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Applied nucleation as a forest restoration strategy

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ABSTRACT

The pace of deforestation worldwide has necessitated the development of strategies that restore forest cover quickly and efficiently. We review one potential strategy, applied nucleation, which involves planting small patches of trees as focal areas for recovery. Once planted, these patches, or nuclei, attract dispersers and facilitate establishment of new woody recruits, expanding the forested area over time. Applied nucleation is an attractive option in that it mimics natural successional processes to aid woody plant recolonization. To date, results of experimental tests of applied nucleation are consistent with theoretical predictions and indicate that the density and diversity of colonists is higher in planted nuclei than in areas where no planting takes place (e.g. passive restoration). These studies suggest that the applied nucleation strategy has the potential to restore deforested habitats into heterogeneous canopies with a diverse community composition, while being cheaper than projects that rely on plantation designs. We recommend several areas where research would aid in refining the methodology. We also call for further comparisons as nuclei age beyond the 2–13 years that have been studied, thus far, in order to confirm that practical applications continue to match theoretical predictions. Finally, we suggest that applied nucleation could be effective in the restoration of a variety of habitat types or species guilds beyond the ones to which it has been applied thus far.

1. Introduction

Deforestation is recognized as a prime element of human-caused global change affecting biodiversity, carbon storage, soil erosion, habitat connectivity, and soil nutrient dynamics (Foley et al., 2005). Whereas preventing conversion of forest into pastures, urban habitat, or other non-forested land must be a key element of efforts to reduce future impacts, restoration of formerly forested land is increasingly recognized as a parallel strategy that can have significant benefits (Chazdon, 2008). However, the scale of the challenge facing efforts to restore cleared habitats is daunting. Purely passive restoration relying on natural succession results in highly variable recovery rates which may take several decades (Holl, 2007; Jones and Schmitz, 2009) or degraded ecosystems may remain in an alternative stable state (Suding and Hobbs, 2009). Meanwhile, the area of land in need of restoration is so large that intensive replanting programs are only feasible in specifically-targeted circumstances. For these reasons, cost-effective methods to facilitate forest recovery are greatly needed.

Recent discussions highlighting the links between succession and restoration have emphasized the potential to utilize natural processes governing dispersal, establishment, resource availability and community assembly to achieve specific management strategies (e.g. Luken, 1990; Walker et al., 2007). Often the most efficient restoration strategies, in terms of cost and effectiveness, facilitate natural successional processes (Chazdon, 2008; Lamb et al., 2005). Applied nucleation (i.e. establishing small patches of shrubs and/or trees to serve as focal areas for recovery) is a strategy that uses principles of colonization of non-forested landscapes by woody vegetation to restore forest cover. It borrows elements of both natural pathways of succession and active restoration to influence the direction and rate of natural succession. We propose that it has the potential to succeed to a greater extent, from a management perspective, than if either passive restoration or intense active management was undertaken by itself.

We review nucleation as a natural process of succession and discuss how it can be applied in a restoration context. We also review the ways in which applied nucleation may be more or less effective than common management strategies designed to restore deforested landscapes, primarily natural recovery and large-scale tree plantings. Finally, we offer suggestions as to how further research can help refine applied nucleation as a strategy to restore deforested areas and develop applications for a wider range of habitat or species types.

2. Nucleation as a natural process

Natural forest recovery, including colonization of open habitats created by natural and anthropogenic disturbances, frequently has been observed to take place in a discrete pattern whereby initial

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colonization by pioneer species creates "clumps" or clusters of vegetation around which other species establish (e.g. Archer et al., 1988; Castellanos and Figueroa, 1994; Del Moral and Bliss, 1993; Franks, 2003; Yarranton and Morrison, 1974). Yarranton and Morrison (1974) referred to the initial colonists as "nuclei", and the process of cluster development and expansion as "nucleation", analogous to the use of the terms in the physical sciences. Once a persistent colonist establishes, further colonization within a nucleus can be facilitated via capture of wind-blown seeds (Yarranton and Morrison, 1974; Del Moral and Bliss, 1993; Franks, 2003) or attraction of birds or other animals that may disperse seeds (Cabral et al., 2003; Carrière et al., 2002b; Fuentes et al., 1986; Guevara et al., 1986; McDonnell and Stiles, 1983; Puyravaud et al., 2003; Slocum, 2001).

The nuclei can also be formed by remnants that survive the initial disturbance (Carrière et al., 2002b; Del Moral and Bliss, 1993; Guevara et al., 1986; Janzen, 1988; Schlawin and Zahawi, 2008; Slocum, 2001; Toh et al., 1999). For example, succession of tropical pastures is strongly influenced by the presence of remnant trees that serve as "recruitment foci" (*sensu* Guevara et al., 1986) by enhancing seed rain of animal-dispersed seeds and facilitating seedling establishment. The use of "seed-trees" in managed temperate coniferous forests can perform the same function, enhancing seed sources and structural diversity compared to clear-cutting (Gillis, 1990; Sullivan et al., 2000).

