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A call for practical spatially patterned forest restoration methods

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2

3 **Title: A call for practical spatially patterned forest restoration methods**

4

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24 PHSB edited the manuscript.

25 **Running-head:** Spatially patterned methods for practical restoration

26

27 **Abstract**

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

41

42 **Key Words:** Applied nucleation, assisted natural regeneration, cost, large-scale restoration, strip  
43 planting

44

45

## 46 **Implications for Practice**

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

## 57 **Introduction**

58 Given ambitious international commitments and regional policies to restore forests and other  
59 ecosystems globally (e.g., Bonn Challenge, UN Decade on Ecosystem Restoration, European  
60 Union Nature Restoration Law), there is a critical need for practical and cost-effective methods  
61 that are scalable to hundreds or thousands of hectares (Brancalion & Holl 2024). Many forest  
62 restoration projects plant native tree seedlings to both reintroduce a subset of desired species and  
63 accelerate the recovery process, but major challenges to the rapid scaling of these efforts include  
64 budget constraints and an insufficient seed and seedling supply chain (Fargione et al. 2021;  
65 National Academy of Sciences 2023). Alternative strategies that can address these constraints  
66 include applied nucleation (i.e., planting patches or clusters of trees) and other spatially patterned  
67 revegetation methods (e.g., strip planting)(Corbin & Holl 2012; Shaw et al. 2020; Fargione et al.  
68 2021). Our and others' work shows that these methods can be effective in catalyzing forest  
69 recovery over the first decade or two in some systems (Table S1; e.g., Saha et al. 2013; Corbin et  
70 al. 2016; Holl et al. 2020). These methods, however, have been primarily tested experimentally  
71 and discussed amongst academics (e.g., Corbin & Holl 2012; Michaels et al. 2021; de Oliveira  
72 Bahia et al. 2023; Michaels et al. 2024), and have rarely been implemented at large spatial scales.  
73 It is critical to move beyond academic discussions and work with practitioners to design and  
74 rigorously evaluate these methodologies in real-world and expansive settings.

## 76 **Varied definitions and past research**

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

89 Michaels et al. (2024) and Eppinga et al. (2023) make the important point that  
90 introducing mutualists, such as mycorrhizae, is critical to the success of nuclei establishment.  
91 They highlight the mechanisms discussed above by which nuclei can facilitate the recovery

92 process, as well as by concentrating resources (e.g., soil nutrients, water) within planted nuclei,  
93 particularly in arid systems. They argue for the importance of distinguishing between “analogy  
94 with nucleation” (i.e., nucleation that depends on outside inputs, such as seed dispersal) and  
95 “autocatalytic nucleation” (i.e., creating positive feedbacks for establishment and growth of  
96 species within the patch). We contend that these mechanisms are not mutually exclusive as  
97 recovery of all ecosystems depends on colonization by the many plant, animal, and microbial  
98 species that are not actively reintroduced in restoration, as well as on suitable habitat for their  
99 establishment.

100 Others have used the term “nucleation” to refer to a more expansive suite of restoration  
101 methods (Bechara et al. 2021; de Oliveira Bahia et al. 2023), which includes not only seeding or  
102 planting vegetation nuclei, but also incorporating various faunal attractants (e.g., bird perches,  
103 bat boxes, brush piles for nesting) and/or transferring small quantities of topsoil, litter, or seed  
104 rain collected from less disturbed habitat. While these methods are interesting, they are not  
105 consistent with the original nucleation model (sensu Yarranton & Morrison 1974), nor are they  
106 scalable. Although bird perches and bat boxes often enhance faunal activity and seed dispersal  
107 over the short-term (Kelm et al. 2008; de Oliveira Bahia et al. 2023; Mayta et al. 2024), they do  
108 not improve local conditions for seedling establishment and growth (Reid & Holl 2013) and have  
109 short-term impacts (e.g., many bird perches decompose within a few years). In contrast, once  
110 established, trees attract dispersers and modify microsite conditions continuously. Moreover, key  
111 to the nucleation model of succession is that vegetation nuclei not only establish, but also spread  
112 over time, which may be slow and highly unpredictable (Rey Benayas et al. 2015; Ursell &  
113 Safford 2022). Yet, few studies have monitored seedling establishment adjacent to actively  
114 restored patches to assess whether they increase in size over time (e.g., Table S1; Mayta et al.  
115 2024). Finally, these methods have mostly been tested in plot sizes <1-2 m<sup>2</sup> (e.g., Pilon et al.  
116 2018; La Mantia et al. 2019; Rojas-Botero et al. 2020) and, to our knowledge, have not been  
117 implemented by practitioners at scale.

