration approaches could have diverging effects on both the pace and
343 trajectory of succession beyond the second decade of recovery.

344 Although previous observations from this study have consistently shown similar effects
345 of the two planting methods on the recovery of seed dispersal and seedlings (e.g., Holl et al.
346 2017, Werden et al. 2022), our comprehensive census reveals subtle compositional differences
347 between applied nucleation and plantation treatments after nearly two decades. First, we found
348 evidence of recruitment limitation as a function of seed size that is curtailed through active
349 planting. Recruit densities of late-successional seedling and sapling species with medium and
350 large seeds were consistently greater in the planted treatments than natural regeneration, and
351 plantation showed comparable densities to reference forest. Our findings support the importance
352 of canopy formation to facilitate colonization of large-seeded species during tropical forest
353 succession, a result consistent with many prior studies (De La Peña-Domene et al. 2016, Rivas-
354 Alonso et al. 2021). Despite increasing canopy cover in applied nucleation plots, plantations
355 continue to have a more uniform canopy cover than applied nucleation in this second decade of
356 recovery (Holl et al. 2020, Zahawi et al. unpublished data). In turn, large birds such as toucans,
357 which are a key disperser of large seeds in our study region, visited plantations more frequently
358 than they did applied nucleation plots over a decade-long period (Reid et al. 2021). Whereas
359 differential seed fates among treatments present an alternative explanation to the observed
360 treatment effects, large-seeded trees are generally not strongly establishment-limited during
361 tropical secondary succession (Pereira et al. 2013, de la Pena-Domene et al. 2018, Metz et al.
362 2023) and prior data from our experiment suggested dispersal- rather than establishment-
363 limitation as the primary driver of variation among treatments (Werden et al. 2020). Recent seed
364 dispersal data (San José et al. unpublished), however, indicate that differences in abundance of
365 medium- and large-seeded, later-successional seeds dispersed to the three treatments have

366 diminished substantially in the past few, suggesting that recruit similarity across restoration
367 treatments may converge over time.

368 A second pattern we observed is that applied nucleation plots tended toward higher
369 densities of early-successional seedlings than plantations, although the difference was not
370 significant due to high within-treatment variation. Given the ubiquitous dispersal of these taxa in
371 our study system (Reid et al. 2015, Werden et al. 2021), their varying recruit densities are
372 indicative of differing ecological filtering between the two planted treatments. Varying canopy
373 development and light environments are often important drivers of tropical forest plant size class
374 distributions, particularly as succession proceeds (Nicotra et al. 1999, Balderrama and Chazdon
375 2005, Van Breugel et al. 2019). The greater canopy cover in plantations corresponds with
376 increased shade and litter depth, both of which inhibit the germination and emergence of early-
377 successional tropical trees with small seeds (Celentano et al. 2011, Muscarella et al. 2013).

378 At the same time, the slightly more open canopy, and in turn light availability, in applied
379 nucleation environments has the potential to enhance growth and transition of recruits to larger
380 size classes (Caughlin et al. 2019). Indeed, there were more early successional trees in applied
381 nucleation and natural regeneration than in plantation plots, and saplings showed a similar trend.
382 However, we observed an overall suppression of natural recruits reaching the canopy in
383 plantations and a trend toward accelerated recruit growth (i.e., more tree-sized stems) in applied
384 nucleation for some later-successional species, which has also been supported by individual
385 sapling measurements over time (Kulikowski et al. 2023). These demographic trade-offs in
386 restoration strategies present important questions about late-successional processes which have
387 rarely been investigated. As seed rain becomes more similar to the restored forest stand over time
388 (Huanca Nuñez et al. 2021), local abiotic and biotic conditions – light availability in particular –

389 will determine which species survive and transition into the canopy layer (Caughlin et al. 2019)
390 while the canopy cover across treatments is also slowly converging over time (Zahawi et al.
391 unpublished data).

392 A major open question in the forest restoration literature is the extent to which active
393 planting interventions have legacy effects on successional trajectories over time as compared to
394 naturally generating forest. In recent years, we have observed high mortality of our two fast-
395 growing planted species, *E. poeppigiana* and *I. edulis*, of which only ~30% survived after 16-18
396 years. Nonetheless the tree layer in plantations remains dominated by planted species, all of
397 which are now reproductive so recruits of these species could influence the successional
398 trajectory. Contrary to expectation, however, abundance of planted tree recruits did not
399 correspond with greater initial planting densities as applied nucleation had greater seedling
400 abundance of these species, which was likely facilitated by the more heterogenous and open
401 canopy during the first decade. That said, the abundance of saplings of planted species was
402 similarly low across restoration treatments which is consistent with our observations of very high
403 seedling mortality of these species that is likely driven by shading and herbivory (Holl et al.
404 2022, Kulikowski et al. 2022).

