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Authors
Holl, Karen D
Reid, J Leighton
Cole, Rebecca J
et al.

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Applied Nucleation Facilitates Tropical Forest Recovery: Lessons Learned from a 15-year Study

K. D. Holl, J. L. Reid, R. J. Cole[3], F. Oviedo-Brenes, J. A. Rosales, R. A. Zahawi

Holl, Karen D. (kholl@ucsc.edu)[1]
Reid, J. Leighton[2,3]
Cole, Rebecca J.[4]
Oviedo-Brenes, Federico[5]
Rosales, J. Abel[5]
Zahawi, Rakan A.[1,5,6]

[1]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA
[2]School of Plant and Environmental Sciences, Virginia Tech, Blacksburg, VA 24061, USA
[3]Missouri Botanical Garden, St. Louis, MO 63110, USA
[4]Osa Conservation, Puerto Jiménez, Golfito, Costa Rica
[5]Las Cruces Biological Station, Organization for Tropical Studies, San Vito, Costa Rica
[6]Lyon Arboretum, University of Hawai'i at Mānoa, Honolulu, HI 96822, USA

Running head: Applied nucleation lessons learned

Keywords: applied nucleation, cluster planting, forest restoration, natural regeneration, rehabilitation, seed dispersal, succession, tree islands

Abstract

1. Applied nucleation, mostly based upon planting tree islands, has been proposed as a cost-effective strategy to meet ambitious global forest and landscape restoration targets.
2. We review results from a 15-yr study, replicated at 15 sites in southern Costa Rica, that compares applied nucleation to natural regeneration and mixed-species tree plantations as strategies to restore tropical forest. We have collected data on planted tree survival and growth, woody vegetation recruitment and structure, seed rain, litterfall, epiphytes, birds, bats, and leaf litter arthropods.
3. Our results indicate that applied nucleation and plantation restoration strategies are similarly effective in enhancing the recovery of most floral and faunal groups, vegetation structure, and ecosystem functions, as compared to natural regeneration.
4. Seed dispersal and woody recruitment are higher in applied nucleation and plantation than natural regeneration treatments; canopy cover has increased substantially in both natural regeneration and applied nucleation treatments; and mortality of planted N-fixing tree species has increased in recent years. These trends have led to rapid changes in vegetation composition and structure and nutrient cycling.
5. The applied nucleation strategy is cheaper than mixed-species tree plantations, but there may be social obstacles to implementing this technique in agricultural landscapes, such as perceptions that the land is not being used productively.
6. Applied nucleation is likely to be most effective in cases where: planted vegetation nuclei enhance seed dispersal and seedling establishment of other species; the spread of nuclei is not strongly inhibited by abiotic or biotic factors; and the approach is compatible with restoration goals and landowner preferences.
7. *Synthesis and Applications*: Results from our 15-yr, multi-site study show that applied nucleation can be a cost-effective strategy for facilitating tropical forest regeneration that holds promise for helping to meet large-scale international forest restoration commitments.

Resumen

1. La nucleación aplicada, basada principalmente en la plantación de islas arbóreas, se ha propuesto como una estrategia económica para cumplir con ambiciosos objetivos mundiales de restauración de bosques y paisajes.
2. Resumimos los resultados de un estudio de 15 años, replicado en 15 sitios en el sur de Costa Rica, que compara la nucleación aplicada con la regeneración natural y las plantaciones de árboles de especies mixtas como estrategias para restaurar el bosque tropical. Hemos recolectado datos sobre la supervivencia y el crecimiento de los árboles plantados, el reclutamiento y la estructura de la vegetación leñosa, la lluvia de semillas, la caída de hojarasca, las epífitas, las aves, los murciélagos y los artrópodos de la hojarasca.
3. Nuestros resultados indican que las estrategias de restauración utilizando la nucleación aplicada y plantaciones son igualmente efectivas para mejorar la recuperación de la mayoría

de los grupos florales y faunísticos, la estructura de la vegetación y las funciones del ecosistema, en comparación con la regeneración natural.

4. La dispersión de semillas y el reclutamiento leñoso son mayores en los tratamientos de nucleación aplicada y de plantación que en los tratamientos de regeneración natural; la cobertura del dosel ha aumentado sustancialmente tanto en la regeneración natural como en los tratamientos de nucleación aplicadas; y la mortalidad de las especies arbóreas fijadores de N plantadas ha aumentado en los últimos años. Estas tendencias han llevado a cambios rápidos en la composición y estructura de la vegetación y el ciclo de nutrientes.
5. La estrategia de nucleación aplicada es más barata que las plantaciones de árboles de especies mixtas, pero pueden existir obstáculos sociales para implementar esta técnica en paisajes agrícolas, como la percepción que la tierra no se está utilizando productivamente.
6. Es probable que la nucleación aplicada sea más efectiva en los casos en que: los núcleos de vegetación plantados mejoran la dispersión de semillas y el establecimiento de plántulas de otras especies; la propagación de los núcleos no está fuertemente inhibida por factores abióticos o bióticos; y el enfoque es compatible con los objetivos de restauración y las preferencias de los propietarios.
7. Síntesis y Aplicaciones: Resultados de nuestro estudio muestran que la nucleación aplicada puede ser una estrategia económica para facilitar la regeneración forestal que promete ayudar a cumplir los compromisos internacionales de restauración forestal a gran escala.

1. INTRODUCTION

An ambitious restoration agenda has been set at the global scale (Chazdon et al., 2017), including the Aichi targets, which propose to restore 15% of the land area worldwide, and the Bonn Challenge, which aims to restore tree cover on 350 million hectares by 2030. These efforts are motivated by varied goals, including conserving biodiversity, improving water quality and supply, sequestering carbon, and improving human livelihoods (Chazdon et al., 2017). To meet these large-scale targets we need restoration strategies that are ecologically sound and economically feasible, especially given the limited resources available (Stanturf, Palik & Dumroese, 2014).

One approach is to plant or seed clusters of plants within a larger area, a strategy that has been variously referred to as applied nucleation (Corbin & Holl, 2012), woodland islets (Rey Benayas, Bullock & Newton, 2008), tree islands (Zahawi & Augspurger, 2006), or cluster planting (Saha, Kuehne & Bauhus, 2016). This approach mimics the natural nucleation process (Yarranton & Morrison, 1974) in which primary colonists establish in patches and spread outward clonally and/or facilitate the colonization of other species. Not only does this methodology better approximate the small-scale heterogeneity of the natural ecosystem recovery (Corbin & Holl, 2012; Holl et al., 2013), it also requires less resources for planting and maintaining seedlings than do standard tree plantations.

Applied nucleation has been tested or proposed for restoration in a range of ecosystem types including tropical forest (Zahawi & Augspurger, 2006; Piiroinen, Nyeko & Roininen, 2015; Ramírez-Soto et al., 2018), temperate forests and woodlands (Robinson & Handel, 2000; Rey Benayas, Bullock & Newton, 2008; Saha, Kuehne & Bauhus, 2016; Aradottir & Halldorsson, 2018), salt marshes (Silliman et al., 2015), arid shrublands (Hulvey et al., 2017), and grasslands (Grygiel, Norland & Biondini, 2018). These studies suggest that in mesic systems where seed dispersal is limiting, tree nuclei enhance dispersal of animal-dispersed seeds and shade out competitive ruderal vegetation (Piiroinen, Nyeko & Roininen, 2015; Reid, Holl & Zahawi, 2015). In systems with harsh microclimatic conditions, plant nuclei can ameliorate stressful abiotic conditions to facilitate seedling establishment (Silliman et al., 2015; Hulvey et al., 2017; Aradottir & Halldorsson, 2018). There are a growing number of applied nucleation studies, but most have not compared the strategy to other restoration approaches and have been conducted at only one or a few sites.

Here we review the lessons learned from a well-replicated, 15-yr study comparing applied nucleation to both natural regeneration and mixed-species tree plantations as strategies to restore tropical forest. We summarize the substantial changes over the first decade and evaluate whether tree nuclei facilitate establishment of other species and increase in size, which is key to the success of this restoration approach. We ask the broad questions of: (1) whether applied nucleation is an effective restoration strategy to facilitate the recovery of abundance, richness, and composition of various floral and faunal groups, as well as ecosystem processes (e.g., litterfall, biomass accumulation), and (2) under what conditions is it a feasible approach to implement at larger scales? We frame this paper around the ecological and management lessons that can be drawn from the more than 50 publications and additional data sets resulting from this study. We refer to other applied nucleation studies throughout to compare where results concur or differ. We conclude by suggesting the conditions under which applied nucleation holds the most promise as a restoration strategy, as well as recommendations for future research directions.

2. STUDY DESIGN

2.1 Study sites

This study was conducted at 15, ~1-ha sites spread across an ~100 km^2 area in southern Costa Rica (Fig. 1) allowing us to overcome the issue of idiosyncratic results of individual sites and generalize across a broader landscape. The forests in this region are at the boundary between Tropical Premontane Wet and Rain Forest zones (Holdridge et al., 1971), range in elevation from 1100-1430 m, and receive mean annual rainfall of 3500-4000 mm with a dry season from December to March. Mean annual temperature is ~21°C. All sites are separated by a minimum of 700 m, and the surrounding landscape is a fragmented mosaic of agricultural fields and pasture interspersed with remnant forest patches (Zahawi, Duran & Kormann, 2015). Forest cover surrounding the plots ranged from 0-85% and 11-89% at 100- and 500-m buffers respectively at the beginning of the study (Table 1).