Biotic and abiotic limitations on establishment may be lower within a nucleus than in surrounding areas. For example, initial colonizers can play a significant role in ameliorating harsh microclimates, stabilizing soil, and providing soil resources during primary succession (e.g. Cutler et al., 2008; Del Moral and Bliss, 1993) and other cases of stressful environmental conditions (e.g. Archer et al., 1988; Callaway, 1992; Castellanos and Figueroa, 1994; Kennedy and Sousa, 2006; Yarranton and Morrison, 1974). In less stressful environments, the nuclei may also reduce competitive inhibition by grasses or other native and non-native ground-level vegetation, thereby enabling the establishment of some species that could not otherwise establish in an opening (Holl, 2002a; Li and Wilson, 1998; Sady et al., 2010; Zahawi and Augspurger, 2006). Seed predation and seedling herbivory may be lower (Callaway, 1992; Garcia and Obeso, 2003) under established woody vegetation than in the open (but see Bartholomew, 1970; Callaway, 1992; Holl, 2002a). The end result is often that abundance, survival, and species richness of seedlings within such colonized nuclei is higher than in unvegetated or open habitat (e.g. Carrière et al., 2002b; Franks, 2003; Hooper et al., 2004; Kennedy and Sousa, 2006; Rubio-Casal et al., 2001; Slocum, 2001).

Once a nucleus forms, it can increase in size via clonal growth or establishment of new seedlings (Archer et al., 1988; Cabral et al., 2003; Castellanos and Figueroa, 1994; Zahawi and Augspurger, 2006). As more nuclei establish, both from dispersal within and outside the site, and grow they will eventually coalesce with neighboring nuclei. In this way, an increasing proportion of a clearing contains species characteristic of the initial nuclei. In older nuclei, processes governing colonization (e.g. dispersal, establishment) give way to processes governing survival (e.g. competition, thinning, mortality) (Archer et al., 1988; Blundon et al., 1993; Castellanos and Figueroa, 1994; Russell-Smith et al., 2004). Thus, nucleation has typically been used to describe relatively early stages of succession (Archer et al., 1988; Cutler et al., 2008; Del Moral and Bliss, 1993; Schweiger et al., 2000; Yarranton and Morrison, 1974; Zobel et al., 1993).

3. Applied nucleation as a restoration tool

The application of nucleation in a restoration context has been suggested as a way to influence the trajectory and pace of restoration (Hooper et al., 2005; Reis et al., 2010; Rey Benayas et al., 2008; Robinson and Handel, 2000; Toh et al., 1999). In this review, we define restoration as assisting the recovery of a degraded, damaged, or destroyed ecosystem (SER, 2004), and aim in particular for a diverse ecosystem that resembles relatively undisturbed nearby forest. Restoration via applied nucleation involves establishing clusters of woody vegetation scattered throughout a clearing. The clusters, or nuclei, will expand via subsequent recruitment of new seedlings in the same way that nucleation in succession takes place (passive restoration and applied nucleation designs, Fig. 1). As reviewed earlier, the introduction of tree clusters can facilitate the establishment of new individuals by ameliorating harsh microclimatic conditions, reducing competition with grasses or other ground-level vegetation, or attracting birds and other animals that might disperse seeds (Duncan and Chapman, 1999). It may also speed the succession from early-arriving ruderal species to "later successional stage" woody vegetation that, under natural conditions, might take place more slowly via the inhibition model of Connell and Slatyer (1977).

Other terms have been suggested for "applied nucleation" including woodland islets (Rey Benayas et al., 2008) and tree or habitat islands (Robinson and Handel, 2000; Zahawi and Augspurger, 2006), but these terms do not reflect the relationship between the restoration strategy and the successional pathways described above. Most often nuclei have been established by planting tree, or sometimes shrub, saplings. Others have suggested introducing nuclei by transplanting soil or introducing bird perches (Bechara et al., 2007; Holl, 1998; Zanini and Ganade, 2005) or brush piles (Uhl et al., 1981) as focal areas for seedling establishment (reviewed in Reis et al., 2010), but these have received minimal testing.

Applied nucleation contrasts with other, more common, methods of forest restoration including passive restoration (*sensu* Rey Benayas et al., 2008) and the planting of trees throughout a clearing (e.g. plantation design) (Fig. 1). There is a large literature on the results of both passive restoration and extensive tree planting as restoration strategies, which we do not aim to review here. We briefly summarize each approach and then contrast them with applied nucleation.

In certain regions of the world, large areas have undergone passive restoration or natural recovery where the only human intervention is to cease ongoing land uses such as grazing, agriculture or logging. For example, the vast majority of forest in the eastern United States was cleared in the late eighteenth and nineteenth centuries before shifting demographic and land-use patterns led to abandonment and natural reforestation of cleared land (Foster et al., 1998, 2004). Today, most of this region is second growth forest, although species composition may be very different from predisturbance conditions or those of less disturbed habitat (Flinn and Marks, 2007; Foster et al., 1998; Fuller et al., 1998). Even in the humid tropics, where deforestation is an ongoing concern, tropical forest cover is increasing in certain regions (Asner et al., 2009; Grau et al., 2003; Hecht et al., 2006). For example, forest cover in Puerto Rico has increased from less than 10% in the 1940's to more than 40% in the present. (Grau et al., 2003).

