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Breaking Sprouters: Proximity to Primary Forest Helps Displace Sprouter Dominance During Natural Regeneration of Degraded Neotropical Sites

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Abstract. Neotropical forests are experiencing increased conversion to agriculture through deforestation, which reduces biodiversity and ecosystem services in these sites. Compared to active restoration, natural regeneration is a more cost-effective approach to restoring abandoned agricultural sites when damage is not extremely significant. However, this passive process can be stagnated, limiting the speed of restoration and impairing the recovery of biodiversity and ecosystem services. Sprouters, individuals that regrow from a stump or roots, may be one reason, as they rapidly resprout and dominate the limited resources following a disturbance. However, literature that makes direct or quantified links between sprouters and stagnation in succession, specifically a decrease in establishment of seeds of other species, is absent. Knowledge on the relative roles of wind and animal dispersal vectors in breaking this dominance is also limited. I conducted a literature review on life history traits of sprouters and seeds, competition between species of different reproductive strategies, animal versus wind dispersal vectors, and the role of proximity in dispersal. I found that sprouters achieve dominance through self-replacement and resource monopolisation; small seeds cannot overcome this barrier while larger seeds likely can, since their seedlings' greater height and shade tolerance allows them to compete against sprouter dominance. Since animal dispersers carrying these large seeds only visit partially recovered sites, proximity to intact forest becomes pivotal, as it controls seed rain supply and thus initial vegetation development through wind-dispersed seeds that attract animal dispersers. Effective natural regeneration would therefore build out from existing intact forests.

Keywords: natural regeneration, sprouters, seed dispersal, forest proximity, secondary succession

1. Introduction

Many tropical landscapes that were initially covered with intact forests are now degraded, mainly due to deforestation during conversion to agriculture. The scale of this issue with deforestation is becoming more common in the neotropics as more forests are converted for agricultural purposes. Degraded tropical forests provide fewer ecosystem services—such as carbon sequestration, water

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regulation, pollination of crops, and habitat for biodiversity [1, 2] than primary forests. When agriculture is abandoned, some of these landscapes begin processes of succession and recover as secondary forests. Though degraded land can be restored through active restoration methods such as tree planting—and such methods are generally needed for more degraded land where large amounts of plant cover and animal species are removed [3]— these methods can be costly and hard due to the scale of certain sites [2-4]. This highlights passive natural regeneration as a promising route to recover ecological functioning and biodiversity as it is cost-effective [3]. The general problem of natural regeneration lies in its variability. Due to the passive nature of the process, recovery outcomes can be unpredictable and context-dependent [5]. Thus, positive recovery outcomes from passive regeneration are more variable and at lower levels compared to active restoration methods [2], leading to failure to regain composition of old growth [6]. This can result in a failure to fully restore biodiversity and ecosystem functions in degraded land.

The slow rate is often due to the stagnation of succession processes [5]. One contributor to stagnation is sprouters—a resprout is an individual that regenerates from a stump or when it was connected by roots at the surface of the soil [7] —that dominate the degraded land at early stages of succession [8]. The sprouters aren't just a short transitional stage. They can maintain dominance for decades [8], which prevents many secondary forests from transitioning to an old growth forest that is able to sequester large amounts of carbon dioxide and sustain diverse biodiversity. These plants favor self-replacement, which is when a species regenerates in the same location from the same individual instead of being replaced by a different individual from the same or different species [7]. This behaviour reduces the species turnover in the secondary forest [7], meaning there are fewer new species that enter the community over time. This means that the forest is unable to move forward in its succession and is stagnant because the same species are continuously replacing themselves.

One possible key to the persistent stagnation of the secondary forest is a self-reinforcing feedback loop where new species are unable to survive in the degraded forest due to the dominating sprouters. If the species needed to break sprouter dominance arrive primarily through animal dispersers [9], and those dispersers require habitat other than sprouters, then a persistent sprouter state could develop. Since animals require a range of environmental conditions that secondary forest in early succession stages with only sprouters does not provide [10, 11], isolated recovering forest fragments in particular are only able to attract a limited number of generalists [12] and dispersers that are tolerant and adapted to degraded areas [12]. They are unable to attract bigger animals that carry with them bigger and shade-tolerant seeds [9] that are likely the species that can overthrow the sprouters and push the succession process [13].