All sites were used for ≥18 years for a mixture of cattle grazing and coffee farming (Table 1). At the start of the study, sites were either dominated by one or a combination of the forage grasses *Axonopus scoparius*, *Pennisetum purpureum*, and *Urochloa brizantha*, or hosted a mixture of grasses, forbs, and the fern *Pteridium arachnoideum*. Most sites are steeply sloped (15-35º). Soils are volcanic in origin, mildly acidic, low in P, and high in organic matter (see Table S1 in Supporting Information, Holl & Zahawi, 2014).

2.2. Experimental design

Because of the scale of this study, the original 15 sites were set up over a 3-yr period: seven sites in 2004, five in 2005, and three in 2006. We currently have 12 active sites remaining; the other three were converted to other land uses within 5-10 years after planting (Reid et al., 2017). At each site we established three 0.25-ha (50×50 m) plots, each separated by a ≥5-m buffer. Each plot received one of three treatments: natural regeneration, applied nucleation, or plantation (Fig. 2). Plantations were uniformly planted with tree seedlings, whereas the applied nucleation treatment was planted with six tree nuclei of three sizes: two each of 4×4, 8×8 and 12×12 m. We planted two later-successional tree species that are widely available in nurseries and planted throughout Central America, *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two fast growing N-fixing species, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae) that are used in agricultural intercropping systems to provide rapid shade cover and increase soil nutrients. Tree spacing was kept constant (~2.8 m); 313 trees were planted in plantation, 86 in applied nucleation, and none in natural regeneration plots. Naturally-establishing vegetation in all plots (including natural regeneration) was cleared to ground level with machetes immediately prior to planting and at ~3-mo intervals for the first 2.5

years to allow planted tree seedlings to grow above existing vegetation; most data collection started after that time. Zahawi et al. (2013) and Holl and Zahawi (2014) provide more details about the experimental design. We also collected data on many variables (see Appendix S1) in plots within reference forests (2 to >300 ha) adjacent to the six restoration sites that have sufficient area of remnant forest nearby; these forests are the most representative habitat available in the region.

By 2019 (13-15 years after plot set up), most natural regeneration plots had patchy canopy cover, primarily in the 2-5 m strata, with dense grass cover in between (Fig. 2, Table 2), but a couple had more extensive cover of trees and shrubs (Holl et al., 2018). In most applied nucleation plots, canopy cover expanded substantially beyond the initial planted area so that by 2019 most of the plots had canopy cover either in the 2-5 or >5 m strata (Fig. 2, Table 2). Most plantation plots had a relatively homogenous tall canopy cover and less mid-story shrub and tree cover than the other treatments (Table 2), likely due to extensive shading, a trend observed in other restoration plantations (de Oliveira et al., 2019).

2.3 Data collection and analysis

We have collected extensive data on vegetation recovery including planted tree survival and growth; woody vegetation recruitment, survival, growth, and structure; and epiphyte species richness. We have monitored abundance, richness and composition of birds and bats, which are important seed dispersers in this system (Cole, Holl & Zahawi, 2010), and leaf litter arthropods, which play a key role in litter decomposition (Cole et al., 2016). We have also measured the effect of restoration treatments on seed dispersal, a common limiting factor in tropical forest recovery (Holl, 2007), and litterfall biomass and nutrients, as an indication of the recovery of nutrient cycling processes. Some data were collected at all sites (e.g., planted tree growth, seedling recruitment), whereas other data sets that require more intensive sampling were collected at a subset of sites (e.g., leaf litter arthropods, nutrient inputs, seed rain). Accordingly, sample size for the studies reviewed here ranges from 4 to 15 sites.

The study is set up as a randomized block design with treatment (natural regeneration, applied nucleation, plantation, reference forest) as a fixed effect and site as the random block effect. We have generally used two-way analysis of variance and general linear mixed models (including surrounding forest cover as an additional continuous explanatory variable) to analyse response variables and used post-hoc multiple-comparison procedures to compare different treatments. Data about nuclei spread were analysed using a one-way analysis of variance (ANOVA) with location within applied nucleation plots (within small, medium, or large nuclei; 2, 4, 6, or 12 m from nuclei edge) as the explanatory variable. If response variables did not meet assumptions of normality and homoscedasticity, they were either transformed or a different error distribution (e.g. binomial) was used. Because of high variability in tree growth rates, mean tree height and cover development overlapped substantially among planting years (Holl et al., 2011; Holl & Zahawi, 2014), so planting year was not included in most analyses. Means ± 1 SE are reported throughout.

A detailed presentation of all data collection and analysis procedures for the numerous variables summarized here is beyond the scope of this review. In Supporting Information Appendix S1, we provide an overview of methods for the previously-published data reviewed here, along with references to the original publications where all methods are described in detail. Appendix S1 also includes detailed collection and analysis methods for the few new data presented here.

3. LESSONS LEARNED

3.1 Efficacy of applied nucleation in facilitating forest recovery

Lesson 1: Applied nucleation and plantation restoration strategies are similarly effective in enhancing the recovery of several floral and faunal groups, vegetation structure, and ecosystem functions.

Most floral and faunal groups we measured had similar abundance and/or rarefied species richness in applied nucleation and plantation treatments by the end of the first decade of recovery, and in some cases even sooner (Fig. 3). For example, applied nucleation and plantation treatments attracted similar abundances of seed-dispersing birds and bats (Fig. 3A-B), resulting in comparable abundance and species richness of animal-dispersed seed deposition and seedling recruitment (Fig. 3C-D; Reid et al., 2014; Reid, Holl & Zahawi, 2015; Reid et al., 2015; Holl et al., 2017). Likewise, applied nucleation and plantation treatments resulted in equivalent vascular epiphyte richness, litterfall production, and litterfall nutrient inputs (Fig. 3E, Fig. 4A-D; Reid et al., 2016; Lanuza et al., 2018). A few variables, however, showed different patterns. For example, leaf litter arthropods showed a trend toward higher abundance and richness in applied nucleation than in plantations (Fig. 3F; Cole et al., 2016). Not surprisingly, above-ground biomass accumulation of planted trees in plantations was twice that in applied nucleation plots by the end of the first decade (AN: 2.35 ± 0.50; PL: 4.98 ± 0.73 Mg ha^{-1} yr^{-1}) (Holl & Zahawi, 2014); in contrast, biomass of naturally recruiting trees was much lower and did not differ significantly across the three restoration treatments (NR: 0.84 ± 0.26; AN: 0.83 ± 0.17; PL: 0.72 ± 0.37 Mg ha^{-1} yr^{-1}).

Moreover, applied nucleation and plantations have both accelerated recovery relative to natural regeneration thus far. Most bird (Fig. 3A; Reid et al., 2014) and leaf litter arthropod variables (Fig. 3F; Cole et al., 2016), tree recruitment (Fig. 3D; Holl et al., 2017), epiphyte richness (Fig. 3E; Reid et al., 2016), and litterfall inputs (Fig. 4; Lanuza et al., 2018) showed a much higher degree of recovery in applied nucleation and plantation treatments than in natural regeneration plots. For example, leaf litter arthropod abundance and richness in applied nucleation plots were double the values in natural regeneration (Cole et al., 2016).

Species composition of birds (Reid et al., 2014, unpub. data), seed rain (Reid, Holl & Zahawi, 2015), tree recruits (Holl et al., 2017), and leaf litter arthropods (Cole et al., 2016) differed substantially from reference forests in all restoration treatments after 8-14 years, with forest dependent species underrepresented in all restoration treatments (Reid et al., 2014; Reid et al., 2015; Holl et al., 2017). For example, both seed rain and tree recruitment studies noted a paucity of later successional, large-seeded species in all restoration treatments, particularly in natural regeneration (Fig. 3C-D). These differences are not surprising given that tropical forests take many decades to hundreds of years to recover prior levels of biodiversity (Dent & Wright, 2009).

A few past studies show that planting tree clusters facilitates plant recruitment as compared to natural regeneration (Robinson & Handel, 2000; Zahawi & Augspurger, 2006; Piiroinen, Nyeko & Roininen, 2015; Aradottir & Halldorsson, 2018), but that the facilitative effect of plantings can decline over time (Corbin et al., 2016). However, most of these studies have not compared the outcomes of applied nucleation to other restoration strategies nor have they compared them to reference ecosystems, making it difficult to ascertain the effects of applied nucleation on successional trajectories in other ecosystems.

Lesson 2: A minimum nucleus size is needed to enhance seed dispersal and seedling recruitment.