405 Beyond the initial two decades of forest recovery, tropical forest succession is largely
406 dependent on the mortality of pioneers and planted tree species to drive gap dynamic processes
407 and growth of later successional species (Finegan 1996, Philipson et al. 2012, Swinfield et al.
408 2016). Until now, however, canopy openings created by *E. poeppigiana* and *I. edulis* mortality
409 have been filled quickly by the expanding crowns of *V. guatemalensis* and early-successional
410 trees, such as *Koanophyllon pittieri*, *Hampea appendiculata*, and *Heliocarpus* spp. (Lanuza et al.
411 2018). Whether gap dynamics occur naturally or are facilitated by subsequent felling by

412 restoration managers to enhance growth of later-successional species will depend on the specific
413 tree species used in restoration interventions and long-term project goals.

414 Many past studies show that natural regeneration, while often a cost-effective restoration
415 option, can have highly unpredictable recovery outcomes (e.g., Chazdon and Guariguata 2016,
416 Chazdon et al. 2020, Atkinson et al. 2022). Additionally, in the absence of active management,
417 there is a much stronger likelihood that succession under natural regeneration will become
418 arrested or not proceed along a timeline that is relevant to restoration goals (Benayas et al. 2009,
419 Meli et al. 2017). Natural regeneration plots in our study consistently supported substantial
420 abundance of early-successional trees and some seedlings and saplings of later-successional
421 species, suggesting that succession is progressing, albeit slowly. Yet, natural regeneration had
422 more variable composition among plots for seedling and saplings than did both planted
423 treatments. Even under conditions with high natural regeneration potential, the stochastic
424 recovery pattern can produce alternative successional trajectories that are dependent on local
425 seed sources, the regional species pool, and land use history (Mesquita et al. 2015, Norden et al.
426 2015, Atkinson et al. 2022). These variable trajectories can include facilitating actively invading
427 non-native species, which tend to have pioneer life history strategies (Catterall 2016). Indeed,
428 our natural regeneration plots assembled communities that were disproportionately dominated by
429 early-successional species compared to active restoration and also showed a propensity to
430 amplify legacies from prior land-use conditions. Namely, several natural regeneration plots had
431 substantial abundances of non-native (albeit naturalized) species such as *E. poeppigiana*, *Citrus*
432 spp., and *Syzygium jambos* that are common in agricultural landscapes. *E. poeppigiana* and
433 *Citrus* spp. primarily occurred from resprouting of cut stems established before restoration had
434 begun, whereas *S. jambos* established from seeds dispersed by bats. Importantly, actively

435 restored plots had fewer individuals of these non-native species growing past the seedling stage.
436 In sum, the greater likelihood of poor outcomes such as stalled recovery or invasion make natural
437 regeneration a potentially risky strategy for restoration practitioners aiming to achieve specific
438 long-term restoration outcomes, although allowing recovery to proceed for a couple of years
439 before choosing whether intervention is necessary can help to reduce this uncertainty (Holl et al.
440 2018), and thereby allocate limiting resources more effectively. Such preparatory monitoring
441 periods also provide an opportunity to identify naturally regenerating trees, which can be assisted
442 (e.g., grass clearing, preventing fires) in tandem with more targeted plantings in areas with sparse
443 seedling growth.

444

445 **Conclusions and Management Recommendations**

446 Our study is one of the few with the longevity, replication, and thorough sampling to
447 compare the effects of restoration interventions on mid-successional filtering, revealing several
448 key management implications. First, we show in a multi-site experiment that earlier patterns of
449 active tree planting (applied nucleation and plantation strategies) accelerating recovery over
450 natural regeneration continue through the second decade. Planting only four species of trees
451 substantially increased the number of species and individuals of later-successional species and,
452 importantly, reduced variability in recovery across sites. This contrasts with prior meta-analyses
453 of active vs. passive tree planting strategies that mostly compared results from sites with
454 different land use histories and studies of single restoration interventions and suggested that
455 natural regeneration results in similar or faster recovery rates to active tree planting (Meli et al.
456 2017, Crouzeilles et al. 2017). Given the highly variable recovery patterns in natural

457 regeneration, active planting strategies should be encouraged when land use history and seed
458 sources are either poorly documented or known to be unfavorable.

459 Second, whereas both applied nucleation and plantation restoration strategies accelerated
460 recovery, nuanced ecological tradeoffs emerged in the second decade. We found a new trend of
461 greater abundance of larger-seeded, late-successional species in plantation than applied
462 nucleation plots but longer-term data are needed to determine whether these comparatively rich
463 understory communities will transition into mature canopy trees more rapidly than in applied
464 nucleation. In fact, data presented here and growth measurements of marked recruits over time
465 (Kulikowski et al. 2023) suggest that recruits are likely to mature more rapidly in the slightly
466 more open canopy of the applied nucleation treatment. Given that the plantation treatment
467 canopy remains dominated by planted species, canopy thinning might help to further accelerate
468 recovery processes (Swinfield et al. 2016), but needs testing.