Proximity to intact forest is increasingly being recognized as a key landscape predictor of recovery [8, 14, 15]. Seed rain—the seeds dispersed by wind or animals—in areas proximal to intact forest patches tend to receive seed that is distinct from its community [8], thereby potentially leading to new species arriving and establishing. Literature has identified a diverse range of other mechanisms of how proximity also affects the recovery process: soil amendments [16], beneficial edge effects due to more abundant and diverse seed rain [15], ectomycorrhizal fungal colonizations that aid seedling physiological performance [17], and many others. A majority of the literature discusses the role of seed dispersal in the benefits of proximity in which topics are debated: higher quantity of seed rain [18] versus disperser mediated quality and diversity of seed rain population [15]; wind dispersal route where proximity enhances edge effect; [18] versus animal dispersal route where proximity enhances connectivity [19]. However, the literature on how proximity could impact sprouter dominance or the dominance of a species with a particular functional trait is lacking.

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There are a few questions that this research paper aims to address. First, how does the sprouter dominance create a 'trap' in which the secondary forest is unable to move in the successional process. I hypothesize that sprouters dominate with their ability to resprout rapidly following a disturbance and suppressing seed recruitment by taking up the limited resources at the site. By inhibiting the establishment of new colonists, sprouters decrease species turnover and stagnate community compositional change. Second, how does the proximity to a forest fragment or old growth forest break the dispersal 'trap' through mechanism of seed rain (through vectors of wind and animal dispersal agents) and how this promotes degraded site recovery through increasing species richness and functional diversity. I expect that proximity to forest fragments or old growth forests may break this feedback loop in two ways: increasing the abundance and diversity of incoming wind-dispersed seeds, which create structural changes in the recovering forest when animal dispersers are absent.

To address these questions, I conducted a focused literature review on studies examining life history traits of sprouters and seeds of different sizes, competition between species of different reproductive strategies during the successional process, animal dispersal vectors versus wind dispersal vectors, and the possible role of proximity in facilitating dispersal of seeds and animals. I searched on Semantic Scholar using key words sprouter, seed size, succession, stagnation, functional trait, seed rain, frugivore dispersal, gape size, wind dispersal, and proximity. I prioritized recent peer reviewed studies and empirical studies and synthesized the evidence narratively by dividing them into a few claims that formed a chain of reason. I consider my results in the context of implications for human actions in targeting degraded areas utilizing knowledge of the impact proximity has on the natural regeneration of secondary forests.

2. Sprouters tend to dominate for extended periods and reduce species turnover

Sprouters tend to dominate degraded land because their life-history strategy suits disturbed ground. Following a disturbance, sprouters quickly fill gaps with shoots sprouting from surviving meristems and stored reserves in roots rather than with seedlings [8]; for example, root starch concentrations can be 4X-higher in sprouters than in non-sprouters [20]. Sprouters can also remobilize the surviving shoots above ground to continue photosynthesis [8]. Due to their established large root systems, sprouters are also better able to access soil resources than non-sprouters [21]. This allows sprouters to dominate in areas where soil is less productive, whereas in more productive sites they can be outcompeted by species that regenerate through seeds [21].

For a secondary forest to regenerate, new species have to replace the ones that colonize first, a process called species turnover. Essentially, species turnover is a door with two locks and both locks need to be opened: the environmental conditions at the secondary forest need to be suitable (niche differentiation) and the seeds need to actually arrive at the secondary forest (dispersal).

Niche differentiation is when the availability of resources change and plants are filtered based on the different functional strategies they employ during the succession process [5]. Established sprouters prevent this process by occupying space for long periods [8], which lowers the probability that new species arriving from nearby forests can establish. The SORTIE model, which simulates crown competition for light and seedling recruitment limited by dispersal and light requirements, predicted that different disturbance regimes produce drastically different forest compositions once sprouting is factored in [8]. Sprouting is therefore a determining factor — not a minor trait — in shaping which species dominate the forest, because it limits the light other plants need to establish.

However, niche differentiation only explains species turnover when it is predictable, which is usually not the case with natural succession. Seed dispersal introduces the chance factor: whether a

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species establishes depends on species-specific reproduction — a species' own pattern and timing of seed production — and on whether its seeds actually reach the secondary forest [5]. Sprouter dominance can persist because the arrival of new species that could replace them depends on unpredictable chance. This is why proximity to an intact forest matters: a secondary forest depends on seed dispersal from adjacent forest to gain new species and drive turnover [7].