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

### 127 **Application in restoration projects**

129 While academic discussions of spatially patterned methods continue and claim to inform  
130 restoration efforts (Holl et al. 2020; de Oliveira Bahia et al. 2023; Michaels et al. 2024), they are  
131 largely divorced from the reality of practitioners implementing restoration projects, who are  
132 increasingly working at scales of hundreds to thousands of hectares to meet growing restoration  
133 demand. Based on our implementation of experiments using spatially patterned restoration  
134 methods to restore tropical forests in three countries (0.25-1.5 ha plots in Brazil, Costa Rica, and  
135 Ecuador), and conversations with multiple restoration practitioners who have tried to apply these  
136 methods in projects ranging from tens to hundreds of hectares in Brazil, we assert that the factors  
137 affecting implementation of spatially patterned restoration differ substantially from those being

138 discussed in the academic literature. Not surprisingly, practitioners face mostly social and  
139 logistical, rather than ecological constraints.

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

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

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

168

### 169 **Transforming spatially patterned methods into scalable strategies**

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

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

181 Second, collaborative research between scientists and practitioners is key to guiding the  
182 amount and spatial distribution of revegetation efforts across a given site. Past research suggests  
183 that a minimum nuclei size of ~64 m<sup>2</sup> is needed to attract seed dispersing birds and shade out

184 pasture grasses in tropical moist forests (Zahawi & Augspurger 2006; Holl et al. 2020), but the  
185 minimum vegetation patch size will vary with ecosystem type and disperser behavior (Morán-  
186 López et al. 2023). More research is needed on the rate of spread of planted vegetation, which  
187 affects appropriate spacing, as well as whether planting in strips, nuclei, or other spatial  
188 arrangements is most effective in a given system (Corbin & Holl 2012; Holl et al. 2020).  
189 Incorporating such considerations into restoration planning will help guide the important  
190 question of the minimum area that needs to be planted. For example, in some projects in Brazil  
191 practitioners are only planting 1-5% of the overall restored area, which is unlikely to catalyze  
192 forest recovery within a reasonable time frame (Procknow et al. 2023, Brancalion & Holl unpub.  
193 data). Most academic studies have focused on systematic planting in clusters or strips, when the  
194 most practical and cost-effective designs will be tailored to local within-site heterogeneity (e.g.  
195 soils, topography, pre-existing vegetation), such as actively planting areas where natural  
196 regeneration is slow and planting along topographic contours or waterways to minimize erosion  
197 and improve water quality (Wilson et al. 2021). Rapidly evolving drone technologies that allow  
198 targeted seeding to small-scale, within-site heterogeneity, hold promise for cost-effectively  
199 implementing spatially patterned methods, but need additional testing (Castro et al. 2024).

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

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

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

227 In summary, applied nucleation specifically, and spatially patterned restoration methods  
228 more generally, offer a promising intermediate-intervention restoration approach with the  
229 potential to actively introduce some species, accelerate natural recovery of others, increase

230 carbon accumulation, and reduce variability in recovery rates, as compared to natural  
231 regeneration. These approaches also enhance habitat heterogeneity (Holl et al. 2013) and reduce  
232 project costs and seedling supply needs relative to standard plantation-style restoration.  
233 However, scaling up spatially patterned methods will require education and training for  
234 restoration implementation groups and landholders who are not familiar with these approaches  
235 (Ramírez-Soto et al. 2018; Wilson et al. 2021). While we recognize that spatially patterned  
236 methods will not be appropriate in all cases (e.g., when rapid carbon sequestration is the primary  
237 goal; where key seed dispersing fauna have been extirpated; where natural regeneration is  
238 dominated by invasive species), they should be considered within the toolbox of restoration  
239 methods with the planting shape, size, and area adjusted to local ecological and social conditions  
240 and project budget constraints.