Results of our study (Fink et al., 2009; Cole, Holl & Zahawi, 2010; Zahawi et al., 2013) and of Zahawi and Augspurger (2006), who studied applied nucleation in tropical forests in Honduras, show that larger tree nuclei (64 and 144 m^2 planted area) have much higher visitation rates by birds, dispersal of animal-dispersed seeds, and seedling recruitment than smaller nuclei (4 and 16 m^2). In the first few years of our study, seed rain and seedling recruitment values in the large and medium nuclei were two to three times those for small nuclei, which were similar to those outside the planted area (Fig. 5A&B). This result was likely due to greater percent canopy cover in large and medium nuclei (Fig. 5C), which both attracts seed dispersers (Fink et al., 2009) and shades out light demanding and highly competitive pasture grasses (Fig. 5D). Since tree nuclei cover increased rapidly and differentially in the first few years (next section), many merged and it was not possible to compare the effect of individual planted nuclei size on recruitment beyond the first few years.

Lesson 3: Tree nuclei are spreading over time.

The original nucleation model of succession (Yarranton & Morrison, 1974) was based on the idea that existing tree nuclei would increase in size over time through both planted tree growth and new tree recruitment, and we have observed this pattern in our sites. We planted only ~20% of the area in applied nucleation plots, and analyses from drone overflights after 7-9 years showed that canopy cover >2 m had increased substantially to 45.5 ± 9.0% in these plots, as compared to 14.2 ± 6.1% in natural regeneration plots and 78.2 ± 9.1% in plantation plots (Zahawi et al., 2015). Ground-measured data after 13-15 years showed a dramatic increase in canopy cover in both the natural regeneration and applied nucleation plots, particularly in the 2-5 m layer (Table 1).

Most past studies of applied nucleation have been of short duration so they have not monitored nuclei spread over time. The other two long-term nucleation studies show that recruitment within and outside tree nuclei is highly variable across ecosystem types. Corbin et al. (2016) reported a considerable increase in canopy cover and higher recruitment of animal-dispersed species within the area of the original planted tree nuclei after 19 years in a temperate forest study in the United States, but they did not find greater numbers of woody recruits near the edge of the planted area compared to further away. In contrast, Rey Benayas et al. (2015) found minimal woody recruitment within or outside planted oak (*Quercus ilex*) nuclei in Spain after 21 years largely due to high seed predation and seedling herbivory, particularly at nuclei edges, as well as stressful microclimate conditions and competition from trees in established nuclei.

3.2 Changing patterns of recovery

Lesson 4: Treatment effects change rapidly during the first decade of recovery.

Recovery patterns changed dramatically over the first decade. For example, the number of animal-dispersed seeds arriving in natural regeneration plots more than doubled between 2-4 years (Cole, Holl & Zahawi, 2010) and 6-9 years following the start of the study (Reid, Holl & Zahawi, 2015). At the first sampling period, seed rain of small (≤5 mm), animal-dispersed seeds was 2.4 times greater in applied nucleation and 3 times greater in plantation as compared to natural regeneration plots (Cole, Holl & Zahawi, 2010), whereas by the second sampling period the number of small, animal-dispersed seeds did not differ significantly across restoration treatments (Reid, Holl & Zahawi, 2015). Likewise, the number of recruited trees increased by a factor of 2.5 between 4-6 years and 9-11 years following the end of site management (Zahawi et al., 2013; Holl et al., 2017), and approximately 20% of recruited seedlings died during that same 5-yr interval (Holl & Zahawi, unpub. data).

The composition of overstory species also changed substantially. Whereas all planted tree species had >80% survival in both applied nucleation and plantation treatments after 3 years (Holl et al., 2011), the survival of the two N-fixing species dropped to approximately half after 12-14 years (*E. poeppigiana* 50.5 ± 7.6%; *I. edulis* 52.7 ± 7.9%); this temporarily increased light availability, thereby increasing growth of the two remaining planted species and establishment and growth of naturally recruiting species. Such rapid changes are not surprising, as it is well known that forests are highly dynamic early in the successional process (Finegan, 1984; van Breugel, Bongers & Martinez-Ramos, 2007; Letcher & Chazdon, 2009), and highlight the importance of longer-term studies to compare restoration strategies.

Lesson 5: Planted trees had weak effects on nutrient inputs and self-recruitment after a decade.

One concern about planting trees to accelerate forest recovery is that the species selected may affect the trajectories of nutrient cycling and vegetation composition (Cusack & Montagnini, 2004; Boley, Drew & Andrus, 2009; Sansevero et al., 2011). Because less area is planted in the applied nucleation approach, we anticipated that these effects would be reduced compared to the plantation treatment. Indeed, at ~5 years into recovery we saw a strong effect of planted trees on litterfall biomass and nutrient inputs (Fig. 4, Celentano et al., 2011); litterfall biomass and all macronutrient (N, P, Ca, Mg, K) inputs were highest in plantations, intermediate in applied nucleation, and lowest in natural regeneration plots. After 10-12 years, however, litterfall biomass and inputs of N, P, and C in applied nucleation and plantation treatments were comparable (Fig. 4, Lanuza et al., 2018), as a result of the mortality of planted N-fixing trees (discussed above) and the increase in litterfall from naturally-recruiting species; values remained significantly lower in natural regeneration plots.

Thus far, planted species have minimally affected species composition of recruiting trees, as evidenced by the similar recruit species composition in applied nucleation and plantation plots (Holl et al., 2017). Moreover, recruits of planted species have comprised <2% of all recruits across the three restoration treatments (Holl et al., 2017). Nearly all are *Inga edulis* or *Erythrina poeppigiana,* both of which are ubiquitous in the agricultural landscape so they recruit into all restoration treatments, including natural regeneration. The vast majority (>90%) of recruits of these species die within a year, likely due to shade intolerance. Hence, our results suggest that the "legacy" effects of the planted trees, at least in terms of nutrient cycling and self-recruitment, are short lived.

3.3 Practicality of implementing applied nucleation at larger scales

Whereas our and other studies suggest that applied nucleation is an ecologically-sound and effective approach to facilitating ecosystem recovery, we are aware of only a few cases to date in which restoration practitioners are using this approach at a large scale (e.g., Osa Conservation in Costa Rica, Green Again Madagascar). As with all restoration strategies it is critical to consider socioeconomic incentives and barriers to adoption, so we review a few key lessons on this topic.

Lesson 6: Applied nucleation is less costly to implement than tree plantations.

Cost-effective restoration approaches are needed to restore forests at the scales proposed by international agreements (Stanturf, Palik & Dumroese, 2014; Brancalion et al., 2019). In our study, the nursery, planting and maintenance costs of applied nucleation were approximately a third the cost of plantations (Zahawi & Holl, 2009), although the relative cost depends on the proportion of the area planted in the applied nucleation strategy. Of course, certain forest restoration costs, such as land acquisition and fencing to exclude domestic livestock, are the same regardless of restoration approach, and natural regeneration is the cheapest approach if the ecosystem recovers at a pace that is acceptable for both social and ecological restoration objectives (Chazdon & Guariguata, 2016).

Lesson 7: Logistical and social challenges can limit the success of applied nucleation.

Restoration companies and practitioners that undertake restoration are more accustomed to the widely-used approach of planting trees in rows which are more orderly than tree clusters. Hence, additional training may be needed at the outset so that restoration teams clearly understand the rationale and layout of the applied nucleation approach (Ramírez-Soto et al., 2018). For example, a less systematic planting design means that people who clear vegetation around the planted seedlings during the first year must be well informed about spacing so they do not inadvertently damage seedlings (Holl et al., 2011). These issues can be surmounted, particularly if applied nucleation is implemented at a large scale and practitioners become familiar with the technique.

A more challenging issue is landowner perception. When an area is planted entirely with trees, it is apparent to both the landowner and neighbours that the land is being used for what people commonly consider a productive land use, namely growing trees. In contrast, we have found that people often perceive natural regeneration and applied nucleation sites as unused land and consider them “messy” (Zahawi, Reid & Holl, 2014), which has clear implications for the longevity of plantings. At the outset of our study, we had to explain to some landowners repeatedly why we did not plant trees throughout the entire plot and did not clear naturally establishing vegetation around the planted trees after the first couple of years. We also had to be vigilant about preventing livestock entry, particularly in natural regeneration and applied nucleation plots, where the more abundant grass was perceived by farmers as unused. In recent years we have had to talk with neighbours about not cutting large trees in the plantations for wood, which can be an important social objective of restoration, but is not part of our study.

3.4 Conditions where applied nucleation is likely to accelerate recovery

Studies to date indicate that applied nucleation is a successful restoration strategy in some but not all situations. We draw on the results of our and other studies to suggest conditions under which applied nucleation is more likely to succeed in meeting restoration goals.

Condition 1: Woody vegetation nuclei are lacking.