The rate of natural recovery, however, is notoriously variable. In some cases, tropical forest biomass and species composition in secondary forests may resemble old-growth forests within decades (Letcher and Chazdon, 2009; Marín-Spiotta et al., 2008), whereas in other cases the areas may remain in a state where woody vegetation is absent or sparse due to minimal dispersal of forest seeds, highly degraded soils, competition with aggressive ruderal species, and lack of remnant trees to serve as recruitment foci (Chazdon, 2008; Duncan and Chapman, 1999; Lamb et al., 2005; Zahawi and Augspurger, 1999). Even in the case of increasing Puerto Rican forest cover, the regrown forests are relatively homogeneous with

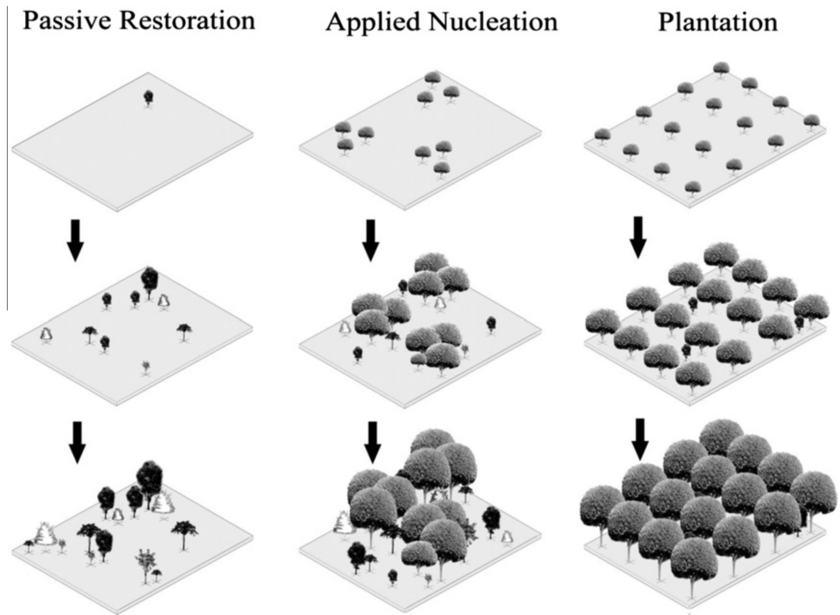

Fig. 1. Time sequence of three common strategies to restore forest cover: passive restoration, applied nucleation, and plantation. As each design ages (from top to bottom), tree cover expands via tree growth and colonization. Passive restoration produces a diverse forest community, although with the least forest cover of the three scenarios. By contrast, applied nucleation results in greater forest cover compared to passive restoration, and lower cover but a more diverse community compared to the plantation. For the sake of simplicity, only one tree type is planted in the applied nucleation and all the other species colonize naturally. In reality, nuclei and plantations could vary in species composition and the number of trees planted.

higher abundance of non-native species compared to mature old-growth forests (Grau et al., 2003). In such cases, human intervention may serve to facilitate forest recovery.

The most common active forest restoration strategy is to plant large numbers of seedlings, or occasionally seeds, in cleared areas. Design of such plantings can range from monocultures of non-native or native species to dense plantings of 20–200 species that represent a range of ecological guilds (Barbier et al., 2008; Golet et al., 2008; Lamb et al., 2005; Rodrigues et al., 2009). A variety of studies in boreal, temperate, and tropical habitats have documented that timber and restoration plantations can facilitate native woody seedling recruitment (e.g. Augusto et al., 2001; Barbier et al., 2008; Carnus et al., 2006; Chapman and Chapman, 1996; Lugo, 1997; Parrotta et al., 1997; Robinson and Handel, 1993). Incorporation of such strategies as mixed-species plantings and planting species characteristic of mature forest has the potential to significantly enhance the physical structure and biodiversity compared to single-species plantations (Lamb, 2010). For example, the number of species planted in subtropical eastern Australian plantations has been shown to be positively correlated with diversity of size classes, degree of canopy closure, and dominance by shrubs over grasses (Kanowski et al., 2003). Omeja et al. (2011) reported recruitment of tree seedlings, including those dispersed by birds and other animals, in Ugandan tropical forests less than 15 years after planting with five native tree species.

We are aware of four experimental tests of applied nucleation to restore forest cover. These four experiments were conducted in three different vegetation types – tropical forest (Cole et al., 2010; Holl et al., 2011; Zahawi and Augspurger, 2006), Mediterranean woodland (Rey Benayas et al., 2008), and temperate deciduous forest (Robinson and Handel, 2000) – and report data from 2–13 years since establishment. The results from these relatively early stages are consistent with patterns observed in naturally-recovering systems. Seed dispersal and seedling survival were consistently higher within planted nuclei than in areas without nuclei; and in each case species density within the nuclei was higher than both the number of species initially planted and the number found in areas outside nuclei. It remains to be seen, however, whether experimentally-planted nuclei expand beyond their initial boundaries and the total canopy area increases. Zahawi and Augspurger (2006) found higher seed density up to 1 m beyond nuclei edges, whereas Holl et al. (2011) found that nuclei expansion (0–3 m beyond initial nuclei dimensions) took place largely via growth of the canopy of trees that were initially planted. Ultimately, the success of applied nucleation as a restoration strategy will be greatest if the initial management can serve as a kind of "activation energy" to begin the restoration process so that natural dispersal and expansion of nuclei subsequently proceed without further need for management.