241

242 **Literature Cited**

- 243 Archer S, Scifres C, Bassham CR, Maggio R (1988) Autogenic succession in a subtropical  
244 savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58:111-128
- 245 Barrera-Cataño JI, Garibello J, Moreno-Cárdenas C, Basto S (2023) Trade-offs at applying tree  
246 nucleation to restore degraded high Andean forests in Colombia. *Restoration Ecology*  
247 31:e13753
- 248 Bechara FC, Trentin BE, Lex Engel V, Estevan DA, Ticktin T (2021) Performance and cost of  
249 applied nucleation versus high-diversity plantations for tropical forest restoration. *Forest*  
250 *Ecology and Management* 491:119088
- 251 Brancalion PHS, Amazonas NT, Chazdon RL, Van Melis J, Rodrigues RR, Silva CC, *et al.*  
252 (2020) Exotic eucalypts: From demonized trees to allies of tropical forest restoration?  
253 *Journal of Applied Ecology* 57:55-66
- 254 Brancalion PHS, Holl K, D. (2024) Upscaling ecological restoration by integrating with  
255 agriculture. *Frontiers in Ecology and the Environment*:In press
- 256 Castro J, Alcaraz-Segura D, Baltzer JL, Amorós L, Morales-Rueda F, Tabik S (2024) Automated  
257 precise seeding with drones and artificial intelligence: a workflow. *Restoration Ecology*  
258 32:e14164
- 259 Chaves RB, Durigan G, Brancalion PHS, Aronson J (2015) On the need of legal frameworks for  
260 assessing restoration projects success: new perspectives from São Paulo state (Brazil).  
261 *Restoration Ecology* 23:754-759
- 262 Chazdon RL, Lindenmayer D, Guariguata MR, Crouzeilles R, Rey Benayas JM, Lazos Chavero  
263 E (2020) Fostering natural forest regeneration on former agricultural land through economic  
264 and policy interventions. *Environmental Research Letters* 15:043002
- 265 Corbin JD, Holl KD (2012) Applied nucleation as a forest restoration strategy. *Forest Ecology*  
266 *and Management* 265:37-46
- 267 Corbin JD, Robinson GR, Hafkemeyer LM, Handel SN (2016) A long-term evaluation of applied  
268 nucleation as a strategy to facilitate forest restoration. *Ecological Applications* 26:104-114
- 269 De Oliveira Bahia T, Martins C, Antonini Y, Cornelissen T (2023) Contribution of nucleation  
270 techniques to plant establishment in restoration projects: an integrative review and meta-  
271 analysis. *Restoration Ecology* 31:e13932
- 272 Eppinga MB, Michaels TK, Santos MJ, Bever JD (2023) Introducing desirable patches to initiate  
273 ecosystem transitions and accelerate ecosystem restoration. *Ecological Applications*  
274 33:e2910
- 275 Fargione J, Haase DL, Burney OT, Kildisheva OA, Edge G, Cook-Patton SC, *et al.* (2021)  
276 Challenges to the reforestation pipeline in the United States. *Frontiers in Forests and Global*  
277 *Change* 4:10.3389/ffgc.2021.629198
- 278 Franks SJ (2003) Facilitation in multiple life-history stages: evidence for nucleated succession in  
279 coastal dunes. *Plant Ecology* 168:1-11
- 280 Gornish ES, Shaw J, Gillespie BM (2019) Using strip seeding to test how restoration design  
281 affects randomness of community assembly. *Restoration Ecology* 27:1199-1205
- 282 Hill MD. (2018) Forest restoration in eastern Madagascar: post-fire survival of select Malagasy  
283 tree species. M.S. Thesis, University of Minnesota
- 284 Holl KD, Reid JL, Cole RJ, Oviedo-Brenes F, Rosales JA, Zahawi RA (2020) Applied nucleation  
285 facilitates tropical forest recovery: Lessons learned from a 15-year study. *Journal of Applied*  
286 *Ecology* 57:2316-2328