469 Finally, the fact that we observed ~90% of reference forest species in our restored plots
470 after less than two decades supports the potential for tropical forests to recover from intensive
471 prior agricultural land-use. Nonetheless, we hasten to reiterate that the overall structure and
472 composition of all our restoration treatments are still substantially different from reference forest,
473 and full recovery is likely to take several decades to centuries (Elsy et al. 2024). Moreover, the
474 rapid recolonization rate of a diverse suite of species is partly a function of the extensive seed
475 sources remaining in remnant forests, along fence lines, and in active agricultural lands in the
476 region (Zahawi et al. 2015a, 2021), and would likely be substantially slower in more deforested
477 landscapes (Pardini et al. 2010). So, protecting existing tropical forests must be the first priority
478 (Brancalion and Holl 2020, Di Sacco et al. 2021). Taken together, our results highlight (1) the
479 value of multi-decadal, well-replicated studies to evaluate the effect restoration on successional

480 trajectories, and (2) the importance of long-term commitments to forest restoration to achieve
481 promised biodiversity outcomes.

482

483 **ACKNOWLEDGEMENTS**

484 This research was supported by the US National Science Foundation (DEB 20-16623). We thank
485 C. Blebea, J. Flores, F. Joyce, T. Loik, V. Morales, K. Navarro, E. Quiros, A. Ramos, B. Ramos,
486 J. Rosales-Umaña, and M. San José for fieldwork and data entry assistance. C. Blebea, J. Funk,
487 F. Joyce, C. Seither and two anonymous reviewers provided helpful comments on earlier
488 versions of the manuscript.

489

490 **AUTHOR CONTRIBUTIONS**

491 Karen D. Holl and Rakan A. Zahawi conceived the study, designed the protocol for sampling,
492 and contributed to the writing and revision of the final manuscript. F. Oviedo Brenes oversaw the
493 botanical identification. All authors contributed to data collection. Spencer C. Schubert analyzed
494 the data and led the writing and revision of the manuscript.

495

496 **CONFLICT OF INTEREST STATEMENT**

497 The authors declare no conflict of interest.

498

499 **REFERENCES**

- 500 Aguirre-Gutiérrez, J., N. Stevens, and E. Berenguer. 2023. Valuing the functionality of tropical
501 ecosystems beyond carbon. *Trends in Ecology & Evolution* 38:1109–1111.
- 502 Atkinson, J., L. A. Brudvig, M. Mallen-Cooper, S. Nakagawa, A. T. Moles, and S. P. Bonser.
503 2022. Terrestrial ecosystem restoration increases biodiversity and reduces its variability,
504 but not to reference levels: A global meta-analysis. *Ecology Letters* 25:1725–1737.
- 505 Balderrama, S. I. V., and R. L. Chazdon. 2005. Light-dependent seedling survival and growth of
506 four tree species in Costa Rican second-growth rain forests. *Journal of Tropical Ecology*
507 21:383–395.
- 508 Benayas, J. M. R., J. M. Bullock, and A. C. Newton. 2008. Creating woodland islets to reconcile
509 ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and*
510 *the Environment* 6:329–336.
- 511 Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity
512 and ecosystem services by ecological restoration: a meta-analysis. *Science* 325:1121–
513 1124.
- 514 Blackham, G. V., E. L. Webb, and R. T. Corlett. 2014. Natural regeneration in a degraded
515 tropical peatland, Central Kalimantan, Indonesia: Implications for forest restoration.
516 *Forest Ecology and Management* 324:8–15.
- 517 Bradfer-Lawrence, T., N. Gardner, and D. H. Dent. 2018. Canopy bird assemblages are less
518 influenced by habitat age and isolation than understory bird assemblages in Neotropical
519 secondary forest. *Ecology and Evolution* 8:5586–5597.
- 520 Brancalion, P. H., and K. D. Holl. 2020. Guidance for successful tree planting initiatives. *Journal*
521 *of Applied Ecology* 57:2349–2361.

522 Brancalion, P. H., A. Niamir, E. Broadbent, R. Crouzeilles, F. S. Barros, A. M. Almeyda
523 Zambrano, A. Baccini, J. Aronson, S. Goetz, and J. L. Reid. 2019. Global restoration
524 opportunities in tropical rainforest landscapes. *Science Advances* 5:eaav3223.

525 Carlo, T. A., and J. M. Morales. 2016. Generalist birds promote tropical forest regeneration and
526 increase plant diversity via rare-biased seed dispersal. *Ecology* 97:1819–1831.