As noted earlier, succession in most habitat types occurs naturally through the establishment of patches of native vegetation that grow and coalesce over time. In sites with a long history of human disturbance, where natural regeneration is slow, actively establishing vegetation nuclei can accelerate recovery by serving as sources of seeds and facilitating dispersal and establishment of other species (Rey Benayas et al., 2020). Alternatively, some ecosystems and sites, particularly where there are nearby seed sources and the land has been used less intensively and for a shorter period of time (e.g., shifting agriculture), nuclei of native vegetation often establish quickly on their own, making it unnecessary to actively seed or plant (Chazdon et al., 2020). In such cases, a more cost-effective strategy may be to allow early-successional species to establish and provide canopy cover, and then seed or plant large-seeded, later-successional species, epiphytes, or other plant groups that are more establishment limited (Bonilla-Moheno & Holl, 2010; Duarte & Gandolfi, 2017; Fernandez Barrancos, Reid & Aronson, 2017). That said, we have found high variability in the rate of natural establishment and spread of tree nuclei in natural regeneration plots even within our small region in southern Costa Rica, and that the number of tree recruits and canopy cover that establish in the first 1.5 years are good predictors of the rate of forest recovery over the next several years (Holl et al., 2018). Hence, a good strategy is to leave a site for a year or two in order to document natural recovery before deciding whether to actively introduce vegetation nuclei.

Condition 2: Nuclei enhance dispersal of animal-dispersed seeds.

For planted woody vegetation nuclei to enhance dispersal requires the presence of dispersers and connectivity between seeds sources and regenerating sites. As such, applied nucleation is unlikely to work in locations where many of the native dispersers have been extirpated (e.g. Guam, Hawaii, Kaiser-Bunbury, Traveset & Hansen, 2010) or overhunting (Brodie et al., 2009; Caughlin et al., 2015); where the system is dominated by wind dispersed species (Corbin et al., 2016); or where vast, inhospitable landscapes make seed dispersal improbable. In cases where animal-mediated seed dispersal is unlikely, restoration efforts will need to actively reintroduce most desired species.

Condition 3: Nuclei facilitate rather than inhibit native species recruitment.

The nucleation model is a promising approach when vegetation nuclei provide more favourable conditions for seedling recruitment. In our system, tree nuclei shade out pasture grasses, thereby reducing competition for newly-recruited tree seedlings (Zahawi et al., 2013). In locations with more extreme microclimatic conditions, tree and shrub nuclei may ameliorate temperature and moisture conditions, reduce wind, and trap organic matter and nutrients, thereby facilitating the establishment of naturally-recruiting species (Gomez-Aparicio, 2009; Aradottir & Halldorsson, 2018), but they also may compete for resources (Rey Benayas et al., 2015). The species selected for planting should be chosen carefully, as in some cases, naturally establishing vegetation nuclei of highly competitive species can inhibit the establishment of a diverse suite of native species (e.g., Zahawi & Augspurger, 1999).

Condition 4: Spread of nuclei is not inhibited by herbivory, invasive species competition, or fire.

The spread of vegetation nuclei either via new recruitment or clonal spread of planted species is key to ecosystem recovery. Woody cover will increase slowly, if at all, in areas where nuclei spread is inhibited by herbivory (Rey Benayas et al., 2015), fire (Hill, 2018), or competition with invasive or other ruderal species (Corbin & Holl, 2012). For example, trees planted on the edges of nuclei in eastern Madagascar suffered greater mortality during a wildfire due to the greater abundance of fine fuels (ruderal ferns) in the spaces between nuclei (Hill 2018). Planting tree nuclei for forest restoration may slowly shade out highly competitive grass, fern, and other herbaceous species at the edge of nuclei, permitting spread, whereas in open canopy systems, such as savannas and grasslands, invasive grasses inhibit the recruitment of native species at nuclei edges (Holl & Lesage, unpub. data), so more widespread planting or seeding is needed.

Condition 5: Applied nucleation is compatible with landowner preferences and restoration goals

It is widely recognized that the selection of restoration approaches needs to include stakeholders from the outset and consideration of both biophysical and socioeconomic outcomes (e.g., Mansourian & Vallauri, 2014; Holl, 2020). Applied nucleation will only be appropriate if it is compatible with the goals of specific restoration projects and landowner needs and preferences. In areas of high human population density, where landowners depend on land for income and resources, forest and landscape restoration efforts will likely need to focus on native species that provide resources to landowners (e.g. fruit, firewood, timber) (Mansourian & Vallauri, 2014). Hence, applied nucleation is more appropriate for degraded land that was recently added to a reserve or national park, where funding to restore a large area is limited, and where the ultimate goal of restoration is conservation or watershed protection. In highly degraded areas, such as post-mining, it is typically necessary to use more intensive restoration strategies, such as restoring topography, planting the entire area, and using erosion control measures to maintain water quality (Holl, 2020).

4. RESEARCH DIRECTIONS TO SCALE UP APPLIED NUCLEATION

Whereas research on applied nucleation and its utility in facilitating forest regeneration is growing, there are still numerous unanswered questions. We highlight a few key research areas.

4.1 Optimal species composition for applied nucleation

One avenue for future research is to evaluate which combinations of species make the most effective nuclei. Some authors have suggested planting tree species that produce preferred fruits for a range of animals to encourage more abundant and diverse seed dispersal (Howe, 2017; Zahawi & Reid, 2018). Some past studies have shown that overstory composition in native tree plantations can influence the mix of recruiting species (Cusack & Montagnini, 2004; Sansevero et al., 2011), whereas Li et al. (2018) found minimal differences in tree recruitment in plots planted entirely with animal-dispersed or wind-dispersed tree species in Mexico. We advocate using planting mixes that represent diverse species, genetics, and functional traits. But, we are not aware of studies that have compared vegetation nuclei with different plant species and/or plant functional traits, such as dispersal-mode, growth-rate, evergreen vs. deciduous, and N-fixation, which might affect their efficacy in facilitating succession.

4.2 Alternative planting configurations

Our research project and Zahawi and Augspurger (2006) compared different nuclei sizes, but we know of no studies that have compared different distances separating nuclei. Whereas the rate of nuclei spread was variable in our sites, woody cover reached over 90% in most applied nucleation plots after 15 years (Table 1). The ideal distance of nuclei spacing will depend on several factors, including the extent of site disturbance, dispersal distances of planted species, the rate of nuclei spread, and the resources available for tree planting. It is likely that planting a larger percentage of a restoration site with nuclei will result in faster recovery but optimal spacing of tree nuclei needs to be tested, and these considerations clearly impact project costs.

Other potential planting designs besides applied nucleation that could achieve the goals of facilitating establishment of other species, creating more heterogeneous habitat, and reducing restoration costs also warrant further testing. For example, planting strips or rows of vegetation with intervening open areas that are allowed to recover naturally has been used in grassland restoration (Rayburn & Laca, 2013), and this approach may be more feasible to implement since farmers and restoration practitioners are more accustomed to planting in rows.

4.3 Comparisons to other restoration methods at larger scales

In a meta-analysis of tropical forest restoration, Shoo and Catterall (2013) found few studies that compared different active tropical forest restoration strategies to each other and to natural regeneration. The same is true for most past studies of applied nucleation. To conclude more broadly about the efficacy of applied nucleation will require more studies that directly test whether it enhances the rate of recovery of both species composition and ecosystem processes as compared to natural regeneration, and whether it is similarly effective to more intensive restoration strategies. These comparisons ideally should be done in the context of actual restoration projects to evaluate ecological and socioeconomic outcomes at a sufficiently large scale to inform restoration practice. A potential major advantage of applied nucleation is the lower planting and seedling maintenance costs, which should enable larger areas to be restored. However, documentation of costs from these comparative restoration projects, rather than just scientific studies, are needed. As the calls from the scientific community, business leaders, and politicians to plant billions to trillions of trees increase (Holl & Brancalion, 2020), such studies are critical to evaluate whether and how to most strategically plant those trees to facilitate forest recovery.

Author's Contributions

K.D.H. and R.A.Z. designed the initial study. All authors helped develop data collection protocols and collected data over many years. K.D.H. led the writing of the manuscript. J.L.R., R.A.Z., and R.J.C. contributed to the drafts.

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Data

Data are archived at our permanent data repository for the study merritt.cdlib.org/m/ucsc_lib_hollzahawi (Holl & Zahawi, 2020) [seed rain: n2t.net/ark:/13030/m5z04pcs, planted trees: n2t.net/ark:/13030/m5xs6056, tree recruits: n2t.net/ark:/13030/m5dk03kt, epiphytes: n2t.net/ark:/13030/m5p88rbz, litterfall: n2t.net/ark:/13030/m5md3vvs, mycorrhizae: n2t.net/ark:/13030/m5jb0vc2, soil nutrients: n2t.net/ark:/13030/m5qz2dzt; birds: n2t.net/ark:/13030/m5mk6jms and n2t.net/ark:/13030/m5673mww, bats: n2t.net/ark:/13030/m57w6g68, leaf litter arthropods: n2t.net/ark:/13030/m5dg1czd; canopy cover: n2t.net/ark:/13030/m5hn0h17]

References

Aradottir, A.L. & Halldorsson, G. (2018) Colonization of woodland species during restoration: seed or safe site limitation? Restoration Ecology, 26**,** S73-S83. doi: 10.1111/rec.12645

Boley, J.D., Drew, A.P. & Andrus, R.E. (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. doi: 10.1016/j.foreco.2009.02.035

Bonilla-Moheno, M. & Holl, K.D. (2010) Direct seeding to restore tropical mature-forest species in areas of slash-and-burn agriculture Restoration Ecology, 18**,** 438-445. doi: 10.1111/j.1526-100X.2009.00580.x