3. Larger sized seeds can help break sprouter dominance

Larger seeds can break sprouter dominance because their greater seedling height and shade tolerance let them establish and survive under sprouter cover. Experimental evidence shows that larger seeds produce seedlings with higher survival rates under competition, shading, drought, and burial by soil or litter [22].

Firstly, larger seeds gain a competitive advantage in microhabitats with low ground cover because of their greater seedling height: small differences in height in low vegetation correlate with drastic changes in light conditions [22]. Taller seedlings from larger seeds can grow above and overshadow their neighbors [23], including dominating sprouters. This is one way larger seeds break sprouter dominance.

Secondly, larger seeds survive longer periods in low-light conditions [23], which lets them persist under established sprouter cover and eventually break through. Grime and Jeffrey [22] showed that seed size correlates with both maximum seedling height under deep shade and the greatest stem elongation. Gross [24] similarly found that competitive cover suppressed the growth of larger-seeded species less than smaller-seeded ones, and that initial seed weight predicted final seedling weight under cover — evidence that seed size confers competitive ability. Two mechanisms explain this shade tolerance. First, large seeds carry reserves that let seedlings survive in a net carbon deficit while shaded, sustaining them until a canopy gap opens above [23]. Under 99% shade, increasing seed size from 0.03 mg to 30 mg extended survival from 10–15 days to 30–40 days — quadrupling the chance of persisting until a gap forms [23]. Second, larger reserves also support stronger etiolation responses — stems elongate and leaf number drops, letting shoots reach for light faster before their energy runs out [23]. Only larger-seeded species showed this response under shade [23]. Larger seeds also establish more readily in shade in the first place. Small seeds require light to germinate and are limited to bare soil or disturbed patches with high light (Gorski, Gorska, and Rybicki 1978; Grime et al., 1981, cited in [24], p. 384). Larger seeds do not need high light and can establish across a wider range of conditions (cited in [24], p. 384).

4. However, large seeds rarely reach degraded sites

Despite these advantages, larger seeds face an earlier bottleneck: they depend on frugivores that rarely reach degraded sites until later in succession. Reduced visitation rates of frugivores in areas of deforestation are correlated with a reduction in recruitment of larger-seeded tree species [25], indicating that larger seeds depend on frugivores for dispersal. Frugivores rarely enter degraded land because the larger fruits their diet requires only appear later in succession [11]. A positive feedback loop forms: lack of larger fruits result in reduced visitation rates of frugivores, which causes a reduced recruitment of seeds that produce the larger fruits they consume, leading to further reduction in the visitation of these frugivores [25]. The size of the seed dispersed also depends on the disperser: larger animal dispersers carry larger and more diverse seeds. Bird species with broader gapes (the width of the open mouth) consume a wider range of fruits and larger fruits on average [9]. Larger fruits attract fewer dispersers as a result [9], leaving them dependent on a few specialized

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large-bodied birds. Consequently, recruitment of frugivore-dispersed trees with larger seeds shows the greatest reduction in degraded land [25] — the largest fruits are the most vulnerable to disturbance and the hardest to recruit into a recovering site.

5. Proximity to undisturbed forest increases dispersal of seeds through increasing wind dispersal

If proximity is going to help at all, it will have to work through small-seeded species — but small seeds cannot readily displace sprouters on their own, because both of their key advantages, rapid colonization of bare ground and fast seedling growth, diminish under the conditions sprouters create. Many small-seeded species are monocarpic (i.e., they only set seed once) and depend on continuous re-colonization of bare ground, so their persistence is bounded by a narrow "window in time" after disturbance; once bare ground closes as sprouters establish, seeds become dormant as part of the seedbank [26]. Once sprouters shade the site, small-seeded species lose their growth-rate advantage, which depends on favorable light, while larger seeds gain the upper hand through their stored reserves [23].