527 Carrick, P. J., and K. J. Forsythe. 2020. The species composition-ecosystem function
528 relationship: A global meta-analysis using data from intact and recovering ecosystems.
529 *PLoS One* 15:e0236550.

530 Catterall, C. P. 2016. Roles of non-native species in large-scale regeneration of moist tropical
531 forests on anthropogenic grassland. *Biotropica* 48:809–824.

532 Caughlin, T. T., M. De La Peña-Domene, and C. Martínez-Garza. 2019. Demographic costs and
533 benefits of natural regeneration during tropical forest restoration. *Ecology Letters* 22:34–
534 44.

535 Celentano, D., R. A. Zahawi, B. Finegan, R. Ostertag, R. J. Cole, and K. D. Holl. 2011. Litterfall
536 dynamics under different tropical forest restoration strategies in Costa Rica. *Biotropica*
537 43:279–287.

538 César, R. G., V. S. Moreno, G. D. Coletta, R. L. Chazdon, S. F. Ferraz, D. R. de Almeida, and P.
539 H. Brancalion. 2018. Early ecological outcomes of natural regeneration and tree
540 plantations for restoring agricultural landscapes. *Ecological Applications* 28:373–384.

541 Chao, A., R. L. Chazdon, R. K. Colwell, and T.-J. Shen. 2005. A new statistical approach for
542 assessing similarity of species composition with incidence and abundance data. *Ecology*
543 *Letters* 8:148–159.

544 Chazdon, R. L. 2008. Beyond deforestation: restoring forests and ecosystem services on
545 degraded lands. *Science* 320:1458–1460.

546 Chazdon, R. L., P. H. Brancalion, D. Lamb, L. Laestadius, M. Calmon, and C. Kumar. 2017. A
547 policy-driven knowledge agenda for global forest and landscape restoration.
548 *Conservation Letters* 10:125–132.

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

551 Chazdon, R. L., D. Lindenmayer, M. R. Guariguata, R. Crouzeilles, J. M. R. Benayas, and E. L.
552 Chavero. 2020. Fostering natural forest regeneration on former agricultural land through
553 economic and policy interventions. *Environmental Research Letters* 15:043002.

554 Clement, R. M., and S. P. Horn. 2001. Pre-Columbian land-use history in Costa Rica: a 3000-
555 year record of forest clearance, agriculture and fires from Laguna Zoncho. *The Holocene*
556 11:419–426.

557 Corbin, J. D., and K. D. Holl. 2012. Applied nucleation as a forest restoration strategy. *Forest*
558 *Ecology and Management* 265:37–46.

559 Corbin, J. D., G. R. Robinson, L. M. Hafkemeyer, and S. N. Handel. 2016. A long-term
560 evaluation of applied nucleation as a strategy to facilitate forest restoration. *Ecological*
561 *Applications* 26:104–114.

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

566 Cusack, D., and F. Montagnini. 2004. The role of native species plantations in recovery of
567 understory woody diversity in degraded pasturelands of Costa Rica. *Forest Ecology and*
568 *Management* 188:1–15.

569 De La Peña-Domene, M., E. S. Minor, and H. F. Howe. 2016. Restored connectivity facilitates
570 recruitment by an endemic large-seeded tree in a fragmented tropical landscape. *Ecology*
571 97:2511–2517.

572 Dent, D. H., S. J. DeWalt, and J. S. Denslow. 2013. Secondary forests of central Panama
573 increase in similarity to old-growth forest over time in shade tolerance but not species
574 composition. *Journal of Vegetation Science* 24:530–542.

575 Di Sacco, A., K. A. Hardwick, D. Blakesley, P. H. S. Brancalion, E. Breman, L. Cecilio Rebola,
576 S. Chomba, K. Dixon, S. Elliott, G. Ruyonga, K. Shaw, P. Smith, R. J. Smith, and A.
577 Antonelli. 2021. Ten golden rules for reforestation to optimize carbon sequestration,
578 biodiversity recovery and livelihood benefits. *Global Change Biology* 27:1328–1348.

579 Edwards, D. P., G. R. Cerullo, S. Chomba, T. A. Worthington, A. P. Balmford, R. L. Chazdon,
580 and R. D. Harrison. 2021. Upscaling tropical restoration to deliver environmental benefits
581 and socially equitable outcomes. *Current Biology* 31:1326–1341.

582 Elsy, A. D., M. Pfeifer, I. L. Jones, S. J. DeWalt, O. R. Lopez, and D. H. Dent. 2024. Incomplete
583 recovery of tree community composition and rare species after 120 years of tropical
584 forest succession in Panama. *Biotropica* 56:36–49.

585 Finegan, B. 1996. Pattern and process in neotropical secondary rain forests: the first 100 years of
586 succession. *Trends in Ecology & Evolution* 11:119–124.