Applied nucleation has the potential to be a lower-cost forest restoration strategy than plantations. The costs of plantations can be high – ranging from $400 to over $3000 per ha for the first 2–3 years for seedlings and labor (Montagnini and Finney, 2011; Olschewski et al., 2010; Omeja et al., 2011; Rodrigues et al., 2011; Vieira et al., 2009). Using these numbers as an illustration, replanting the estimated 27.2 million ha of forest in the humid tropics that was cleared between 2000 and 2005 (Hansen et al., 2008) would cost between $10 and $82 billion. By focusing the plantings within distinct areas and leaving other areas to be colonized with new recruits as nuclei expand, planting and management costs associated with applied nucleation would be substantially lower than most plantation designs (Parrotta et al., 1997; Rey Benayas et al., 2008). For example, Holl et al. (2011) estimated that their applied nucleation design would cost a quarter to a third of a typical plantation, though the precise cost comparison would vary from site to site with costs proportional to the area devoted to planted nuclei.

On the other hand, the irregular spacing of nucleation plantings can present other challenges that may impact a project's cost. For example, planting in clusters may require greater supervision of planting crews accustomed to planting in systematic rows. Row planting may also have other practical advantages such as proximity to irrigation lines or fencing to reduce damage by herbivores. Finally, the less uniform planting arrangement of a nucleation

Table 1
Research questions to refine and implement applied nucleation as a restoration strategy.

A. Planting design
- How do the intensity of past disturbance and the surrounding land uses affect the relative efficacy of applied nucleation, as compared to other restoration strategies, in achieving restoration goals (e.g. facilitating the development of forest that resembles relatively undisturbed stands)?
- What characteristics of the planted nuclei (e.g. nuclei size, density, spacing) are most likely to achieve desired results?
- How does species composition (e.g. diversity, successional stage, functional group) influence restoration success?

B. Patterns of recovery in applied nucleation over longer time scales (as compared to passive restoration and plantation designs)
- Do longer-term outcomes of applied nucleation follow theoretical predictions? Specifically, do planted nuclei spread?
- To what degree are nuclei limiting over the long-term in unmanaged habitats? Would sufficient nuclei form through natural processes without intervention?
- Does applied nucleation result in a forest that more closely resembles intact forest in terms of species composition and habitat heterogeneity, and/or at a faster rate, than other methods? Are projects using applied nucleation more vulnerable to invasion by non-native species?
- How does applied nucleation compare to other methods in terms of providing desired ecosystem services (e.g. pollination, nutrient cycling, carbon sequestration) and affecting biotic interactions (e.g. disease spread, herbivory)?

C. Generalization to other habitat types
- What habitat characteristics, including those of non-forested habitats, are appropriate for applied nucleation?
- What other vegetation types besides forests are appropriate targets for applied nucleation?

design may make seedlings more vulnerable to accidental damage during follow-up clearing to control ruderal vegetation (Holl et al., 2011). In most cases, these logistical challenges associated with applied nucleation will still be lower than the cost of supplying more seedlings to a large-scale planting project (Holl et al., 2011). As long as applied nucleation is at least as effective in achieving restoration goals (see below), it may be a more cost-effective option.

In summary, past research suggests that natural succession often proceeds in a manner that resembles the nucleation model; that this model can be applied in a restoration context; and that in some cases, applied nucleation has the potential to achieve common restoration goals more effectively and/or at a lower cost than large-scale plantings or passive restoration. Therefore, we assert that applied nucleation should be considered as a restoration technique more often than it is. Given the small number of studies to date on applied nucleation, however, research is needed to provide more specific guidelines regarding applied nucleation planting designs (Table 1A). Such research should consider the effects of the surrounding landscape and how the number of nuclei, their size, and their distance from seed sources influence the likelihood of restoration success. Longer-term monitoring of applied nucleation is critical to evaluate whether this strategy increases both the rate of forest recovery and the similarity to intact forest species composition and functions compared to other restoration approaches (Table 1B). Finally, further testing of applied nucleation in a range of habitat types is needed (Table 1C). We explore these questions and relevant literature in more detail below.

4. Planting design considerations

4.1. Influence of disturbance intensity and the surrounding landscape

The intensity and spatial extent of the disturbances that led to forest clearing influences the rate and direction of forest recovery (Chazdon, 2008; Holl, 2007; Parrotta, 1992). For example, areas that have been used for mining, pasture, or industrial scale agriculture for many years may require extensive intervention, such as planting trees throughout to ameliorate stressful soil conditions or to shade out pasture grasses. By contrast, sites that were used less intensively or for shorter periods of time are likely to have sufficient natural establishment of forest species that passive restoration, with no effort to establish nuclei, may be sufficient (Gill and Marks, 1991; Holl, 2007). We hypothesize that sites with an intermediate level of disturbance are most likely to be appropriate for an applied nucleation approach.

