RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

OPINION ARTICLE

A call for practical spatially patterned forest restoration methods

Karen D. Holl[1,2], J. Leighton Reid[3], Rakan A. Zahawi[1,4,5], Ludmila P. de Siqueira[6,7], Pedro H. S. Brancalion[7,8]

Applied nucleation and other spatially patterned restoration methods are promising approaches for scaling up projects to meet ambitious international restoration commitments in an ecologically and economically sound manner. Much of the corresponding literature to date, however, has centered around theoretical discussions and small-scale studies that are largely divorced from constraints faced by restoration practitioners. We briefly review recent academic literature about applied nucleation and other spatially patterned restoration methods and discuss practical challenges to their implementation. We offer several recommendations to move spatially patterned restoration from an academic conversation to scalable application, including: (1) comparing different planting designs and natural regeneration within the same system at an appropriate scale; (2) monitoring ecological outcomes throughout the restored area over sufficient time to evaluate recovery; (3) quantifying costs and documenting other logistical constraints to implementation; and (4) exploring methods for using unplanted areas to provide benefits to landholders until planted vegetation establishes.

Key words: applied nucleation, assisted natural regeneration, cost, large-scale restoration, strip planting

Implications for Practice

- Spatially patterned restoration methods should be included in the toolbox of restoration approaches and used more widely when they are consistent with project goals.
- Collaborations between academic researchers and restoration practitioners are key to developing spatially patterned restoration methods that are scalable, cost-effective, and tailored to local ecological, social, and logistical conditions.
- Planting designs should be tailored to heterogeneous site conditions such as land contour, soils, hydrology, and preexisting or rapidly regenerating vegetation.
- Implementing spatially patterned restoration methods will require training restoration crews and educational outreach to local landholders and communities.

Introduction

Given ambitious international commitments and regional policies to restore forests and other ecosystems globally (e.g. the Bonn Challenge, the UN Decade on Ecosystem Restoration, and the European Union Nature Restoration Law), there is a critical need for practical and cost-effective methods that are scalable to hundreds or thousands of hectares (Brancalion & Holl 2024). Many forest restoration projects plant native tree seedlings to both reintroduce a subset of desired species and accelerate the recovery process, but major challenges to the rapid scaling of these efforts include budget constraints and an insufficient seed and seedling supply chain (Fargione et al. 2021; National Academy of Sciences 2023). Alternative strategies that can address these constraints include applied nucleation (i.e. planting patches or clusters of trees) and other spatially patterned revegetation methods (e.g. strip planting) (Corbin & Holl 2012; Shaw et al. 2020; Fargione et al. 2021). Our and others' work shows that these methods can be effective in catalyzing forest recovery over the first decade or two in some systems (Table S1; e.g. Saha et al. 2013; Corbin et al. 2016; Holl et al. 2020). These methods, however, have been primarily tested experimentally and discussed amongst academics (e.g. Corbin & Holl 2012; Michaels et al. 2021, 2024; de Oliveira Bahia et al. 2023), and have rarely been implemented at large spatial scales. It is critical to move beyond academic conversations and work with practitioners to design and rigorously evaluate these methodologies in real-world and expansive settings.

Author contributions: KDH conceived of the paper, the content of which draws heavily on prior discussions with JLR, RAZ, LPdS, PHSB; KDH wrote and revised the manuscript; JLR, RAZ, LPdS, PHSB edited the manuscript.

[1]Environmental Studies Department, University of California, Santa Cruz, CA, U.S.A.
[2]Address correspondence to K. D. Holl, email kholl@ucsc.edu
[3]School of Plant and Environmental Sciences, Virginia Tech, Blacksburg, VA, U.S.A.
[4]Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador
[5]School of Life Sciences, University of Hawaii at Mānoa, Honolulu, HI, U.S.A.
[6]Conservation International, Campinas, SP, Brazil
[7]Department of Forest Sciences, "Luiz de Queiroz" College of Agriculture, University of São Paulo, Piracicaba, SP, Brazil
[8]Re.green, Rio de Janeiro, RJ, Brazil

doi: 10.1111/rec.14266
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14266/suppinfo