587 Fuss, S., A. Golub, and R. Lubowski. 2021. The economic value of tropical forests in meeting
588 global climate stabilization goals. *Global Sustainability* 4:1–11.

589 Gann, G. D., T. McDonald, B. Walder, J. Aronson, C. R. Nelson, J. Jonson, J. G. Hallett, C.
590 Eisenberg, M. R. Guariguata, and J. Liu. 2019. International principles and standards for
591 the practice of ecological restoration. *Restoration Ecology* 27:S1–S46.

592 Gilman, A. C., S. G. Letcher, R. M. Fincher, A. I. Perez, T. W. Madell, A. L. Finkelstein, and F.
593 Corrales-Araya. 2016. Recovery of floristic diversity and basal area in natural forest
594 regeneration and planted plots in a Costa Rican wet forest. *Biotropica* 48:798–808.

595 González-Castro, A., S. Yang, and T. A. Carlo. 2019. How does avian seed dispersal shape the
596 structure of early successional tropical forests? *Functional Ecology* 33:229–238.

597 Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang, and J. A. Tosi Jr. 1971. Forest
598 environments in tropical life zones: a pilot study. Pergamon Press, Oxford, England.

599 Holl, K. D., M. E. Loik, E. H. V. Lin, and I. A. Samuels. 2000. Tropical montane forest
600 restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration*
601 *Ecology* 8:339–349.

602 Holl, K. D., J. C. Luong, and P. H. Brancalion. 2022. Overcoming biotic homogenization in
603 ecological restoration. *Trends in Ecology & Evolution* 37:777–788.

604 Holl, K. D., J. L. Reid, J. M. Chaves-Fallas, F. Oviedo-Brenes, and R. A. Zahawi. 2017. Local
605 tropical forest restoration strategies affect tree recruitment more strongly than does
606 landscape forest cover. *Journal of Applied Ecology* 54:1091–1099.

607 Holl, K. D., J. L. Reid, R. J. Cole, F. Oviedo-Brenes, J. A. Rosales, and R. A. Zahawi. 2020.
608 Applied nucleation facilitates tropical forest recovery: Lessons learned from a 15-year
609 study. *Journal of Applied Ecology* 57:2316–2328.

610 Holl, K. D., J. L. Reid, F. Oviedo-Brenes, A. J. Kulikowski, and R. A. Zahawi. 2018. Rules of
611 thumb for predicting tropical forest recovery. *Applied Vegetation Science* 21:669–677.

612 Holl, K. D., and R. A. Zahawi. 2014. Factors explaining variability in woody above-ground
613 biomass accumulation in restored tropical forest. *Forest Ecology and Management*
614 319:36–43.

615 Holl, K. D., R. A. Zahawi, R. J. Cole, R. Ostertag, and S. Cordell. 2011. Planting seedlings in
616 tree islands versus plantations as a large-scale tropical forest restoration strategy.
617 *Restoration Ecology* 19:470–479.

618 Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and*
619 *Systematics* 13:201–228.

620 Hsieh, T. C., K. H. Ma, and A. Chao. 2016. iNEXT: an R package for rarefaction and
621 extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*
622 7:1451–1456.

623 Huanca Nuñez, N., R. L. Chazdon, and S. E. Russo. 2021. Seed-rain–successional feedbacks in
624 wet tropical forests. *Ecology* 102:e03362.

625 Ingle, N. R. 2003. Seed dispersal by wind, birds, and bats between Philippine montane rainforest
626 and successional vegetation. *Oecologia* 134:251–261.

627 Koch, A., and J. O. Kaplan. 2022. Tropical forest restoration under future climate change. *Nature*
628 *Climate Change* 12:279–283.

629 Kulikowski, A. J., R. A. Zahawi, and K. D. Holl. 2022. Effects of insect herbivory on seedling
630 mortality in restored and remnant tropical forest. *Restoration Ecology* 30:e13467.

631 Kulikowski, A. J., R. A. Zahawi, L. K. Werden, K. Zhu, and K. D. Holl. 2023. Restoration
632 interventions mediate tropical tree recruitment dynamics over time. *Philosophical*
633 *Transactions of the Royal Society B* 378:20210077.

634 Lanuza, O., F. Casanoves, R. A. Zahawi, D. Celentano, D. Delgado, and K. D. Holl. 2018.
635 Litterfall and nutrient dynamics shift in tropical forest restoration sites after a decade of
636 recovery. *Biotropica* 50:491–498.

637 Lenth, R. V. 2021. Estimated marginal means, aka least-squares means [R Package Emmeans
638 Version 1.6. 0]. Comprehensive R Archive Network (CRAN).