Even so, proximity to intact forest can boost small-seed dispersal enough for some to establish, because proximity boosts seed dispersal by letting recovering sites benefit from the concentrated seed rain at the forest edge. Once sprouters dominate, small-seeded pioneers depend on numbers to break through, since no single seed can outcompete a sprouter. Small-seeded species therefore establish disproportionately in degraded areas because they simply have a higher probability of arriving. A 10-fold increase in seed mass corresponds to a 10-fold decrease in the number of seeds a plant produces per unit canopy per year [27]. The probability of seedling occurrence rises with proximity to a seed source [28]. The mechanism behind this edge effect involves wind: as vegetation changes at the forest edge, winds shift from the vertical patterns produced by tall trees in undisturbed forest to the horizontal patterns of open, reforested fields [18]. This wind transition drives the high wind-dispersed seed rain observed at edge areas of both sites [18]. In the reforested field, captured seed numbers dropped drastically beyond 5 m from the forest edge [18]. Edge density is therefore a resource that recovering sites can tap for both seed abundance and diversity [15]. Because seed density concentrates at the edge, a degraded area near an undisturbed forest is better positioned to receive these seeds. Seed abundance matters because low seed numbers cannot support widespread succession: at Kibale, hundreds of seeds are needed for a single one to establish [29]. The structural complexity of the source forest also matters. A structurally complex forest generates a more diverse seed rain than a less diverse plantation [18], so a more diverse source raises the probability that diverse species disperse into the recovering site. For wind-dispersed diversity, proximity to a structurally complex forest matters more than mere distance to any intact forest.

6. Wind dispersed pioneer species restructure degraded site to attract more animal dispersers that carry larger seeds

Pioneer trees, which usually have small seeds [13], are carried long distances by wind and colonize bare sites, establishing low-diversity communities [30-32]. These pioneers then set up the conditions that attract animal dispersers, which bring in seeds of the tropical trees and shrubs that build a site's later diversity [10, 11]. In a study in northern Mexico, after 20 months in plots with planted pioneers, natural recruitment increased because the plantings provided perches, cover, and foraging sites for birds that eat both insects and fruit [13]. Once the pioneers begin fruiting, they attract bats and birds that rely on fruit and can import the larger seeds [13] capable of breaking sprouter

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dominance. Because degraded sites have high temperatures, low humidity, direct solar radiation, and little leaf litter — conditions that prevent late-successional species from germinating and establishing — pioneers also restructure the environment into something more favorable for the shade-tolerant colonists that animal dispersers bring in [33]. Late-successional species carried by animal dispersers accumulated at pioneer-planted sites 10 times faster than in plots without pioneers [13].

7. Proximity to undisturbed forest also increases dispersal of seeds through increasing animal dispersal

Proximity to intact forest also matters because it can increase the dispersal of large seeds into recovering sites by increasing animal dispersal. A study at Kibale found that recruitment density of animal-dispersed species increases as distance from the forest edge decreases [34]. Two mechanisms drive this pattern.

First, proximity reduces animal dispersers' reluctance to enter degraded land when attractants are present. Forest frugivores rarely visit degraded areas because fruit abundance is low there [35] and the open landscape exposes them to greater predation risk [36]. However, when pioneer species provide attractants — perches, food, and cover — early in succession, frugivores are more likely to cross into the site. In southern Queensland, early successional regeneration clustered around scattered trees that served as perches and contributed to seed input [37]. But isolated trees only work when they are within reach of a source: a Brazilian study found that isolated trees attracted more bird dispersers than forest fragments or live fences did, yet how much these seeds contributed to seed rain depended on their degree of isolation [38]. Proximity to intact forest and the strength of animal-dispersed input therefore rise together.

Second, proximity to undisturbed forest generates cross-habitat spillover as animal dispersers move between forest fragments. In Brazil, avian spillovers from secondary forest into degraded sites exceeded the reverse [39]. So a degraded site close to an intact forest — one that acts as a source for animal populations — would receive more seeds through spillover. In Costa Rica, adjacent pastures served as pathways along which frugivorous birds moved between larger forested areas and defecated or regurgitated seeds of 28 plant species onto stumps scattered across the pasture [40]. A degraded site near primary forest therefore has the chance to receive seed dispersal from the animal dispersers that populate those forests.

Bats and birds play different roles at different successional stages. Bats readily cross into open areas early in succession and disperse pioneer trees and shrubs. Birds require some vegetation structure — such as trees to perch on — and arrive to disperse later-successional species. Proximity to intact forest is essential to both, but their contributions to natural regeneration are timed differently.