287 Holl KD, Stout VM, Reid JL, Zahawi RA (2013) Testing heterogeneity-diversity relationships in  
288 tropical forest restoration. *Oecologia* 173:569–578

289 Holl KD, Zahawi RA, Cole RJ, Ostertag R, Cordell S (2011) Planting seedlings in tree islands  
290 versus plantations as a large-scale tropical forest restoration strategy. *Restoration Ecology*  
291 19:470-479

292 Hulvey KB, Leger EA, Porensky LM, Roche LM, Veblen KE, Fund A, *et al.* (2017) Restoration  
293 islands: a tool for efficiently restoring dryland ecosystems? *Restoration Ecology* 25:S124-  
294 S134

295 Kelm DH, Wiesner KR, Von Helversen O (2008) Effects of artificial roosts for frugivorous bats  
296 on seed dispersal in a Neotropical forest pasture mosaic. *Conservation Biology* 22:733-741

297 La Mantia T, Rühl J, Massa B, Pipitone S, Lo Verde G, Bueno RS (2019) Vertebrate-mediated  
298 seed rain and artificial perches contribute to overcome seed dispersal limitation in a  
299 Mediterranean old field. *Restoration Ecology* 27:1393-1400

300 Mayta C, López CL, Villegas M, Aguirre LF, Hensen I, Gallegos SC (2024) Bird perches and  
301 artificial bat roosts increase seed rain and seedling establishment in tropical bracken-  
302 dominated deforested areas. *Restoration Ecology* In press:e14197

303 Michaels TK, Eppinga MB, Angelini C, Holl KD, Bever JD (2021) Can nucleation bridge to  
304 desirable alternative stable states? Theory and applications. *Bulletin of the Ecological*  
305 *Society of America* 103:e01953

306 Michaels TK, Eppinga MB, Bever JD (2024) When patches grow themselves: from analogy to  
307 autocatalytic processes, the relevance of ecological nucleation for restoration practices.  
308 *Restoration Ecology* 32:e14066

309 Morán-López T, Rodríguez-Pérez J, Donoso I, Martínez D, Manuel Morales J, García D (2023)  
310 Forest recovery through applied nucleation: Effects of tree islet size and disperser mobility  
311 on tree recruitment in a temperate landscape. *Forest Ecology and Management* 550:121508

312 National Academy of Sciences. (2023) An Assessment of Native Seed Needs and the Capacity  
313 for Their Supply: Final Report. The National Academies Press, Washington, DC

314 Piaia BB, Rovedder APM, Procknow D, Camargo B, Gazzola MD, Croda JP, *et al.* (2020)  
315 Natural regeneration as an indicator of ecological restoration by applied nucleation and  
316 passive restoration. *Ecological Engineering* 157:105991

317 Pilon NaL, Buisson E, Durigan G (2018) Restoring Brazilian savanna ground layer vegetation by  
318 topsoil and hay transfer. *Restoration Ecology* 26:73-81

319 Procknow D, Rovedder APM, Piaia BB, Camargo B, De Moraes Stefanello M, Da Silva MPKL,  
320 *et al.* (2023) Monitoring ecological restoration of riparian forest: Is the applied nucleation  
321 effective ten years after implementation in the Pampa? *Forest Ecology and Management*  
322 538:120955

323 Ramírez-Soto A, Lucio-Palacio CR, Rodríguez-Mesa R, Sheseña-Hernández I, Farhat FN, Villa-  
324 Bonilla B, *et al.* (2018) Restoration of tropical montane cloud forests: a six-prong strategy.  
325 *Restoration Ecology* 26:206-211

326 Reid JL, Holl KD (2013) Arrival ≠ survival. *Restoration Ecology* 21:153-155

327 Rey Benayas JM, Martínez-Baroja L, Pérez-Camacho L, Villar-Salvador P, Holl KD (2015)  
328 Predation and aridity slow down the spread of 21-year-old planted woodland islets in  
329 restored Mediterranean farmland. *New Forests* 46:841-853