639 Li, L., M. W. Cadotte, C. Martínez-Garza, M. de la Peña-Domene, and G. Du. 2018. Planting
640 accelerates restoration of tropical forest but assembly mechanisms appear insensitive to
641 initial composition. *Journal of Applied Ecology* 55:986–996.

642 Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Benthem, B.
643 Bolker, M. Brooks, and M. M. Brooks. 2017. R Package ‘glmmTMB’ Version 0.2.0.
644 Comprehensive R Archive Network (CRAN).

645 Martin, M. P., D. J. Woodbury, D. A. Doroski, E. Nagele, M. Storace, S. C. Cook-Patton, R.
646 Pasternack, and M. S. Ashton. 2021. People plant trees for utility more often than for
647 biodiversity or carbon. *Biological Conservation* 261:109224.

648 Martínez-Garza, C., and H. F. Howe. 2003. Restoring tropical diversity: beating the time tax on
649 species loss. *Journal of Applied Ecology*:423–429.

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

653 Mesquita, R. de C. G., P. E. dos S. Massoca, C. C. Jakovac, T. V. Bentos, and G. B. Williamson.
654 2015. Amazon rain forest succession: stochasticity or land-use legacy? *BioScience*
655 65:849–861.

656 Metz, M. R., S. J. Wright, J. K. Zimmerman, A. Hernández, S. M. Smith, N. G. Swenson, M. N.
657 Umaña, L. R. Valencia, I. Waring-Enriquez, M. Wordell, M. Zambrano, and N. C.
658 Garwood. 2023. Functional traits of young seedlings predict trade-offs in seedling
659 performance in three neotropical forests. *Journal of Ecology* 111:2568–2582.

660 Muscarella, R., M. Lohbeck, M. Martínez-Ramos, L. Poorter, J. E. Rodríguez-Velázquez, M.
661 Van Breugel, and F. Bongers. 2017. Demographic drivers of functional composition
662 dynamics. *Ecology* 98:2743–2750.

663 Muscarella, R., M. Uriarte, J. Forero-Montaña, L. S. Comita, N. G. Swenson, J. Thompson, C. J.
664 Nytch, I. Jonckheere, and J. K. Zimmerman. 2013. Life-history trade-offs during the
665 seed-to-seedling transition in a subtropical wet forest community. *Journal of Ecology*
666 101:171–182.

667 Nicotra, A. B., R. L. Chazdon, and S. V. B. Iriarte. 1999. Spatial heterogeneity of light and
668 woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.

669 Norden, N., H. A. Angarita, F. Bongers, M. Martínez-Ramos, I. Granzow-de la Cerda, M. Van
670 Breugel, E. Lebrija-Trejos, J. A. Meave, J. Vandermeer, and G. B. Williamson. 2015.
671 Successional dynamics in Neotropical forests are as uncertain as they are predictable.
672 *Proceedings of the National Academy of Sciences* 112:8013–8018.

673 Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O’Hara, P.
674 Solymos, M. Stevens, and E. Szoecs. 2022. *Vegan: Community Ecology Package* (R
675 Package Version 2.6-2). 2022. Comprehensive R Archive Network (CRAN).

676 Osuri, A. M., S. Kasinathan, M. K. Siddhartha, D. Mudappa, and T. S. Raman. 2019. Effects of
677 restoration on tree communities and carbon storage in rainforest fragments of the Western
678 Ghats, India. *Ecosphere* 10:e02860.

679 Palma, A. C., M. Goosem, R. J. Fensham, S. Goosem, N. D. Preece, P. R. Stevenson, and S. G.
680 Laurance. 2021. Dispersal and recruitment limitations in secondary forests. *Journal of*
681 *Vegetation Science* 32:e12975.

682 Pardini, R., A. de A. Bueno, T. A. Gardner, P. I. Prado, and J. P. Metzger. 2010. Beyond the
683 fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented
684 landscapes. *PloS One* 5:e13666.

685 Parrotta, J. A., O. H. Knowles, and J. M. Wunderle Jr. 1997. Development of floristic diversity
686 in 10-year-old restoration forests on a bauxite mined site in Amazonia. *Forest Ecology*
687 *and Management* 99:21–42.

688 de la Pena-Domene, M., C. Martínez-Garza, L. M. Ayestarán-Hernández, and H. F. Howe. 2018.
689 Plant attributes that drive dispersal and establishment limitation in tropical agricultural
690 landscapes. *Forests* 9:620.

691 de la Peña-Domene, M., C. Martínez-Garza, and H. F. Howe. 2013. Early recruitment dynamics
692 in tropical restoration. *Ecological Applications* 23:1124–1134.

693 Pereira, S. R., V. A. Laura, and A. L. T. Souza. 2013. Establishment of Fabaceae tree species in a
694 tropical pasture: influence of seed size and weeding methods. *Restoration Ecology*
695 21:67–74.