Varied Definitions and Past Research

Ecosystems often regenerate patchily where initial vegetation colonists establish in clusters that spread over time (e.g. Archer et al. 1988; Franks 2003), a process referred to as "nucleation" (Yarranton & Morrison 1974). We and others have used the term applied nucleation to refer to a restoration approach in which patches of vegetation (referred to variably as "nuclei," "tree islands," or "woodland islets") are actively seeded or planted to accelerate forest recovery (Robinson & Handel 2000; Corbin & Holl 2012; Rey Benayas et al. 2015). This definition follows on the model of Yarranton and Morrison (1974), namely that initial vegetation clusters facilitate recovery by multiple mechanisms, including attracting seed dispersing animals thereby enhancing seed dispersal, creating favorable conditions for seedling recruitment both within and at the edge of nuclei (e.g. reducing grass competition, moderating microclimatic extremes, and increasing nutrient availability), and spreading over time through the growth of planted vegetation and enhanced recruitment within and at the edge of nuclei.

Michaels et al. (2024) and Eppinga et al. (2023) make the important point that introducing mutualists, such as mycorrhizae, is critical to the success of nuclei establishment. They highlight the mechanisms discussed above by which nuclei can facilitate the recovery process, as well as by concentrating resources (e.g. soil nutrients and water) within planted nuclei, particularly in arid systems. They argue for the importance of distinguishing between "analogy with nucleation" (i.e. nucleation that depends on outside inputs, such as seed dispersal) and "autocatalytic nucleation" (i.e. creating positive feedbacks for the establishment and growth of species within the patch). We contend that these mechanisms are not mutually exclusive, as recovery of all ecosystems depends on colonization by the many plant, animal, and microbial species that are not actively reintroduced in restoration, as well as on suitable habitat for their establishment.

Others have used the term "nucleation" to refer to a more expansive suite of restoration methods (Bechara et al. 2021; de Oliveira Bahia et al. 2023), which includes not only seeding or planting vegetation nuclei, but also incorporating various faunal attractants (e.g. bird perches, bat boxes, and brush piles for nesting) and/or transferring small quantities of topsoil, litter, or seed rain collected from less disturbed habitat. While these methods are interesting, they are not consistent with the original nucleation model (sensu Yarranton & Morrison 1974), nor are they scalable. Although bird perches and bat boxes often enhance faunal activity and seed dispersal over the short-term (Kelm et al. 2008; de Oliveira Bahia et al. 2023; Mayta et al. 2024), they do not improve local conditions for seedling establishment and growth (Reid & Holl 2013) and have short-term impacts (e.g. many bird perches decompose within a few years). In contrast, once established, trees attract dispersers and modify microsite conditions continuously. Moreover, key to the nucleation model of succession is that vegetation nuclei not only establish but also spread over time, which may be slow and highly unpredictable (Rey Benayas et al. 2015; Ursell & Safford 2022). Yet, few studies have monitored seedling establishment adjacent to actively restored patches to assess whether they increase in size over time (e.g. Table S1; Mayta et al. 2024). Finally, these methods have mostly been tested in plot sizes less than 1–2 m^2 (e.g. Pilon et al. 2018; La Mantia et al. 2019; Rojas-Botero et al. 2020) and, to our knowledge, have not been implemented by practitioners at scale.

Shaw et al. (2020) highlight that vegetation can be planted or seeded in alternative patterns besides clusters (e.g. strips), achieving a similar effect of establishing vegetation in a portion of a restored area that facilitates recovery both within and beyond the edges of the planted area, a term they call "spatially patterned restoration methods." We adopt this broader terminology, recognizing that to be most effective and scalable, planting designs should be site and ecosystem specific. Spatially patterned restoration methods, including applied nucleation, have been discussed in a range of ecosystems, including grasslands, shrublands, and wetlands (e.g. Hulvey et al. 2017; Gornish et al. 2019; Michaels et al. 2021), though here we focus on forests.