Brancalion, P.H.S., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F.S.M., Almeyda Zambrano, A.M., . . . Chazdon, R.L. (2019) Global restoration opportunities in tropical rainforest landscapes. Science Advances, 5**,** eaav3223. doi: 10.1126/sciadv.aav3223

Brodie, J.F., Helmy, O.E., Brockelman, W.Y. & Maron, J.L. (2009) Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. Ecological Applications, 19**,** 854-863. doi: 10.1890/08-0955.1

Caughlin, T.T., Ferguson, J.M., Lichstein, J.W., Zuidema, P.A., Bunyavejchewin, S. & Levey, D.J. (2015) Loss of animal seed dispersal increases extinction risk in a tropical tree species due to pervasive negative density dependence across life stages. Proceedings of the Royal Society B, 282**,** 20142095. doi: 10.1098/rspb.2014.2095

Celentano, D., Zahawi, R.A., Finegan, B., Ostertag, R., Cole, R.J. & Holl, K.D. (2011) Litterfall dynamics under different tropical forest restoration strategies in Costa Rica. Biotropica, 43**,** 279-287. doi: 10.1111/j.1744-7429.2010.00688.x

Chazdon, R.L., Brancalion, P.H.S., Lamb, D., Laestadius, L., Calmon, M. & Kumar, C. (2017) A policy-driven knowledge agenda for global forest and landscape restoration. Conservation Letters, 10**,** 125-132. doi: 10.1111/conl.12220

Chazdon, R.L. & Guariguata, M.R. (2016) Natural regeneration as a tool for large-scale forest restoration in the tropics: Prospects and challenges. Biotropica, 48**,** 716-730. doi: 10.1111/btp.12381

Chazdon, R.L., Lindenmayer, D., Guariguata, M.R., Crouzeilles, R., Rey Benayas, J.M. & Lazos Chavero, E. (2020) Fostering natural forest regeneration on former agricultural land through economic and policy interventions. Environmental Research Letters, 15**,** 043002. doi: 10.1088/1748-9326/ab79e6

Cole, R.J., Holl, K.D. & Zahawi, R.A. (2010) Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecological Applications, 20**,** 1255-1269. doi: 10.1890/09-0714.1

Cole, R.J., Holl, K.D., Zahawi, R.A., Wickey, P. & Townsend, A.R. (2016) Leaf litter arthropod responses to tropical forest restoration. Ecology and Evolution, 6**,** 5158-5168. doi: 10.1002/ece3.2220

Corbin, J.D. & Holl, K.D. (2012) Applied nucleation as a forest restoration strategy. Forest Ecology and Management, 265**,** 37-46. doi: 10.1016/j.foreco.2011.10.013

Corbin, J.D., Robinson, G.R., Hafkemeyer, L.M. & Handel, S.N. (2016) A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. Ecological Applications, 26, 104-114. doi: 10.1890/15-0075

Cusack, D. & Montagnini, F. (2004) The role of native species plantations in recovery of understory woody diversity in degraded pasturelands of Costa Rica. Forest Ecology and Management, 188**,** 1-15. doi: 10.1016/S0378-1127(03)00302-5

de Oliveira, C.D.C., de Oliveira, I.R.C., Suganuma, M.S. & Durigan, G. (2019) Overstory trees in excess: A threat to restoration success in Brazilian Atlantic forest. Forest Ecology and Management, 449**,** 117453. doi: 10.1016/j.foreco.2019.117453

Dent, D.H. & Wright, S.J. (2009) The future of tropical species in secondary forests: A quantitative review. Biological Conservation, 142**,** 2833-2843. doi: 10.1016/j.biocon.2009.05.035

Duarte, M.M. & Gandolfi, S. (2017) Diversifying growth forms in tropical forest restoration: Enrichment with vascular epiphytes. Forest Ecology and Management, 401**,** 89-98. doi: 10.1016/j.foreco.2017.06.063

Fernandez Barrancos, E.P., Reid, J.L. & Aronson, J. (2017) Tank bromeliad transplants as an enrichment strategy in southern Costa Rica. Restoration Ecology, 25**,** 569-576. doi: 10.1111/rec.12463

Finegan, B. (1984) Forest succession. Nature, 312**,** 109-114.

Fink, R.D., Lindell, C.A., Morrison, E.B., Zahawi, R.A. & Holl, K.D. (2009) Patch size and tree species influence the number and duration of bird visits in forest restoration plots in southern Costa Rica. Restoration Ecology, 17**,** 479-486. doi: 10.1111/j.1526-100X.2008.00383.x

Gomez-Aparicio, L. (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology, 97**,** 1202-1214. doi: 10.1111/j.1365-2745.2009.01573.x

Grygiel, C.E., Norland, J.E. & Biondini, M.E. (2018) Precision prairie reconstruction (ppr): 15 years of data. Ecological Restoration, 36**,** 276-283. doi: 10.3368/er.36.4.276

Hill, D.M. (2018) *Forest restoration in eastern Madagascar: post-fire survival of select Malagasy tree species.* M.S. Thesis, University of Minnesota.

Holdridge, L.R., Grenke, W.C., Hatheway, W.H., Liang, T. & Tosi, J.A., Jr. (1971) *Forest environments in tropical life zones.* Pergamon Press, Oxford.

Holl, K.D. (2007) Oldfield vegetation succession in the Neotropics. *Old fields* (eds R.J. Hobbs & V.A. Cramer), pp. 93-117. Island Press, Washington, DC.

Holl, K.D. (2020) Primer of ecological restoration. Island Press, Washington, D.C.

Holl, K.D. & Brancalion, P.H.S. (2020) Tree planting is not a simple solution. Science, 368**,** 580-581. doi: 10.1126/science.aba8232

Holl, K.D., Reid, J.L., Chaves-Fallas, J.M., Oviedo-Brenes, F. & Zahawi, R.A. (2017) Local tropical forest restoration strategies affect tree recruitment more strongly than does landscape forest cover. Journal of Applied Ecology, 54**,** doi: 1091-1099. 10.1111/1365-2664.12814

Holl, K.D., Reid, J.L., Oviedo-Brenes, F., Kulikowski, A.J. & Zahawi, R.A. (2018) Rules of thumb for predicting tropical forest recovery. Applied Vegetation Science, 21**,** 669-677. doi: 10.1111/avsc.12394

Holl, K.D., Stout, V.M., Reid, J.L. & Zahawi, R.A. (2013) Testing heterogeneity-diversity relationships in tropical forest restoration. Oecologia, 173**,** 569–578. doi: 10.1007/s00442-013-2632-9

Holl, K.D. & Zahawi, R.A. (2014) Factors explaining variability in woody above-ground biomass accumulation in restored tropical forest. Forest Ecology and Management, 319**,** 36-43. doi: 10.1016/j.foreco.2014.01.024

Holl, K.D. & Zahawi, R.A. (2020) Holl and Zahawi: tropical forest restoration data. Merritt data repository. https://merritt.cdlib.org/m/ucsc_lib_hollzahawi.

Holl, K.D., Zahawi, R.A., Cole, R.J., Ostertag, R. & Cordell, S. (2011) Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. Restoration Ecology, 19**,** 470-479. doi: 10.1111/j.1526-100X.2010.00674.x

Howe, H.F. (2017) Fruit-eating birds in experimental plantings in southern Mexico. Journal of Tropical Ecology, 33**,** 83-88. doi: 10.1017/s0266467416000596

Hulvey, K.B., Leger, E.A., Porensky, L.M., Roche, L.M., Veblen, K.E., Fund, A., . . . Gornish, E.S. (2017) Restoration islands: a tool for efficiently restoring dryland ecosystems? Restoration Ecology, 25**,** S124-S134. doi: 10.1111/rec.12614

Kaiser-Bunbury, C.N., Traveset, A. & Hansen, D.M. (2010) Conservation and restoration of plant–animal mutualisms on oceanic islands. Perspectives in Plant Ecology, Evolution and Systematics, 12**,** 131-143. doi: 10.1016/j.ppees.2009.10.002

Lanuza, O., Casanoves, F., Zahawi, R.A., Celentano, D., Delgado, D. & Holl, K.D. (2018) Litterfall and nutrient dynamics shift in tropical forest restoration sites after a decade of recovery. Biotropica, 50**,** 491-498. doi: 10.1111/btp.12533

Letcher, S.G. & Chazdon, R.L. (2009) Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. Biotropica, 41, 608-617. doi: 10.1111/j.1744-7429.2009.00517.x

Li, L., Cadotte, M.W., Martínez-Garza, C., Peña-Domene, M. & Du, G. (2018) Planting accelerates restoration of tropical forest but assembly mechanisms appear insensitive to initial composition. Journal of Applied Ecology, 55, 986-996. doi: 10.1111/1365-2664.12976

Mansourian, S. & Vallauri, D. (2014) Restoring forest landscapes: important lessons learnt. Environmental Management, 53, 241-251. doi: 10.1007/s00267-013-0213-7

Mendenhall, C.D., Sekercioglu, C.H., Brenes, F.O., Ehrlich, P.R. & Daily, G.C. (2011) Predictive model for sustaining biodiversity in tropical countryside. Proceedings of the National Academy of Sciences of the United States of America, 108, 16313-16316. doi: 10.1073/pnas.1111687108

Piiroinen, T., Nyeko, P. & Roininen, H. (2015) Natural establishment of indigenous trees under planted nuclei: A study from a clear-felled pine plantation in an afrotropical rain forest. Forest Ecology and Management, 345, 21-28. doi: 10.1016/j.foreco.2015.02.027

Ramírez-Soto, A., Lucio-Palacio, C.R., Rodríguez-Mesa, R., Sheseña-Hernández, I., Farhat, F.N., Villa-Bonilla, B., . . . Ruelas Inzunza, E. (2018) Restoration of tropical montane cloud forests: a six-prong strategy. Restoration Ecology, 26, 206-211. doi: 10.1111/rec.12660

Rayburn, A.P. & Laca, E.A. (2013) Strip-seeding for grassland restoration: past successes and future potential. Ecological Restoration, 31, 147-153.