The composition of the surrounding landscape, including the amount of remaining forest cover and the other types of land-uses, also strongly affects dispersal and establishment of forest species, and in turn the selection of a restoration strategy (Holl and Aide, 2011). Extensive past research suggests that seed rain of temperate and tropical forest species is quite low in open agricultural areas and drops dramatically even at short distances (e.g. 5–10 m) from the forest edge (Holl, 2007; Meiners et al., 2002; Myster, 1993), particularly for large-seeded, animal-dispersed species (Cordeiro and Howe, 2001; Cramer et al., 2007; McEuen and Curran, 2004). Seed inputs into nuclei embedded in highly disturbed or fragmented landscapes may be low due to reduced population sizes or altered behaviors of dispersing animals (e.g. Kirika et al., 2008). In such circumstances, new recruits may derive largely from the progeny of planted individuals rather than from species found in distant remnant stands, although this has not been demonstrated empirically (Table 1A). In addition to proximity to remnant forest, the types of agricultural land-uses in the surrounding landscape (e.g. shade vs. sun coffee, amount of tree cover in pastures) will affect the ability of seed-dispersing animals to move through the landscape and utilize tree nuclei (DeClerck et al., 2010).

Based on the above findings, one would predict and one past study has shown (Robinson and Handel, 2000) that nuclei closer to source populations of forest species have higher seed rain and seedling establishment. In contrast, two other studies (Cole et al., 2010; Zahawi and Augspurger, 2006) did not detect an effect of proximity to forest remnants on seed rain and seedling establishment in nuclei. The inconsistency may be a function of the study duration: the latter two studies spanned only the first few years of succession when source populations of early successional species may be relatively widely distributed throughout the landscape and their establishment less distance-dependent. Alternatively, the ability of nuclei to attract birds could overcome the effects on recruitment of distance to forest remnants (Duncan and Chapman, 1999).

Whereas past studies of landscape effects and habitat fragmentation on forest recovery have focused largely on seed dispersal, other large-scale factors may affect the efficacy of different restoration strategies, including applied nucleation. In landscapes with a high percentage of urban or intensive agricultural land-uses altered flows of water, nutrients, or chemicals into a restored site may require strategies to ameliorate high flows or filter inputs. Likewise, the surrounding land uses may affect biological interactions such as disease spread, herbivory, and pollination (Holl et al., 2003; Luken, 1990). How surrounding habitat fragmentation might affect these physical and biological processes in sites using the applied nucleation approach versus other strategies is essentially unknown.

4.2. Planting design considerations

Thus far, theory (e.g. MacArthur and Wilson, 1967) and two practical studies in Central America (Cole et al., 2010; Zahawi and Augspurger, 2006) indicate that larger nuclei are colonized by a larger number of individuals and animal-dispersed species than are smaller nuclei. Small nuclei appear to be less attractive to seed-dispersing birds (Fink et al., 2009) and neither ameliorate stressful microclimatic conditions (light, temperature, humidity) nor shade out ruderal ground-level vegetation to the same degree as larger nuclei (Holl, 2002a; Zahawi and Augspurger, 2006). Very small nuclei are also problematic from a practical standpoint, as they are harder to locate for maintenance, and mortality of one or two seedlings more strongly affects the overall nuclei structure (Holl et al., 2011). The two Central American studies (Cole et al., 2010; Zahawi and Augspurger, 2006) suggest that nuclei smaller than 8 m × 8 m may be significantly less effective in fostering reforestation than larger nuclei, but further work on appropriate nuclei sizes is needed in a range of systems. Moreover, both the density of and spacing among nuclei may affect movement of seed dispersers and seedling establishment, and warrant further experimentation.

4.3. Species composition

Many studies of both remnant trees and plantations demonstrate the strong effect of initial species on the composition of seed rain and naturally colonizing seedlings. Incoming seed rain is a function of the degree to which the planted species attract birds, bats, and other dispersal agents (e.g. Carrière et al., 2002a; Cole et al., 2010), as well as the height of the nuclei (McDonnell and Stiles, 1983; Robinson and Handel, 1993, 2000; Toh et al., 1999). The number of recruits underneath planted species and their diversity is strongly affected by the species composition of the overstory (Barbier et al., 2008; Cusack and Montagnini, 2004; Lemenih et al., 2004; Parrotta, 1995; Silver et al., 2004; Wang et al., 2009). For example, Cusack and Montagnini (2004) found a fourfold range in the abundance of understory recruits under various timber plantation trees at three sites in Costa Rica. Moreover, the choice of species, particularly nitrogen fixers, can strongly affect nutrient cycling within nuclei and plantations (Celentano et al., 2011; Siddique et al., 2008) and successional pathways (Chapin et al., 1994). Therefore, the choice of species to be planted will certainly affect colonization and community development and should be carefully considered as part of the restoration planning process to increase the likelihood of achieving restoration goals.