Application in Restoration Projects

While academic discussions of spatially patterned methods continue and claim to inform restoration efforts (Holl et al. 2020; de Oliveira Bahia et al. 2023; Michaels et al. 2024), they are largely divorced from the reality of practitioners implementing restoration projects, who are increasingly working at scales of hundreds to thousands of hectares to meet growing restoration demand. Based on our implementation of experiments using spatially patterned restoration methods to restore tropical forests in three countries (0.25–1.5 ha plots in Brazil, Costa Rica, and Ecuador), and conversations with multiple restoration practitioners who have tried to apply these methods in projects ranging from tens to hundreds of hectares in Brazil, we assert that the factors affecting implementation of spatially patterned restoration differ substantially from those being discussed in the academic literature. Not surprisingly, practitioners face mostly social and logistical, rather than ecological constraints.

First, with spatially patterned restoration approaches—as well as natural regeneration and assisted natural regeneration—landholders often perceive the unplanted area as "messy" and "unproductive" land that should be used for grazing livestock, agriculture, or other uses (Zahawi et al. 2014; Chazdon et al. 2020). This increases the risk of livestock damaging plantings (Zahawi et al. 2014). Second, unplanted areas often have a dense cover of invasive grasses, ferns, and other ruderal vegetation, which is objectionable to some landowners and increases the risk of accidental or intentional fire (Hill 2018) that can set back forest recovery in both unplanted and planted areas. Controlling this vegetation increases project costs. Third, planting or seeding in nuclei rather than straight lines can be more challenging and make it more difficult to locate planted seedlings, which may result in inadvertent seedling damage when controlling competitive vegetation during the first few years (Holl et al. 2011).

Finally, the most appropriate spatial planting pattern depends heavily on local constraints, such as tree growth rates, terrain, planting methods, costs, and plant availability, rather than theoretical predictions from academic models. For example, Brancalion and Holl (unpublished data) compared planting nuclei and strips of tree seedlings on flat terrain in semi-deciduous Brazilian Atlantic forest where planting and soil preparation are mechanized in rows and found that the cost of planting nuclei was 1.5–1.7 times greater than planting a similar area in strips. In contrast, in mountainous regions with undulating terrain where planting is done manually (e.g. Costa Rica and Ecuador), planting nuclei or in other spatial patterns tailored to the topography is more feasible and cost-effective.

Despite these obstacles, interest remains high amongst practitioners to develop practical, spatially patterned restoration methods, largely because of the insufficient seed and seedling supply chain, as well as limited funding for full planting and maintenance of native species. That said, many restoration projects are under substantial pressure to meet strict short-term objectives (e.g. the amount of trees planted or carbon sequestered) or compliance with legal requirements (Chaves et al. 2015). These make it untenable to use spatially patterned restoration or assisted natural regeneration methods that are minimally tested and often have more variable outcomes (Chazdon et al. 2020; Bechara et al. 2021).

Transforming Spatially Patterned Methods Into Scalable Strategies

Given the urgent need to develop practical methods to restore ecosystems at scale to meet restoration commitments, slow down biodiversity loss, mitigate greenhouse gas emissions, and more, it is time to move beyond terminology and theoretical academic discussions to develop spatially patterned restoration methods that are ecologically sound, as well as socially and economically viable. We offer several recommendations to achieve this transformation (Table 1).

First, research should focus on testing methods that are logistically, financially, and socially acceptable at scale (Ramírez-Soto et al. 2018). These methods should be compared to standard approaches of natural regeneration and plantation-style tree planting either in large experimental plots or in restoration projects in collaboration with practitioners. Of course, which methods are feasible at different locations will depend on project goals, landholding size, terrain, and many other factors.