One nuance concerns fragment size, not distance: proximity to smaller forest fragments works nearly as well as proximity to larger ones. In one study, Chaves et al. [12] showed that brown howlers did not disperse fewer seeds into smaller forest fragments in comparison with larger ones. The monkeys compensated for a shortage of preferred native fruit in smaller fragments by consuming second-choice native fruits or cultivated alien fruits. Their generalist, adaptive diet actually let them disperse more large seeds from cultivated alien species in smaller fragments. Overall, alpha diversity of dispersed seeds — especially of rare species — was similar or numerically higher in smaller fragments than in larger ones. Even small fragments therefore serve as reservoirs of plant propagules with a similar seed diversity to larger fragments, so proximity to them still aids dispersal.

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8. Synthesis and conclusion

Through my literature review, I showed how sprouter dominance can limit succession and described a mechanism by which sprouter dominance — which I call "the dispersal trap" — is able to be broken by proximity to intact forest. Proximity to an intact forest allows a degraded site to benefit from the forest's abundant and diverse seed rain through wind dispersal, aiding seed establishment in the site. Such wind-dispersed pioneer species, typically small in size, are unable to break the dominance of sprouters but can set up the conditions that attract animal dispersers that carry larger and more shade tolerant seeds, which in turn may be able to compete against sprouters and unblock succession.

A major caveat to the mechanism is that sprouters can be beneficial in a circumstance where the differential roles and distinct physiology of seed and sprout regeneration result in a supportive relationship. Sprouters, because they are spatially bound to the location where the original tree was, are limited in their dispersal ability [21, 41]. The spatial gaps in which the sprouters can't colonize are thus filled in by non-sprouters [11] who are favored to do so due to their greater seed production. Results show that seed regeneration did not affect the growth of sprouts while sprouts increased the seed regeneration density [21]. Sprouts were able to aid seedlings because seed regeneration benefits from the moderated temperature and moisture level provided by the partial shading of sprouters that has a faster growth rate initially [42]. The lack of competition, as shown from the results, between the two regeneration strategies is because sprouters have already established root systems from parent trees and thus can access water and nutrients from deeper soil [43, 44], which leaves the resources from surface soils available for the roots of seed regeneration which are usually less-established [21]. The established root systems of sprouters provide an additional benefit to regenerating seeds by releasing water from the deeper soil layers to the shallower layers where the root systems of seed regeneration lie, allowing seeds to have greater water availability [21, 45].

A second caveat is that there is no single source in the literature review that states that proximity to old growth is able to break sprouter dominance. Instead, the mechanism is pieced together using various sources supporting connecting claims.

There are several knowledge gaps that need further research. Critically, I did not identify an empirical study on whether larger seeds are able to compete well against sprouters specifically and whether higher proximity leads to higher probability of wind-dispersed seedling establishment through abundance. There is also little research quantifying the level of proximity that matters, though some researchers quantify an optimal level of proximity that describes a threshold to access higher seed availability from an undisturbed forest [15]. This optimal range may be impactful to future forest restoration methods as the context-dependent nature of natural regeneration means that the process can occur in different forms and at different rates in sites with different conditions.

My results indicate that a cost-effective method in restoration would be building out from existing fragments for natural regeneration as this allows higher connectivity and thus benefits in seed dispersal through wind and frugivores. Another study argues for prioritizing natural regeneration near forest edges as it can moderate harsh stressors, such as high elevation and microclimate extremes after a disturbance, that reduces seedling survival [15]. Expanding restoration outward from these undisturbed forests would thus improve seedling establishment without the need of artificial shading or microclimate amelioration that can be costly and cause disturbance to local biodiversity. When a degraded site is not close to an existing forest fragment however, active restoration may be needed—especially the addition of mature trees with abundant

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and complex seed rain—to break the sprouter dominance as a very little amount of seed is able to establish and build the mechanism to break the 'dispersal trap.'

References

[1] Rosan, T. M., Vedovato, L. B., Heinrich, V. H. A., Silva-Junior, C. H. L., Brancalion, P. H. S., Sitch, S., & Aragão, L. E. O. C. (2026). Forest connectivity boosts carbon recovery in regenerating Atlantic forests. *Communications Earth & Environment, 7*(1), Article 627. https://doi.org/10.1038/s43247-026-03480-5

[2] Miguel, M. F., Butterfield, H. S., & Lortie, C. J. (2020). A meta-analysis contrasting active versus passive restoration practices in dryland agricultural ecosystems. *PeerJ, 8*, Article e10428. https://doi.org/10.7717/peerj.10428