Among experimental tests of applied nucleation, only two studies varied the species composition of planted nuclei. Robinson and Handel (2000) found no difference in seedling establishment between nuclei that did or did not include N-fixers among their species pool. Zahawi and Augspurger (2006) found differences in species richness, but not number of seedlings, below nuclei planted with two different species; they attribute the higher species richness to a denser canopy and more favorable microhabitat conditions created by one species. Future tests of applied nucleation should further investigate the influence of species composition on nuclei development (Table 1A). For example, does seedling establishment vary with the number of species planted in nuclei? What characteristics of planted trees, such as the ability to attract seed disperser or reduce competition with aggressive understory species, most strongly influence seedling establishment?

An important question for tree planting, either in a plantation or applied nucleation design, is whether to plant: (1) early successional species that are better adapted to stressful microclimatic conditions of clearings, but are more likely to colonize naturally; (2) large-seeded, later successional species that might not otherwise become established on their own but are likely to close canopy more slowly (Martinez-Garza and Howe, 2003); or (3) a mix of life history guilds. The answer is likely to be site-specific and depend on, among other things, the degree to which rapid canopy closure will better achieve restoration goals and to which later successional species are dispersal-limited. In general, planting a greater number of species that also represent different functional groups (e.g. bat- vs. bird-dispersed) is recommended to enhance diversity within a site and attract a wider variety of faunal colonizers. However, in reality, restoration projects are often limited by the number of species available in local nurseries or wild populations.

In summary, no reliable template exists for the design of applied nucleation plantings across the range of habitats in which it might be used. Evidence suggests that: larger nuclei are more effective in attracting seed dispersers than smaller ones and that they more successfully ameliorate harsh environmental conditions; that nuclei should be located as close to remnant seed sources as possible; and that including a variety of species, including late successional species, in the planting mix is more likely to result in a diverse community. In reality, tradeoffs exist between some of these prescriptions – for example, for a given number of trees planted, increasing nucleus size will decrease planting density or number of nuclei. As we have described, further research is required to better understand the nature of these tradeoffs and which design considerations are more important in various circumstances (Table 1A).

5. Patterns of recovery in applied nucleation over longer time scales

5.1. Rate of nuclei spread and establishment

As noted earlier, most studies of applied nucleation have spanned less than a decade following planting. Therefore, long-term monitoring of recovery is needed to answer a host of questions about the efficacy of this restoration method (Table 1B). An important question is whether and at what rate the nuclei spread over time. Experiments suggest that, over the short-term, there is relatively little establishment of seedlings at nuclei edges compared to areas under planted trees (Holl et al., 2011; Robinson and Handel, 2000; Zahawi and Augspurger, 2006), likely due to competition with ruderal vegetation and stressful microclimate conditions. Corbin et al. (unpublished data), sampling a reclaimed landfill in the northeastern US (Robinson and Handel, 2000), found that establishment beyond planted nuclei was highly species-specific; whereas some bird- and a variety of wind-dispersed tree species established outside nuclei, recruitment of others, such as the bird-dispersed tree *Morus* spp., were largely limited to the original area of the nuclei.

Studies to date clearly show that in former agricultural lands where the natural recovery process is slow, planting nuclei helps to increase seed rain and seedling establishment in the first few years after abandonment (see above). It is not clear, however, whether planting nuclei accelerates recovery sufficiently over the long-term to warrant this intervention. In many systems, there may be enough natural nuclei establishing within the first decade that there is little difference in recovery rates two to several decades after planting (e.g. Gill and Marks, 1991). Only with long-term monitoring in different ecosystem types will it be possible to answer this question.

5.2. Legacy of planted species

Long-term studies are important not only to compare the rate but also the trajectory of community composition in passive restoration, applied nucleation, and plantation sites. Restoration projects usually aim to promote the development of ecosystems that resemble intact habitat as closely as possible; however, few projects have the resources to actively restore the full complement of forest species. Accordingly, most restoration planting efforts use a "framework species" approach (Elliott et al., 2003), where a small subset of rapidly growing species are planted that will close canopy within 1–3 years, and facilitate recovery by attracting dispersers and creating microhabitat conditions favorable for forest seedling establishment. Yet, the subset of species planted will inevitably leave a legacy of anthropogenic influence in terms of species composition and the spatial arrangement of planted individuals.