Second, collaborative research between scientists and practitioners is key to guiding the amount and spatial distribution of revegetation efforts across a given site. Past research suggests that a minimum nuclei size of approximately 64 m^2 is needed to attract seed dispersing birds and shade out pasture grasses in tropical moist forests (Zahawi & Augspurger 2006; Holl et al. 2020), but the minimum vegetation patch size will vary with ecosystem type and disperser behavior (Morán-López et al. 2023). More research is needed on the rate of spread of planted vegetation, which affects appropriate spacing, as well as whether planting in strips, nuclei, or other spatial arrangements is most effective in a given system (Corbin & Holl 2012; Holl et al. 2020). Incorporating such considerations into restoration planning will help guide the important question of the minimum area that needs to be planted. For example, in some projects in Brazil, practitioners are only planting 1–5% of the overall restored area, which is unlikely to catalyze forest recovery within a reasonable time frame (Brancalion & Holl unpublished data; Procknow et al. 2023). Most academic studies have focused on systematic planting in clusters or strips, when the most practical and cost-effective designs will be tailored to local within-site heterogeneity (e.g. soils, topography, and pre-existing vegetation), such as actively planting areas where natural regeneration is slow and planting along topographic contours or waterways to minimize erosion and improve water quality (Wilson et al. 2021). Rapidly evolving drone technologies that allow targeted seeding to small-scale, within-site heterogeneity hold promise for cost-effectively implementing spatially patterned methods, but need additional testing (Castro et al. 2024).

Table 1. Recommendations for future spatially patterned restoration research and implementation.

- Conduct collaborative research between academic researchers and restoration practitioners to test methods that are practical and scalable.
- Compare spatially patterned methods to more common restoration approaches (e.g. natural regeneration and plantation-style planting).
- Evaluate spatially patterned methods in different socio-ecological systems (e.g. ecosystem types, native vegetation cover in the landscape, local site resilience, land uses, and regulatory environments).
- Test different planting designs, including shape, size, and distance between planted areas, and percentage area planted, to determine which patterns work most effectively to meet restoration goals in specific systems.
- Evaluate different species compositions for planting, considering effectiveness in enhancing seed dispersal and seedling establishment, shading out ruderal vegetation, sequestering carbon, and/or providing resources to landowners (e.g. fruit and firewood).
- Tailor planting designs to heterogeneous site conditions such as land contour, soils, hydrology, preexisting (e.g. remnant trees), or rapidly regenerating vegetation.
- Quantify costs and other logistical constraints to implement different planting designs.
- Explore methods for using unplanted areas to provide benefits to landholders while native vegetation establishes in planted areas.
- Monitor the effects of spatially patterned restoration throughout a restoration site and not just in actively revegetated areas, and over a sufficient time frame to evaluate the recovery of naturally colonizing species.
- Create education and training materials for restoration staff and community members about cost, benefits, and guidance for implementing spatially patterned planting methods.

Third, it is critical to compare the costs and logistical obstacles of spatially patterned methods to more common restoration approaches (Ramírez-Soto et al. 2018; Shaw et al. 2020; Wilson et al. 2021; Toro et al. 2024). Yet costs are rarely reported (Table S1). One argument favoring applied nucleation is that it is cheaper for a given seedling spacing than fully planting a site, and some of us have written previously that the cost of spatially patterned methods scales to the area planted (Holl et al. 2020). In contrast, some authors in this article (P.H.S.B., L.P.d.S.) and others (Ramírez-Soto et al. 2018) report that spatially patterned restoration plantings are more expensive per area planted relative to plantation-style plantings due to the complex planting pattern and additional weed control required. Relative costs will vary depending on many factors (e.g. labor costs, whether planting can be mechanized, the extent of weed control required), so careful documentation is key to selecting the most practical spatially patterned method in each system.

Fourth, it is important to test strategies for managing unplanted areas of restoration sites that could provide income to landowners and reduce weed control costs in the early years while planted vegetation becomes established, after which these uses would cease. For example, Brancalion et al. (2020) found that interplanting strips of exotic eucalyptus with native Brazilian Atlantic forest tree species and harvesting eucalyptus after 4–5 years defrayed 44–75% of restoration implementation costs without inhibiting recovery in the native tree strips. This approach is now being applied on a large scale in Mato Grosso. Alternatively, unplanted areas could be used for small-scale agricultural production for a few years as a form of agro-successional restoration (Vieira et al. 2009).