Reid, J.L., Chaves-Fallas, J.M., Holl, K.D. & Zahawi, R.A. (2016) Tropical forest restoration enriches vascular epiphyte recovery. Applied Vegetation Science, 19, 508-517. doi: 10.1111/avsc.12234

Reid, J.L., Holl, K.D. & Zahawi, R.A. (2015) Seed dispersal limitations shift over time in tropical forest restoration. Ecological Applications, 25, 1072-1082. doi: 10.1890/14-1399.1

Reid, J.L., Mendenhall, C.D., Rosales, J.A., Zahawi, R.A. & Holl, K.D. (2014) Landscape context mediates avian habitat choice in tropical forest restoration. Plos One, 9, e90573. doi: 10.1371/journal.pone.0090573

Reid, J.L., Mendenhall, C.D., Zahawi, R.A. & Holl, K.D. (2015) Scale-dependent effects of forest restoration on Neotropical fruit bats. Restoration Ecology, 23, 681-689. doi: 10.1111/rec.12235

Reid, J.L., Wilson, S.J., Bloomfield, G.S., Cattau, M.E., Fagan, M.E., Holl, K.D. & Zahawi, R.A. (2017) How long do restored ecosystems persist? Annals of the Missouri Botanical Garden, 102, 258-265. doi: 10.3417/2017002

Rey Benayas, J.M., Altamirano, A., Miranda, A., Catalán, G., Prado, M., Lisón, F. & Bullock, J.M. (2020) Landscape restoration in a mixed agricultural-forest catchment: Planning a buffer strip and hedgerow network in a Chilean biodiversity hotspot. Ambio, 49, 310-323. doi: 10.1007/s13280-019-01149-2

Rey Benayas, J.M., Bullock, J.M. & Newton, A.C. (2008) Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Frontiers in Ecology and Environment, 6, 329-336. doi: 10.1890/070057

Rey Benayas, J.M., Martínez-Baroja, L., Pérez-Camacho, L., Villar-Salvador, P. & Holl, K.D. (2015) Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. New Forests, 46, 841-853. doi: 0.1007/s11056-015-9490-8

Robinson, G.R. & Handel, S.N. (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. Ecological Applications, 10, 174-188.

Saha, S., Kuehne, C. & Bauhus, J. (2016) Lessons learned from oak cluster planting trials in central Europe. Canadian Journal of Forest Research, 47, 139-148. doi: 10.1139/cjfr-2016-0265

Sansevero, J.B.B., Prieto, P.V., de Moraes, L.F.D. & Rodrigues, P.J.P. (2011) Natural regeneration in plantations of native trees in lowland Brazilian atlantic forest: community structure, diversity, and dispersal syndromes. Restoration Ecology, 19, 379-389. doi: 10.1111/j.1526-100X.2009.00556.x

Shoo, L.P. & Catterall, C.P. (2013) Stimulating natural regeneration of tropical forest on degraded land: approaches, outcomes, and information gaps. Restoration Ecology, 21, 670-677. doi: 10.1111/rec.12048

Silliman, B.R., Schrack, E., He, Q., Cope, R., Santoni, A., van der Heide, T., . . . van de Koppel, J. (2015) Facilitation shifts paradigms and can amplify coastal restoration efforts. Proceedings of the National Academy of Sciences, 112**,** 14295-14300. doi: 10.1073/pnas.1515297112

Stanturf, J.A., Palik, B.J. & Dumroese, R.K. (2014) Contemporary forest restoration: a review emphasizing function. Forest Ecology and Management, 331**,** 292-323. doi: 10.1016/j.foreco.2014.07.029

van Breugel, M., Bongers, F. & Martınez-Ramos, M. (2007) Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. Biotropica, 39**,** 610-619. doi: 10.1111/j.1744-7429.2007.00316.x

Yarranton, G.A. & Morrison, R.G. (1974) Spatial dynamics of a primary succession: nucleation. Journal of Ecology, 62**,** 417-428.

Zahawi, R.A. & Augspurger, C.K. (1999) Early plant succession in abandoned pastures in Ecuador. Biotropica, 31**,** 540-552.

Zahawi, R.A. & Augspurger, C.K. (2006) Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. Ecological Applications, 16**,** 464-478. doi: 10.1890/1051-0761

Zahawi, R.A., Dandois, J.P., Holl, K.D., Nadwodny, D., Reid, J.L. & Ellis, E.C. (2015) Using lightweight unmanned aerial vehicles to monitor tropical forest recovery. Biological Conservation, 186**,** 287-295. doi: 10.1016/j.biocon.2015.03.031

Zahawi, R.A., Duran, G. & Kormann, U. (2015) Sixty-seven years of land-use change in southern Costa Rica. Plos One, 10**,** e0143554. doi: 10.1371/journal.pone.0143554

Zahawi, R.A. & Holl, K.D. (2009) Comparing the performance of tree stakes and seedlings to restore abandoned tropical pastures. Restoration Ecology, 17**,** 854-864. doi: 10.1111/j.1526-100X.2008.00423.x

Zahawi, R.A., Holl, K.D., Cole, R.J. & Reid, J.L. (2013) Testing applied nucleation as a strategy to facilitate tropical forest recovery. Journal of Applied Ecology, 50**,** 88-96. doi: 10.1111/1365-2664.12014

Zahawi, R.A. & Reid, J.L. (2018) Tropical secondary forest enrichment using giant stakes of keystone figs. Perspectives in Ecology and Conservation, 16**,** 133-138. doi: 10.1016/j.pecon.2018.06.001

Zahawi, R.A., Reid, J.L. & Holl, K.D. (2014) Hidden costs of passive restoration. Restoration Ecology, 22**,** 284-287. doi: 10.1111/rec.12098

Tables and Figures

Table 1. Site characteristics.

Site	Year planted	Year site lost	Elevation (m)	Forest cover within 500 m (%)	Ref. forest[1]	Past land uses
AC	2005		1430	48-50	No	Corn and beans (4 yr), fallow (12–14 yr), pasture (13 yr)
BB	2004		1290	36-38	No	Pasture (10 yr), coffee (32 yr)
BR	2004	2012	1060	13-17	No	Coffee (35 yr), pasture (20 yr)
CD	2004	2009	1160	32-40	No	Coffee (16 yr), pasture and orange trees (2 yr)
EC	2006		1180	40-48	No	Coffee (16 yr), beans (15 yr), fallow (17 yr)
GN	2005	2015	1170	43-44	No	Pasture (47 yr)
HB	2005		1120	23-25	No	Coffee (25 yr), pasture (8 yr), fallow (4 yr)
JG	2005		1180	65-71	yes	Mixed simultaneous uses: mostly beans (35 yr) and fallow (5 yr), partly coffee (30 yr) and pasture (10 yr)

Table 1. Site Characteristics (continued)

Site	**Year planted**	**Year site lost**	**Elevation (m)**	**Forest within 500 m (%)**	**Ref. forest[1]**	**Past land uses**
LL	2004		1160	50-54	yes	Pasture (17 yr), vegetables (5 yr), coffee (7 yr), beans (5 yr), fallow (15 yr)
MM	2004		1100	71-89	yes	Pasture (>40 yr), fallow (4 yr)
OM	2005		1120	24-25	yes	Beans and corn (10 yr), pasture (5 yr), coffee (5 yr), fallow (5 yr)
RS	2004		1190	36-40	yes	Mixed simultaneous uses: mostly pasture (10 yr), coffee (20 yr), corn and beans (2 yr), intermittently grazed pasture (20 yr)
SC	2006		1110	43-44	no	Pasture (30 yr), beans (3 yr), fallow (4 yr)
SG	2004		1110	11-16	no	Coffee (25 yr), fallow (3 yr), pasture (4 yr)
SP	2006		1330	57-63	yes	Pasture (33 yr)

[1] Indicates whether there is a reference forest plot near the site

Table 2. Percent woody canopy in the 2-5 m, >5 m, and overall canopy strata in three restoration treatments in 2019. Vegetation point-intercepts were recorded at 96 points along systematic transects at n = 12 sites per treatment. Values are means ± 1 SE. Means with the same letter do not differ significantly using Tukey's multiple-comparison test.