Planted trees can influence community composition and ecosystem functioning for decades or longer by supplying propagules (e.g. Parrotta, 1999; Silver et al., 2004), influencing the species composition of plants in the understory (e.g. Barbier et al., 2008; Firn et al., 2007; Gandolfi et al., 2007), and altering nutrient cycling (e.g. Macedo et al., 2008; Parrotta, 1999; Siddique et al., 2008; Silver et al., 2004). For example, Celentano et al. (2011) found higher litter quality (in terms of nutrient availability and C:N ratios) in unplanted secondary tropical forest in Costa Rica, as compared to a nearby mixed-species plantation in which nutrient cycling was dominated by a single, rapidly-growing, N-fixing species. Moreover, planted trees may inhibit the growth and survival of species through allelopathy or providing densely shaded conditions (Ganade and Brown, 2002). Therefore, successional trajectories may be quite different following restoration plantings than where natural processes dominate (Dong et al., 2007; Holl, 2002b; Kanowski et al., 2003; Murcia, 1997; Silver et al., 2004). In this regard, applied nucleation may be influenced by human design to a greater extent than cases where remnant trees or shrubs act as nuclei. Compared to larger-scale plantings, however, applied nucleation holds promise as a method that will produce a more "natural", or less-engineered, endpoint by allowing natural processes to dominate beyond the initial plantings (Fig. 1).

5.3. Habitat heterogeneity

Plantations, particularly when densely planted and tree survival is high, are likely to have lower spatial heterogeneity than applied nucleation or passive restoration (Fig. 1). Planting even-aged stands of a single or few species has been criticized for the negative effects on understory species diversity (Gillis, 1990; Halpern and Spies, 1995). One likely mechanism for relatively low species diversity in such planted systems is low habitat heterogeneity; the diversity of birds is often higher in more complex habitats (Antos et al., 2008; McDonnell, 1986; Razola and Rey Benayas, 2009; Robinson and Handel, 2000; Toh et al., 1999), and understory plant diversity has been shown to be positively correlated with heterogeneity in canopy cover (Halpern and Spies, 1995; Peterson and Reich, 2008). The applied nucleation planting design should produce a more heterogeneous environment than even a mixed-species plantation (Halpern and Spies, 1995), with a mosaic of species composition, community ages, and physical environments (Fig. 1).

We know of no studies comparing habitat heterogeneity in plantation vs. applied nucleation planting designs, but related studies add some insight into this question. Comparisons of stand densities in plantations suggest that species diversity is negatively correlated with planting density. For example, Vesk et al. (2008), surveying replanted habitats in Australia, found that forests with higher stem densities (on a per hectare basis) provided less-suitable habitat for dispersers and had lower rates of shrub and tree recruitment than areas with lower stem densities. Similarly, Lemenih et al. (2004) reported that plantations in southern Ethiopia with relatively open canopies were more successful than those with closed canopies at enhancing understory regeneration. Such patterns suggest that recruitment of a diverse understory may be more likely in an applied nucleation design because the clustering of tree plantings within open habitat results in lower stand-wide tree densities (Fig. 1). On the other hand, variable survival of seedlings, natural self-thinning, or active management (e.g. thinning trees, creating clearings) may serve to increase heterogeneity in plantations over time. Clearly, longer-term monitoring of different planting approaches is needed to compare heterogeneity.

Applied nucleation will also increase the proportion of the restored area that is at an ecotone between forest and non-forest habitat (Rey Benayas et al., 2008; Holl et al., 2011). Such edges may have both positive and negative effects in terms of the recruitment of species into young forests (Murcia, 1995). Recruitment and species diversity is often higher at forest edges than interiors (e.g. Parrotta, 1995; Razola and Rey Benayas, 2009), and edges increase habitat heterogeneity and canopy openness even within a planted cluster (Rey Benayas et al., 2008), providing habitat for different species. Rey Benayas et al. (2008) found that 13 yr-old planted oak tree nuclei in Spain enhanced habitat heterogeneity and herbaceous species richness over no planting. On the other hand, survival of seedlings naturally establishing at the edges of nuclei may be lower than seedlings grown in a plantation design due to microclimatic stresses such as desiccation, heat stress, or photoinhibition, and/or damage from herbivory (Bartholomew, 1970).

Edges may also facilitate the invasion of undesirable species (Cadenasso and Pickett, 2001; Cordeiro et al., 2004; Meekins and McCarthy, 2001). Indeed, applied nucleation may be less effective in reducing cover of existing non-native species, as well as preventing future invasions, than other methods of restoration, which could strongly influence the pace and direction of forest recovery (e.g. Lugo and Helmer, 2004). Restoration plantings that maximize canopy cover throughout an area in the shortest time (i.e. plantations rather than nuclei) are likely to most rapidly reduce cover of shade-intolerant non-native species. However, invasive non-native species that can tolerate the shady conditions of a plantation understory are becoming more prevalent (McClain et al., 2011; Ostertag et al., 2008), making it more difficult to predict the impact of different planting designs on reducing non-native cover.

Many problematic invasive species are dispersed by frugivorous birds (Bartuszevige and Gorchov, 2006; Buckley et al., 2006; McCay et al., 2009), so management designs that increase habitat heterogeneity and/or bird visitation may paradoxically result in greater inputs of non-native seeds (Buckley et al., 2006; With, 2002). For example, abundance of non-native seeds has been found to be higher under natural and artificial perches designed to facilitate native seed dispersal (Dean and Milton, 2000; Deckers et al., 2008; Ferguson and Drake, 1999). Once established, many invasive non-native species populations have been observed to expand in patterns that resemble nucleation - a few colonists establish "satellite outbreaks" or "nascent foci" that expand and coalesce into larger patches via clonal growth or local dispersal (Moody and Mack, 1988; Sakai et al., 2001). The net result is that restoration projects that employ applied nucleation should monitor invasive species, although the same is true for nearly all restoration designs (e.g. Richardson, 1998).