Finally, evaluating the efficacy of different spatially patterned methods requires monitoring both within and outside planted areas over multiple years (Holl et al. 2020), as successful spatially patterned restoration methods must facilitate recovery throughout the restored area and not just the actively revegetated areas that are typically monitored. Whether the recovery process is fast enough to meet restoration goals can only be determined through sufficient spatial and temporal monitoring.

In summary, applied nucleation specifically and spatially patterned restoration methods more generally, offer a promising intermediate-intervention restoration approach with the potential to actively introduce some species, accelerate natural recovery of others, increase carbon accumulation, and reduce variability in recovery rates, as compared to natural regeneration. These approaches also enhance habitat heterogeneity (Holl et al. 2013) and reduce project costs and seedling supply needs relative to standard plantation-style restoration. However, scaling up spatially patterned methods will require education and training for restoration implementation groups and landholders who are not familiar with these approaches (Ramírez-Soto et al. 2018; Wilson et al. 2021). While we recognize that spatially patterned methods will not be appropriate in all cases (e.g. when rapid carbon sequestration is the primary goal; where key seed dispersing fauna have been extirpated; where natural regeneration is dominated by invasive species), they should be considered within the toolbox of restoration methods with the planting shape, size, and area adjusted to local ecological and social conditions and project constraints.

Acknowledgments

This work was supported by the MacArthur Foundation Chair at University of California Santa Cruz held byK.D.H. and by funding from the U.S. National Science Foundation to K.D.H. and R.A.Z. We appreciate helpful feedback on the manuscript from Jeff Corbin, Elise Gornish, and an anonymous reviewer. This research was supported by a University of California Macarthur Foundation Endowed Chair to K.D.H. and U.S. National Science Foundation grants to K.D.H. and R.A.Z.

LITERATURE CITED

Archer S, Scifres C, Bassham CR, Maggio R (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 58:111–128. https://doi.org/10.2307/1942463

Bechara FC, Trentin BE, Lex Engel V, Estevan DA, Ticktin T (2021) Performance and cost of applied nucleation versus high-diversity plantations for tropical forest restoration. Forest Ecology and Management 491:119088. https://doi.org/10.1016/j.foreco.2021.119088

Brancalion PHS, Amazonas NT, Chazdon RL, van Melis J, Rodrigues RR, Silva CC, Sorrini TB, Holl KD (2020) Exotic eucalypts: from demonized trees to allies of tropical forest restoration? Journal of Applied Ecology 57:55–66. https://doi.org/10.1111/1365-2664.13513

Brancalion PHS, Holl KD (2024) Upscaling ecological restoration by integrating with agriculture. Frontiers in Ecology and the Environment 22 (in press). https://doi.org/10.1002/fee.2802

Castro J, Alcaraz-Segura D, Baltzer JL, Amorós L, Morales-Rueda F, Tabik S (2024) Automated precise seeding with drones and artificial intelligence: a workflow. Restoration Ecology 32:e14164. https://doi.org/10.1111/rec.14164

Chaves RB, Durigan G, Brancalion PHS, Aronson J (2015) On the need of legal frameworks for assessing restoration projects success: new perspectives from São Paulo state (Brazil). Restoration Ecology 23:754–759. https://doi.org/10.1111/rec.12267

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

Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. Forest Ecology and Management 265:37–46. https://doi.org/10.1016/j.foreco.2011.10.013

Corbin JD, Robinson GR, Hafkemeyer LM, Handel SN (2016) A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. Ecological Applications 26:104–114. https://doi.org/10.1890/15-0075

de Oliveira Bahia T, Martins C, Antonini Y, Cornelissen T (2023) Contribution of nucleation techniques to plant establishment in restoration projects: an integrative review and meta-analysis. Restoration Ecology 31:e13932. https://doi.org/10.1111/rec.13932