Treatment	**2-5 m**	**>5 m**	**Overall canopy**
Natural regeneration	63.4 ± 5.3[a]	11.0 ± 2.4[a]	73.9 ± 4.7[a]
Applied nucleation	63.2 ± 3.5[a]	35.1 ± 6.0[b]	93.4 ± 2.1[b]
Plantation	43.2 ± 4.9[b]	55.7 ± 5.5[c]	98.7 ± 0.8[c]

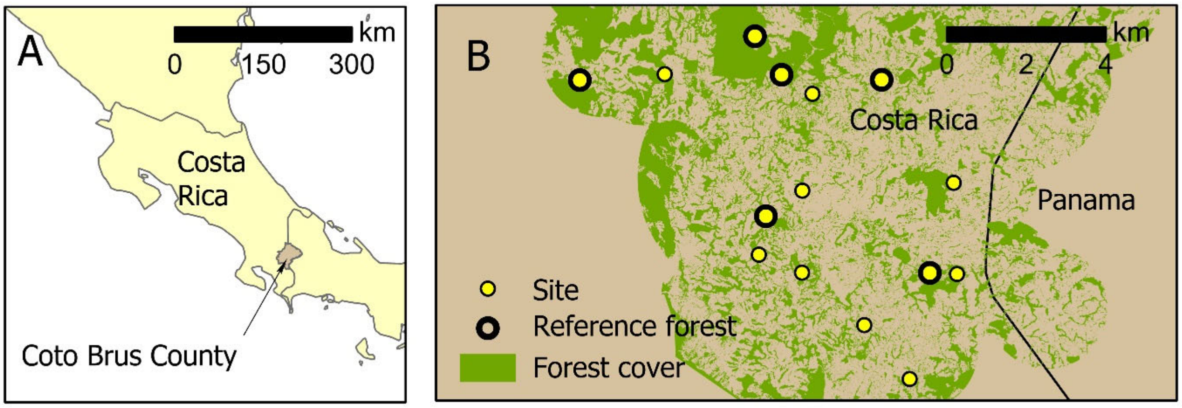
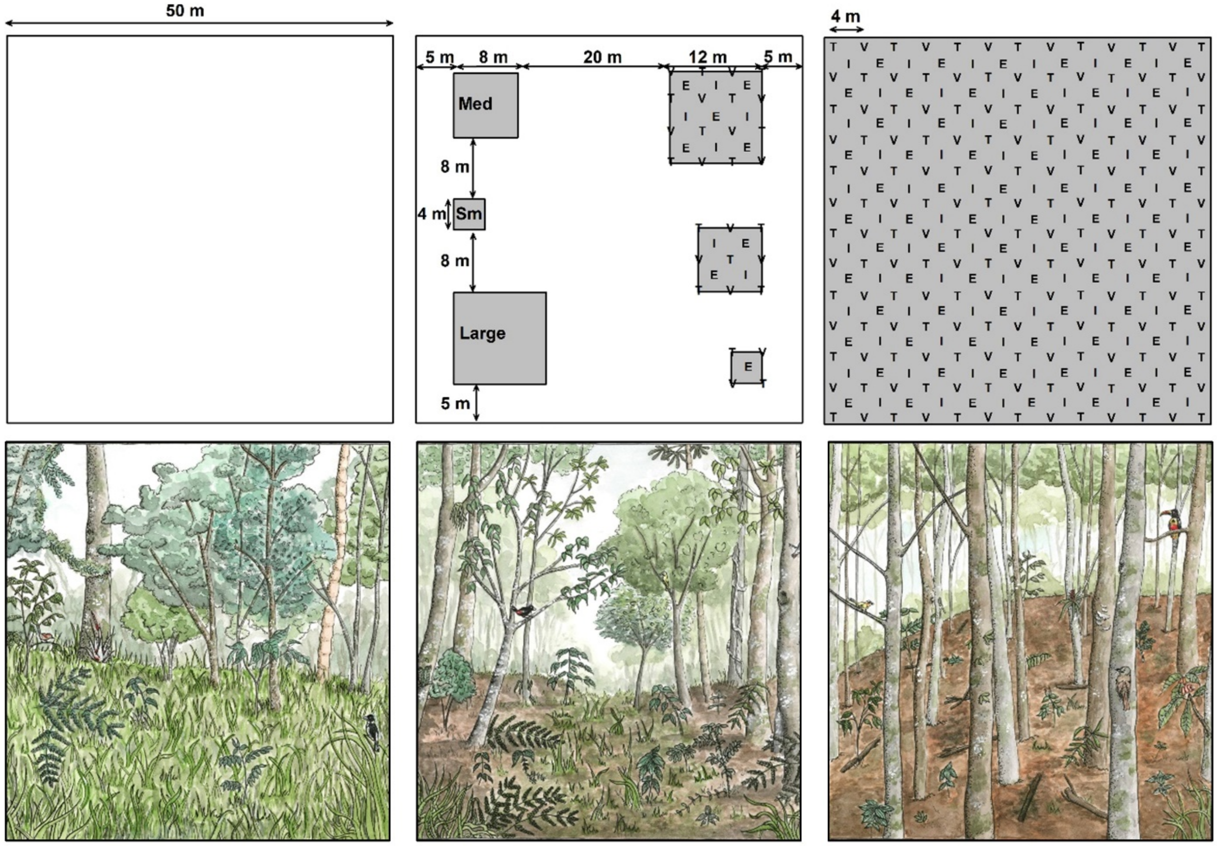


Figure 1. Study area (A) and the 15 study sites from which data were collected in southern Costa Rica (B). Forest cover data are from Mendenhall et al. (2011).



Natural regeneration

Applied nucleation

Plantation

Figure 2. Top panels detail the original planting design and bottom panels illustrate the plots after 15 years showing both planted and naturally recruited vegetation. In top panels gray areas were planted with *Erythrina poeppigiana* (E), *Inga edulis* (I), *Terminalia amazonia* (T), and *Vochysia guatemalensis* (V). Sm = small; Med = medium. Artist credit: Michelle Pastor