696 Philipson, C. D., P. Saner, T. R. Marthews, R. Nilus, G. Reynolds, L. A. Turnbull, and A.
697 Hector. 2012. Light-based regeneration niches: evidence from 21 Dipterocarp species
698 using size-specific RGRs. *Biotropica* 44:627–636.

699 Piironen, T., P. Nyeko, and H. Roininen. 2015. Natural establishment of indigenous trees under
700 planted nuclei: a study from a clear-felled pine plantation in an Afrotropical rain forest.
701 *Forest Ecology and Management* 345:21–28.

702 R Core Team. 2024. R: A language and Environment for Statistical Computing. Vienna, Austria:
703 R Foundation for Statistical Computing. <https://www.R-project.org/>.

704 Ramírez-Soto, A., C. R. Lucio-Palacio, R. Rodríguez-Mesa, I. Sheseña-Hernández, F. N. Farhat,
705 B. Villa-Bonilla, L. Landa Libreros, G. Gutiérrez Sosa, O. Trujillo Santos, and I. Gomez
706 Sanchez. 2018. Restoration of tropical montane cloud forests: a six-prong strategy.
707 *Restoration Ecology* 26:206–211.

708 Reid, J. L., K. D. Holl, and R. A. Zahawi. 2015. Seed dispersal limitations shift over time in
709 tropical forest restoration. *Ecological Applications* 25:1072–1082.

710 Reid, J. L., R. A. Zahawi, D. A. Zárrate-Chary, J. A. Rosales, K. D. Holl, and U. Kormann.
711 2021. Multi-scale habitat selection of key frugivores predicts large-seeded tree
712 recruitment in tropical forest restoration. *Ecosphere* 12:e03868.

713 Rivas-Alonso, E., C. Martínez-Garza, M. de la Peña-Domene, and M. Mendez-Toribio. 2021.
714 Large trees in restored tropical rainforest. *Forest Ecology and Management* 498:119563.

715 Robinson, G. R., and S. N. Handel. 2000. Directing spatial patterns of recruitment during an
716 experimental urban woodland reclamation. *Ecological Applications* 10:174–188.

717 Rozendaal, D. M., F. Bongers, T. M. Aide, E. Alvarez-Dávila, N. Ascarrunz, P. Balvanera, J. M.
718 Becknell, T. V. Bents, P. H. Brancalion, and G. A. Cabral. 2019. Biodiversity recovery
719 of Neotropical secondary forests. *Science Advances* 5:eaau3114.

720 Rüger, N., M. E. Schorn, S. Kambach, R. L. Chazdon, C. E. Farrior, J. A. Meave, R. Muñoz, M.
721 Van Breugel, L. Amissah, F. Bongers, D. Craven, B. Hérault, C. C. Jakovac, N. Norden,
722 L. Poorter, M. T. Van Der Sande, C. Wirth, D. Delgado, D. H. Dent, S. J. DeWalt, J. M.
723 Dupuy, B. Finegan, J. S. Hall, J. L. Hernández-Stefanoni, and O. R. Lopez. 2023.

724 Successional shifts in tree demographic strategies in wet and dry Neotropical forests.
725 *Global Ecology and Biogeography* 32:1002–1014.

726 Shaw, J. A., L. M. Roche, and E. S. Gornish. 2020. The use of spatially patterned methods for
727 vegetation restoration and management across systems. *Restoration Ecology* 28:766–775.

728 Ssekuubwa, E., V. B. Muwanika, J. Esaete, J. R. Tabuti, and M. Tweheyo. 2019. Colonization of
729 woody seedlings in the understory of actively and passively restored tropical moist
730 forests. *Restoration Ecology* 27:148–157.

731 Swinfield, T., R. Afriandi, F. Antoni, and R. D. Harrison. 2016. Accelerating tropical forest
732 restoration through the selective removal of pioneer species. *Forest Ecology and*
733 *Management* 381:209–216.

734 Tonetti, V., B. B. Niebuhr, M. Ribeiro, and M. A. Pizo. 2022. Forest regeneration may reduce
735 the negative impacts of climate change on the biodiversity of a tropical hotspot. *Diversity*
736 *and Distributions* 28:2956–2971.

737 Trujillo-Miranda, A. L., T. Toledo-Aceves, F. López-Barrera, and P. Gerez-Fernández. 2018.
738 Active versus passive restoration: Recovery of cloud forest structure, diversity and soil
739 condition in abandoned pastures. *Ecological Engineering* 117:50–61.

740 Van Breugel, M., D. Craven, H. R. Lai, M. Baillon, B. L. Turner, and J. S. Hall. 2019. Soil
741 nutrients and dispersal limitation shape compositional variation in secondary tropical
742 forests across multiple scales. *Journal of Ecology* 107:566–581.