330 Robinson GR, Handel SN (2000) Directing spatial patterns of recruitment during an  
331 experimental urban woodland reclamation. *Ecological Applications* 10:174-188

332 Rojas-Botero S, Solorza-Bejarano J, Kollmann J, Teixeira LH (2020) Nucleation increases  
333 understory species and functional diversity in early tropical forest restoration. *Ecological*  
334 *Engineering* 158:106031

335 Saha S, Kuehne C, Bauhus J (2013) Tree species richness and stand productivity in low-density  
336 cluster plantings with oaks (*Quercus robur* L. and *Q. petraea* (Mattuschka) Liebl.). *Forests*  
337 4:650-665

338 Shaw JA, Roche LM, Gornish ES (2020) The use of spatially-patterned methods for vegetation  
339 restoration and management across systems. *Restoration Ecology* 28:766-775

340 Toro L, Torres-Romero F, Salinas SM, Avella-Munoz A, Galatowish S, Secchi S, *et al.* (2024)  
341 Cost-effectiveness of management strategies in a nucleation experiment in a tropical dry  
342 forest. *Restoration Ecology* 32:e14094

343 Ursell T, Safford HD (2022) Nucleation sites and forest recovery under high shrub competition.  
344 *Ecological Applications* 32:e2711

345 Vieira DLM, Holl KD, Peneireiro FM (2009) Agro-successional restoration as a strategy to  
346 facilitate tropical forest recovery. *Restoration Ecology* 17:451-459

347 Wilson SJ, Alexandre NS, Holl KD, Reid JL, Zahawi RA, Celentano D, *et al.* (2021) Applied  
348 nucleation guide for tropical forests. Conservation International,

349 Yarranton GA, Morrison RG (1974) Spatial dynamics of a primary succession: nucleation.  
350 *Journal of Ecology* 62:417-428

351 Zahawi RA, Augspurger CK (2006) Tropical forest restoration: tree islands as recruitment foci in  
352 degraded lands of Honduras. *Ecological Applications* 16:464-478

353 Zahawi RA, Reid JL, Holl KD (2014) Hidden costs of passive restoration. *Restoration Ecology*  
354 22:284-287

355

- 356 **Table 1.** Recommendations for future spatially patterned restoration research and  
357 implementation
- 358 • Conduct collaborative research between academic researchers and restoration practitioners to  
359 test methods that are practical and scalable.
  - 360 • Compare spatially patterned methods to more common restoration approaches (e.g., natural  
361 regeneration, plantation-style planting).
  - 362 • Evaluate spatially patterned methods in different socio-ecological systems (e.g., ecosystem  
363 types, native vegetation cover in the landscape, local site resilience, land uses, regulatory  
364 environments).
  - 365 • Test different planting designs, including shape, size, and distance between planted areas, and  
366 percentage area planted, to determine which patterns work most effectively to meet  
367 restoration goals in specific systems.
  - 368 • Evaluate different species compositions for planting, considering effectiveness in enhancing  
369 seed dispersal and seedling establishment, shading out ruderal vegetation, sequestering  
370 carbon, and/or providing resources to landowners (e.g., fruit, firewood).
  - 371 • Tailor planting designs to heterogeneous site conditions such as land contour, soils,  
372 hydrology, pre-existing (e.g., remnant trees) or rapidly regenerating vegetation.
  - 373 • Quantify costs and other logistical constraints to implement different planting designs.
  - 374 • Explore methods for using unplanted areas to provide benefits to landholders while native  
375 vegetation establishes in planted areas.
  - 376 • Monitor the effects of spatially patterned restoration throughout a restoration site and not just  
377 in actively revegetated areas, and over a sufficient time frame to evaluate recovery of  
378 naturally colonizing species.
  - 379 • Create education and training materials for restoration staff and community members about  
380 cost, benefits, and guidance for implementing spatially patterned planting methods.