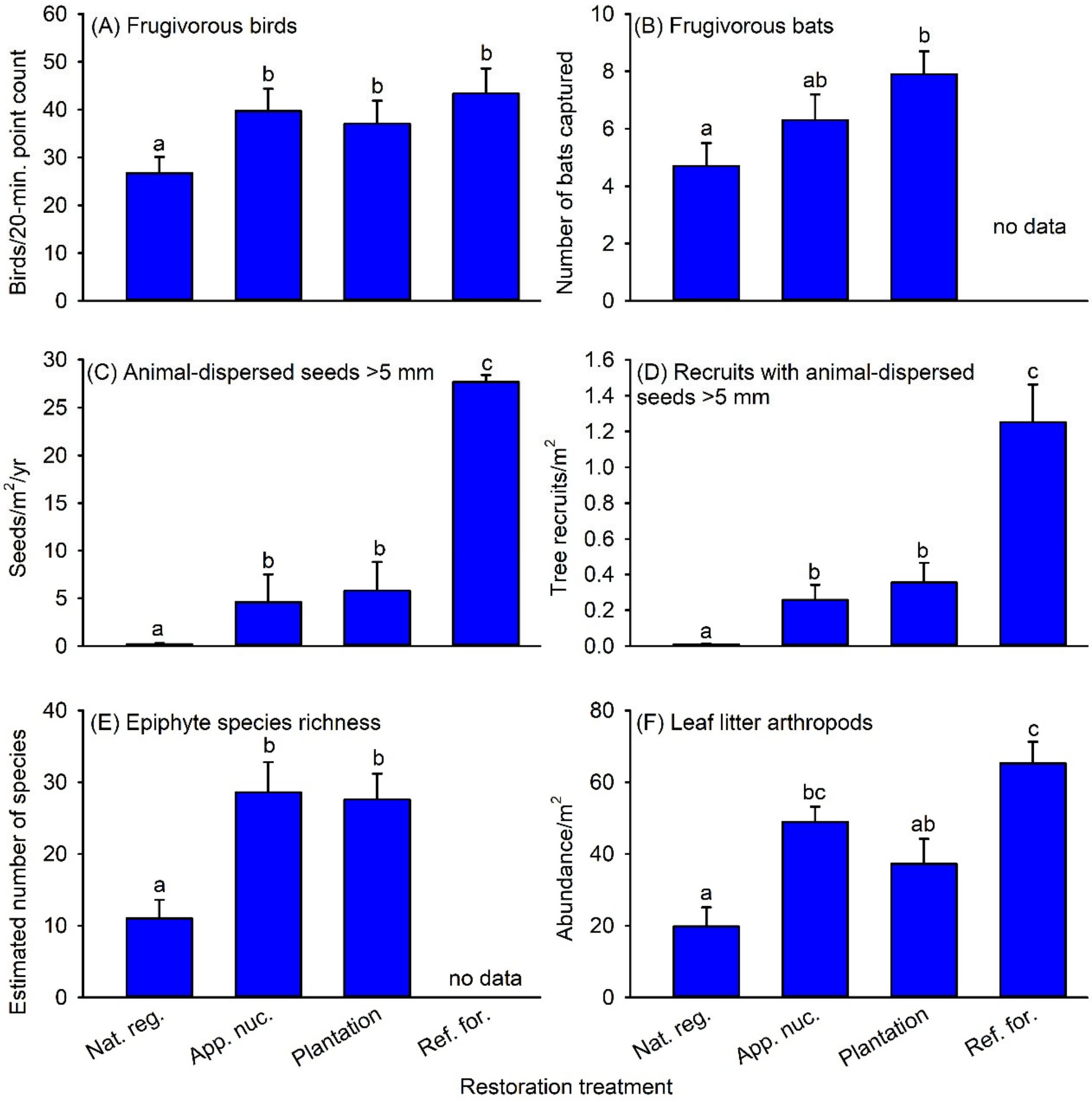


Figure 3. Responses of ecological variables to forest restoration treatments. A. Frugivorous bird abundance in 2016 (n = 11 sites, Reid et al. unpublished data); B. Frugivorous bat abundance in 2009 and 2012 (n = 10, Reid et al., 2015); C. Abundance of animal-dispersed seed >5 mm in 2012-2013 (n = 10, Reid, Holl & Zahawi, 2015); D. Abundance of recruits with animal-dispersed seeds >5 mm in 2015 (n = 13, Holl et al., 2017); E. Estimated species richness of epiphytes in 2015 based on sample-based accumulation curves (n = 13, Reid et al., 2016); and H. Leaf litter arthropods in 2012 (n = 4, Cole et al., 2016). Values are means ± 1 SE. Means with the same letter do not differ significantly using Tukey's multiple-comparison test among treatments.

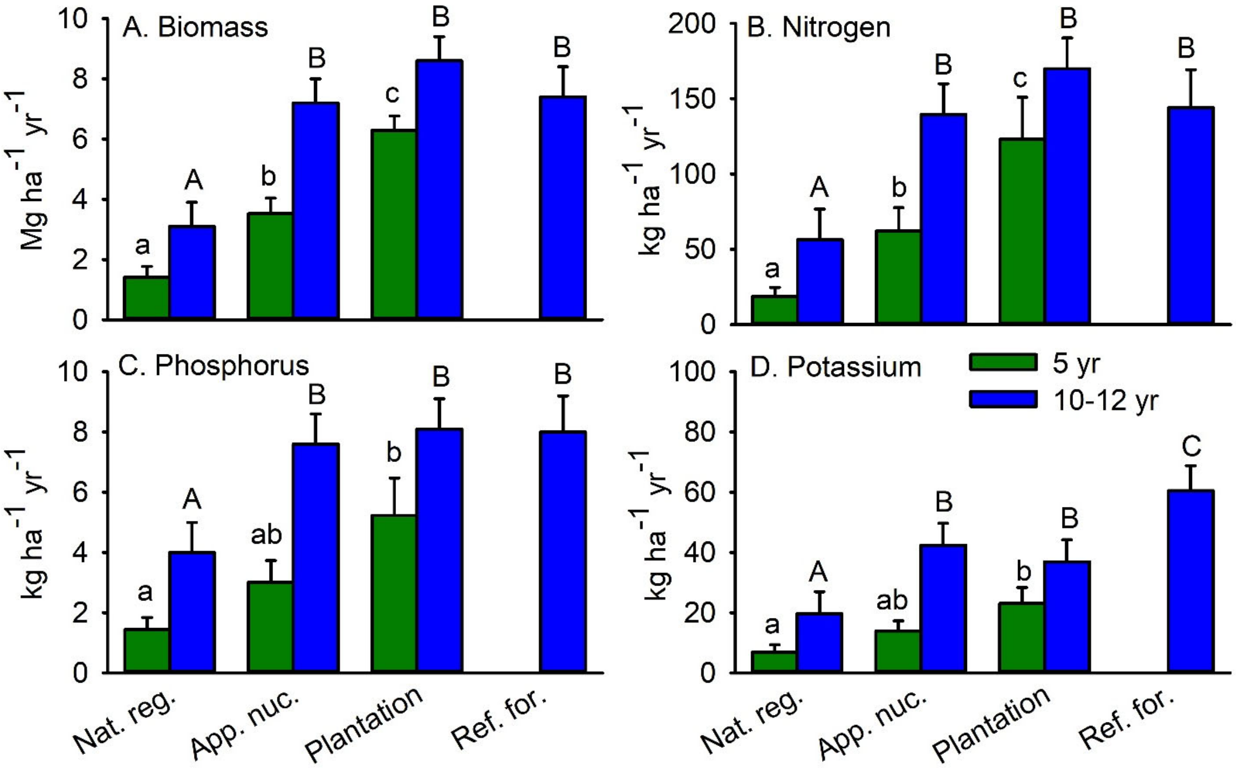


Figure 4. Litterfall biomass and nutrient inputs in restoration treatments after 5 years (n = 6, Celentano et al., 2011) and 10-12 years (n = 5 for restoration treatments, n = 3 for reference forest, Lanuza et al., 2018). Data were only collected in reference forests after 10-12 years. Values are means ± 1 SE. Means with the same letter do not differ significantly using Tukey's multiple-comparison test among treatments; small letters compare 5-yr measurements and capital letters compare 10-12-yr measurements.

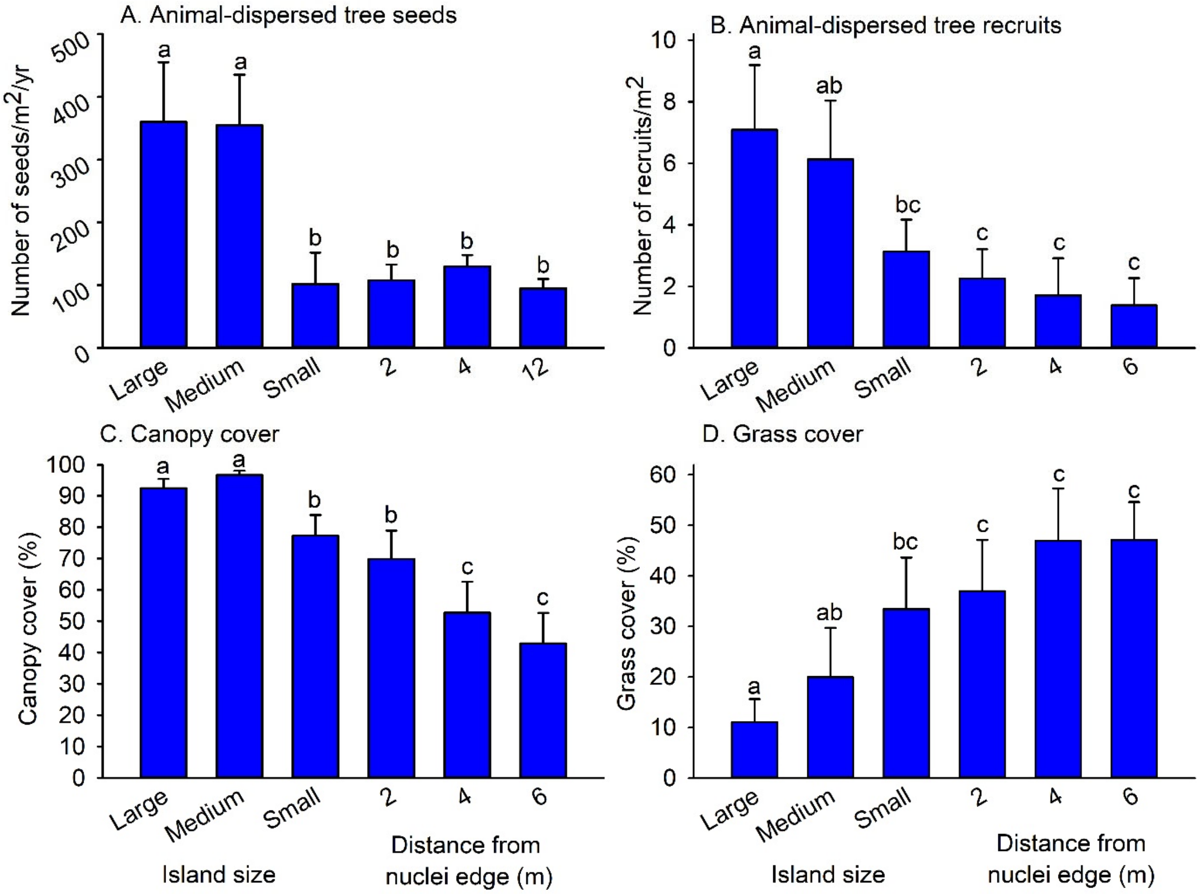


Figure 5. Number of (A) animal-dispersed seeds, (B) tree recruits, (C) canopy cover and (D) grass cover at different locations within applied nucleation plots. Large nuclei = 12 × 12 m planted, medium = 8 × 8 m, small = 4 × 4 m. Values are means ± 1 SE for n = 11 plots for seed deposition in 2006-2008 (Cole, Holl & Zahawi, 2010), n = 8 plots for recruit data and vegetation structure in 2010 (Zahawi et al., 2013, unpub. data). Means with the same letter do not differ significantly using Tukey's multiple-comparison test across locations.