Eppinga MB, Michaels TK, Santos MJ, Bever JD (2023) Introducing desirable patches to initiate ecosystem transitions and accelerate ecosystem restoration. Ecological Applications 33:e2910. https://doi.org/10.1002/eap.2910

Fargione J, Haase DL, Burney OT, Kildisheva OA, Edge G, Cook-Patton SC, et al. (2021) Challenges to the reforestation pipeline in the United States. Frontiers in Forests and Global Change 4:629198. https://doi.org/10.3389/ffgc.2021.629198

Franks SJ (2003) Facilitation in multiple life-history stages: evidence for nucleated succession in coastal dunes. Plant Ecology 168:1–11. https://doi.org/10.1023/A:1024426608966

Gornish ES, Shaw J, Gillespie BM (2019) Using strip seeding to test how restoration design affects randomness of community assembly. Restoration Ecology 27:1199–1205. https://doi.org/10.1111/rec.12988

Hill MD (2018) Forest restoration in eastern Madagascar: post-fire survival of select Malagasy tree species. MS thesis, University of Minnesota, Minneapolis.

Holl KD, Reid JL, Cole RJ, Oviedo-Brenes F, Rosales JA, Zahawi RA (2020) Applied nucleation facilitates tropical forest recovery: lessons learned from a 15-year study. Journal of Applied Ecology 57:2316–2328. https://doi.org/10.1111/1365-2664.13684

Holl KD, Stout VM, Reid JL, Zahawi RA (2013) Testing heterogeneity-diversity relationships in tropical forest restoration. Oecologia 173:569–578. https://doi.org/10.1007/s00442-013-2632-9

Holl KD, Zahawi RA, Cole RJ, 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. https://doi.org/10.1111/j.1526-100X.2010.00674.x

Hulvey KB, Leger EA, Porensky LM, Roche LM, Veblen KE, Fund A, Shaw J, Gornish ES (2017) Restoration islands: a tool for efficiently restoring dryland ecosystems? Restoration Ecology 25:S124–S134. https://doi.org/10.1111/rec.12614

Kelm DH, Wiesner KR, Von Helversen O (2008) Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. Conservation Biology 22:733–741. https://doi.org/10.1111/j.1523-1739.2008.00925.x

La Mantia T, Rühl J, Massa B, Pipitone S, Lo Verde G, Bueno RS (2019) Vertebrate-mediated seed rain and artificial perches contribute to overcome seed dispersal limitation in a Mediterranean old field. Restoration Ecology 27:1393–1400. https://doi.org/10.1111/rec.13009

Mayta C, López CL, Villegas M, Aguirre LF, Hensen I, Gallegos SC (2024) Bird perches and artificial bat roosts increase seed rain and seedling establishment in tropical bracken-dominated deforested areas. Restoration Ecology 32:e14197. https://doi.org/10.1111/rec.14197

Michaels TK, Eppinga MB, Angelini C, Holl KD, Bever JD (2021) Can nucleation bridge to desirable alternative stable states? Theory and applications. Bulletin of the Ecological Society of America 103:e01953. https://doi.org/10.1002/bes2.1953

Michaels TK, Eppinga MB, Bever JD (2024) When patches grow themselves: from analogy to autocatalytic processes, the relevance of ecological nucleation for restoration practices. Restoration Ecology 32:e14066. https://doi.org/10.1111/rec.14066

Morán-López T, Rodríguez-Pérez J, Donoso I, Martínez D, Manuel Morales J, García D (2023) Forest recovery through applied nucleation: effects of tree islet size and disperser mobility on tree recruitment in a temperate landscape. Forest Ecology and Management 550:121508. https://doi.org/10.1016/j.foreco.2023.121508

National Academy of Sciences (2023) An assessment of native seed needs and the capacity for their supply: final report. The National Academies Press, Washington, D.C.