[3] Hobbs, R. J., & Cramer, V. A. (2008). Restoration ecology: Interventionist approaches for restoring and maintaining ecosystem function in the face of rapid environmental change. *Annual Review of Environment and Resources, 33*(1), 39–61. https://doi.org/10.1146/annurev.environ.33.020107.113631

[4] Tabeni, S., Miguel, M. F., Campos, C. M., & Cona, M. (2018). Small mammal abundance and seed predation across boundaries in a restored-grazed woodland interface. *Restoration Ecology, 26*(4), 787–795. https://doi.org/10.1111/rec.12600

[5] Dent, D. H., & Estrada-Villegas, S. (2021). Uniting niche differentiation and dispersal limitation predicts tropical forest succession. *Trends in Ecology & Evolution, 36*(8), 700–708. https://doi.org/10.1016/j.tree.2021.04.001

[6] Hartup, J., Ockendon, N., & Pettorelli, N. (2022). Active versus passive restoration: Forests in the southern Carpathian Mountains as a case study. *Journal of Environmental Management, 322*, Article 116003. https://doi.org/10.1016/j.jenvman.2022.116003

[7] Jakovac, C. C., Peña-Claros, M., Kuyper, T. W., & Bongers, F. (2015). Loss of secondary-forest resilience by land-use intensification in the Amazon. *Journal of Ecology, 103*(1), 67–77. https://doi.org/10.1111/1365-2745.12298

[8] Bond, W. J., & Midgley, J. J. (2001). Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology & Evolution, 16*(1), 45–51. https://doi.org/10.1016/S0169-5347(00)02033-4

[9] Wheelwright, N. T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology, 66*(3), 808–818. https://doi.org/10.2307/1940542

[10] Frankie, G. W., Baker, H. G., & Opler, P. A. (1974). Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *The Journal of Ecology, 62*(3), 881–919. https://doi.org/10.2307/2258961

[11] Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics, 13*(1), 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

[12] Chaves, Ó. M., Bicca-Marques, J. C., & Chapman, C. A. (2018). Quantity and quality of seed dispersal by a large arboreal frugivore in small and large Atlantic forest fragments. *PLOS ONE, 13*(3), Article e0193660. https://doi.org/10.1371/journal.pone.0193660

[13] de la Peña-Domene, M., Martínez-Garza, C., & Howe, H. F. (2013). Early recruitment dynamics in tropical restoration. *Ecological Applications, 23*(5), 1124–1134. https://doi.org/10.1890/12-1728.1

[14] Souza, J. T., Ferraz, E. M. N., Albuquerque, U. P., & Araújo, E. L. (2014). Does proximity to a mature forest contribute to the seed rain and recovery of an abandoned agriculture area in a semiarid climate? *Plant Biology, 16*(4), 748–756. https://doi.org/10.1111/plb.12120

[15] Mandl, L., Cerioni, M., Bače, R., Bončina, A., Brůna, J., Chećko, E., de Koning, J. H. C., Diaci, J., Dobrowolska, D., Fidej, G., Garbarino, M., Jansons, Ā., Keren, S., Kitenberga, M., Klopčič, M., Konôpka, B., Kopecký, M., Köster, K., Kucbel, S., … Senf, C. (2025). The amount of undisturbed forest in proximity of severe disturbance patches enhances their recovery in temperate Europe. *Landscape Ecology, 40*(11), Article 199. https://doi.org/10.1007/s10980-025-02231-9

[16] König, L. A., Medina-Vega, J. A., Longo, R. M., Zuidema, P. A., & Jakovac, C. C. (2023). Restoration success in former Amazonian mines is driven by soil amendment and forest proximity. *Philosophical Transactions of the Royal Society B: Biological Sciences, 378*(1867), Article 20210086. https://doi.org/10.1098/rstb.2021.0086

[17] Cortese, A. M., Drake, J. E., Dovciak, M., Cohen, J. B., & Horton, T. R. (2023). Proximity to an old-growth forest edge and ectomycorrhizal tree islands enhance ectomycorrhizal fungal colonization of Betula lenta L. (black birch) seedlings in secondary forest soils. *Plant and Soil, 493*(1–2), 391–405. https://doi.org/10.1007/s11104-023-06237-7

[18] Setiawan, N. N., & Sulistyawati, E. (2021). A seed rain community in a reforested post-agricultural field and adjacent secondary forest of Mount Papandayan Nature Reserve, West Java, Indonesia. *Journal of Forestry Research, 32*(3), 1013–1023. https://doi.org/10.1007/s11676-020-01151-5