743 Werden, L. K., K. D. Holl, J. M. Chaves-Fallas, F. Oviedo-Brenes, J. A. Rosales, and R. A.
744 Zahawi. 2021. Degree of intervention affects interannual and within-plot heterogeneity of
745 seed arrival in tropical forest restoration. *Journal of Applied Ecology* 58:1693–1704.

746 Werden, L. K., K. D. Holl, J. A. Rosales, J. M. Sylvester, and R. A. Zahawi. 2020. Effects of
747 dispersal- and niche-based factors on tree recruitment in tropical wet forest restoration.
748 *Ecological Applications* 30:e02139.

749 Werden, L. K., S. Zarges, K. D. Holl, C. L. Oliver, F. Oviedo-Brenes, J. A. Rosales, and R. A.
750 Zahawi. 2022. Assisted restoration interventions drive functional recovery of tropical wet
751 forest tree communities. *Frontiers in Forests and Global Change* 5:935011.

752 Williams, B., H. Beyer, M. E. Fagan, R. Chazdon, M. Schmoeller, S. Sprenkle-Hyppolite, B.
753 Griscom, J. Watson, A. Tedesco, and M. Gonzalez-Roglich. 2023. The global potential
754 for natural regeneration in deforested tropical regions. Research Square unpublished.

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

758 Wilson, S. J., and J. M. Rhemtulla. 2016. Acceleration and novelty: community restoration
759 speeds recovery and transforms species composition in Andean cloud forest. *Ecological*
760 *Applications* 26:203–218.

761 Yarranton, G. A., and R. G. Morrison. 1974. Spatial dynamics of a primary succession:
762 nucleation. *Journal of Ecology* 62:417–428.

763 Zahawi, R. A., and C. K. Augspurger. 2006. Tropical forest restoration: tree islands as
764 recruitment foci in degraded lands of Honduras. *Ecological Applications* 16:464–478.

765 Zahawi, R. A., J. P. Dandois, K. D. Holl, D. Nadwodny, J. L. Reid, and E. C. Ellis. 2015a. Using
766 lightweight unmanned aerial vehicles to monitor tropical forest recovery. *Biological*
767 *Conservation* 186:287–295.

768 Zahawi, R. A., G. Duran, and U. Kormann. 2015b. Sixty-seven years of land-use change in
769 southern Costa Rica. *PloS One* 10:e0143554.

770 Zahawi, R. A., L. K. Werden, M. San-José, J. A. Rosales, J. Flores, and K. D. Holl. 2021.
771 Proximity and abundance of mother trees affects recruitment patterns in a long-term
772 tropical forest restoration study. *Ecography* 44:1826–1837.

773 Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in an
774 abandoned pasture in Puerto Rico. *Restoration Ecology* 8:350–360.

775

776 **FIGURE CAPTIONS**

777

778 **Figure 1:** Species accumulation curves for seedling, sapling, and tree recruits for early- (n = 38
779 spp.), mid- (n = 52 spp.), and late-successional species (n = 163 spp.) in natural regeneration
780 (NR), applied nucleation (AN), plantation (PL), and reference forest (RF). Rarefaction was
781 performed across randomized samples of 3 × 3 m quadrats with 95% confidence intervals,
782 displayed as shaded area. Dotted sections of curves indicate extrapolated calculations. See Table
783 S3 for statistical comparisons of species richness estimates.

784

785 **Figure 2:** Non-metric multi-dimensional scaling (NMDS) plot of Chao dissimilarity distances
786 among site community matrices based on total species abundances for (A) seedling, (B) sapling,
787 and (C) tree recruits from natural regeneration (NR), applied nucleation (AN), plantation (PL),
788 and reference forest (RF). Shaded ellipses indicate 95% confidence intervals of within-group
789 variance. Plot values are shown as small circles, and treatment group centroids are large cross-
790 filled squares. Stress = 0.17-0.18 for all three vegetation size classes. See Table S4 for pairwise
791 comparisons of treatments.

792

793 **Figure 3:** Mean stem densities of (A) seedlings, (B) saplings, and (C) trees of planted, early
794 successional, and later-successional species with small (Sm, <5 mm), medium (Md, 5-<10 mm)
795 and large (Lg, ≥10 mm) seeds across the four treatments: natural regeneration (NR), applied
796 nucleation (AN), plantation (PL), and reference forest (RF). Later-successional species include
797 mid- (no cross hatching) and late- (cross hatching) species. Error bars represent 95% confidence
798 intervals. Note different y-axis scales. Means with the same letter do not differ significantly (p >

799 0.05) using pairwise comparisons of estimated marginal means with a Bonferroni correction to
800 resulting p-values. See Fig. S2 for statistical comparisons of mid- and late-successional species
801 separately.