Pilon NAL, Buisson E, Durigan G (2018) Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. Restoration Ecology 26:73–81. https://doi.org/10.1111/rec.12534

Procknow D, Rovedder APM, Piaia BB, Camargo B, De Moraes Stefanello M, Da Silva MPKL, da Silva PS, Croda JP, Dreyer JBB (2023) Monitoring ecological restoration of riparian forest: is the applied nucleation effective ten years after implementation in the Pampa? Forest Ecology and Management 538:120955. https://doi.org/10.1016/j.foreco.2023.120955

Ramírez-Soto A, Lucio-Palacio CR, Rodríguez-Mesa R, Sheseña-Hernández I, Farhat FN, Villa-Bonilla B, et al. (2018) Restoration of tropical montane cloud forests: a six-prong strategy. Restoration Ecology 26:206–211. https://doi.org/10.1111/rec.12660

Reid JL, Holl KD (2013) Arrival ≠ survival. Restoration Ecology 21:153–155. https://doi.org/10.1111/j.1526-100X.2012.00922.x

Rey Benayas JM, Martínez-Baroja L, Pérez-Camacho L, Villar-Salvador P, Holl KD (2015) Predation and aridity slow down the spread of 21-year-old planted woodland islets in restored Mediterranean farmland. New Forests 46:841–853. https://doi.org/10.1007/s11056-015-9490-8

Robinson GR, Handel SN (2000) Directing spatial patterns of recruitment during an experimental urban woodland reclamation. Ecological Applications 10:174–188. https://doi.org/10.1890/1051-0761(2000)010[0174:DSPORD]2.0.CO;2

Rojas-Botero S, Solorza-Bejarano J, Kollmann J, Teixeira LH (2020) Nucleation increases understory species and functional diversity in early tropical forest restoration. Ecological Engineering 158:106031. https://doi.org/10.1016/j.ecoleng.2020.106031

Saha S, Kuehne C, Bauhus J (2013) Tree species richness and stand productivity in low-density cluster plantings with oaks (*Quercus robur* L. and *Q. Petraea* [Mattuschka] Liebl.). Forests 4:650–665. https://doi.org/10.3390/f4030650

Shaw JA, Roche LM, Gornish ES (2020) The use of spatially-patterned methods for vegetation restoration and management across systems. Restoration Ecology 28:766–775. https://doi.org/10.1111/rec.13198

Toro L, Torres-Romero F, Salinas SM, Avella-Munoz A, Galatowish S, Secchi S, Powers JS (2024) Cost-effectiveness of management strategies in a nucleation experiment in a tropical dry forest. Restoration Ecology 32:e14094. https://doi.org/10.1111/rec.14094

Ursell T, Safford HD (2022) Nucleation sites and forest recovery under high shrub competition. Ecological Applications 32:e2711. https://doi.org/10.1002/eap.2711

Vieira DLM, Holl KD, Peneireiro FM (2009) Agro-successional restoration as a strategy to facilitate tropical forest recovery. Restoration Ecology 17:451–459. https://doi.org/10.1111/j.1526-100X.2009.00570.x

Wilson SJ, Alexandre NS, Holl KD, Reid JL, Zahawi RA, Celentano D, Sprenkle-Hyppolite S, Werden L (2021) Applied nucleation guide for tropical forests. Conservation International, Crystal City, Virginia.

Yarranton GA, Morrison RG (1974) Spatial dynamics of a primary succession: nucleation. Journal of Ecology 62:417–428. https://doi.org/10.2307/2258988

Zahawi RA, Augspurger CK (2006) Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. Ecological Applications 16:464–478. https://doi.org/10.1890/1051-0761(2006)016[0464:TFRTIA]2.0.CO;2

Zahawi RA, Reid JL, Holl KD (2014) Hidden costs of passive restoration. Restoration Ecology 22:284–287. https://doi.org/10.1111/rec.12098

Supporting Information

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

Table S1. Summary of published studies comparing the effect of planting nuclei of trees (AN) with natural regeneration (NR) and/or plantation-style (PL) plantings on natural recruitment in forest ecosystems.

Coordinating Editor: Elise Gornish

Received: 11 June, 2024; First decision: 4 July, 2024; Revised: 14 August, 2024; Accepted: 14 August, 2024