6. Generalization beyond forest restoration

Thus far, applied nucleation has been tested in a relatively few habitat types, specifically forests dominated by animal-dispersed tree species. This restoration approach has the potential to be useful in a wider range of ecosystem types, although this remains largely untested (Table 1C). Given the role of nuclei in attracting birds (e.g. McDonnell and Stiles, 1983; Robinson and Handel, 2000), applied nucleation may be most effective in situations where birds are important dispersers. Seed dispersal by bats, in contrast, seems to be less affected by the presence of young trees (Cole et al., 2010).

Wind-dispersed species are less likely to be facilitated by planted nuclei (Robinson and Handel, 2000), although natural nuclei may be important in the establishment of wind-dispersed species in primary succession (Del Moral and Bliss, 1993; Franks, 2003; Yarranton and Morrison, 1974). Further research should test the effectiveness of applied nucleation in facilitating establishment of species dependent on seed caching animals such as squirrels (*Sciurus* spp.) (Rooney and Waller, 2003).

Applied nucleation is likely to prove useful in systems in which seedling establishment is limited by stressful abiotic conditions. As discussed earlier, "nurse plants" in arid and semi-arid shrubland and forest systems have been demonstrated to enhance establishment of other species (Archer et al., 1988; Callaway, 1992; Garcia and Obeso, 2003). Such plantings have been applied in a restoration context, as well (reviewed in Padilla and Pugnaire, 2006). For example, Gomez-Aparicio et al. (2004) found that nurse plants had a significant facultative effect on late-successional woody species in Spanish woodlands. Plantings of larger clusters of shrubs in an applied nucleation design or as part of a multi-layer canopy may provide similar benefits in some habitats. Cluster designs have been shown to increase survival and growth rates of planted mangrove (e.g. *Rhizophora germinans*, *Avicennia germinans*) seedlings (Kumara et al., 2010; Toledo et al., 2001), perhaps due to facilitative interactions within the seedling clusters that reduced the impacts of low redox potential and high soil salinity (Gedan and Silliman, 2009).

Applied nucleation may also be an appropriate restoration strategy for some non-woody ecosystems (Table 1C). For example, natural succession of herbaceous species in such habitats as sand dunes (Franks, 2003; Yarranton and Morrison, 1974) and salt marshes (Castellanos and Figueroa, 1994; Rubio-Casal et al., 2001) have been shown to follow a pattern of nucleation. We are aware of only one study that has applied a modified nucleation technique to the restoration of herbaceous species. Grygiel et al. (2009) planted clusters of native grasses and forbs in a western old field in Minnesota, USA. They found that broadcasting seeds onto simulated small-scale disturbances comprising 25% of the area was as effective as disturbing and seeding the entire area while substantially reducing costs and the amount of seed required. Applied nucleation may be similarly well-suited to restore native species in other habitats, including wetlands or understory forb species absent from secondary temperate forests. We anticipate that nucleation will be most effective in systems where planted species spread quickly via either seed dispersal or spreading rhizomes and where competition with aggressive exotic species is not a major barrier to seedling establishment outside the planted nuclei.

Not all cases where tree or shrub regeneration is low are likely to be appropriate for applied nucleation. For example, where regeneration is limited following alteration of disturbance regime, such as fire suppression in *Pinus palustris* savannas in southeastern North America (Jose et al., 2006) or impoundment of coastal wetlands (Turner and Lewis, 1996), restoration of disturbance regimes is likely to be more effective than planting nuclei. As discussed previously, sites in which soil and hydrologic conditions are severely altered due to mining or other similarly intensive past disturbances are likely to require different restoration actions, such as recontouring the topography, mulching, and fertilizing, in addition to planting, throughout the disturbed area (Parrotta and Knowles, 2001; Robinson and Handel, 2000). Similarly, where excessive herbivory limits woody establishment, such as areas of temperate deciduous forests with high densities of deer (*Odocoileus* spp., *Cervus* spp.) (Rooney and Waller, 2003), protection from browsing is likely required for planting and subsequent establishment of seedlings to be successful. Finally, habitats where passive dispersal modes such as wind, water, or gravity predominate – as opposed to habitats where animal-dispersal predominates – are likely less appropriate venues for the applied nucleation design.

7. Conclusion

The scale of deforestation worldwide necessitates the development of techniques to re-establish forest cover on cleared land at a faster pace than strategies that rely exclusively on natural colonization processes, but at a cheaper cost than planting the entire disturbed area. Thus far, experimental tests suggest that applied nucleation matches theoretical predictions and patterns seen in natural succession; continued monitoring and testing will be useful in determining whether favorable outcomes persist as restoration projects age. Further testing to refine methodologies and apply them to novel habitat types or species guilds is needed. In the meantime, applied nucleation should be considered a viable strategy to restore cleared forests in many regions of the world.

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