DOI: 10.54254/2753-8818/2027.36965

[19] Mayhew, R. J., Tobias, J. A., Bunnefeld, L., & Dent, D. H. (2019). Connectivity with primary forest determines the value of secondary tropical forests for bird conservation. *Biotropica, 51*(2), 219–233. https://doi.org/10.1111/btp.12629
[20] Pate, J. S., Froend, R. H., Bowen, B. J., Hansen, A., & Kuo, J. (1990). Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S. W. Australia. *Annals of Botany, 65*(6), 585–601. https://doi.org/10.1093/oxfordjournals.aob.a087976
[21] Mejstřík, M., Svátek, M., Pollastrini, M., Šrámek, M., & Matula, R. (2024). Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance. *Forest Ecosystems, 11*, Article 100198. https://doi.org/10.1016/j.fecs.2024.100198
[22] Grime, J. P., & Jeffrey, D. W. (1965). Seedling establishment in vertical gradients of sunlight. *The Journal of Ecology, 53*(3), 621–642. https://doi.org/10.2307/2257624
[23] Leishman, M. R., & Westoby, M. (1994). The role of large seed size in shaded conditions: Experimental evidence. *Functional Ecology, 8*(2), 205–214. https://doi.org/10.2307/2389903
[24] Gross, K. L. (1984). Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *The Journal of Ecology, 72*(2), 369–387. https://doi.org/10.2307/2260053
[25] Velho, N., Ratnam, J., Srinivasan, U., & Sankaran, M. (2012). Shifts in community structure of tropical trees and avian frugivores in forests recovering from past logging. *Biological Conservation, 153*, 32–40. https://doi.org/10.1016/j.biocon.2012.04.028
[26] Gross, K. L., & Werner, P. A. (1982). Colonizing abilities of 'biennial' plant species in relation to ground cover: Implications for their distributions in a successional sere. *Ecology, 63*(4), 921–931. https://doi.org/10.2307/1937232
[27] Moles, A. T., & Westoby, M. (2004). Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology, 92*(3), 372–383. https://doi.org/10.1111/j.0022-0477.2004.00884.x
[28] Ursell, T., & Safford, H. D. (2022). Nucleation sites and forest recovery under high shrub competition. *Ecological Applications, 32*(8), Article e2711. https://doi.org/10.1002/eap.2711
[29] Duncan, R. S., & Chapman, C. A. (2002). Limitations of animal seed dispersal for enhancing forest succession on degraded lands. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation* (pp. 437–450). CABI Publishing. https://doi.org/10.1079/9780851995250.0437
[30] Janzen, D. H. (1988). Management of habitat fragments in a tropical dry forest: Growth. *Annals of the Missouri Botanical Garden, 75*(1), 105–116. https://doi.org/10.2307/2399468
[31] Zimmerman, J. K., Pascarella, J. B., & Aide, T. M. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology, 8*(4), 350–360. https://doi.org/10.1046/j.1526-100X.2000.80050.x
[32] Ingle, N. R. (2003). Seed dispersal by wind, birds, and bats between Philippine montane rainforest and successional vegetation. *Oecologia, 134*(2), 251–261. https://doi.org/10.1007/s00442-002-1081-7
[33] Parrotta, J. A., Turnbull, J. W., & Jones, N. (1997). Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology and Management, 99*(1–2), 1–7. https://doi.org/10.1016/S0378-1127(97)00190-4
[34] Zanne, A. E., & Chapman, C. A. (2001). Expediting reforestation in tropical grasslands: Distance and isolation from seed sources in plantations. *Ecological Applications, 11*(6), 1610–1621. https://doi.org/10.1890/1051-0761(2001)011[1610:ERITGD]2.0.CO;2
[35] Da Silva, J. M. C., Uhl, C., & Murray, G. (1996). Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. *Conservation Biology, 10*(2), 491–503. https://doi.org/10.1046/j.1523-1739.1996.10020491.x
[36] Wegner, J. F., & Merriam, G. (1979). Movements by birds and small mammals between a wood and adjoining farmland habitats. *The Journal of Applied Ecology, 16*(2), 349–358. https://doi.org/10.2307/2402513
[37] Toh, I., Gillespie, M., & Lamb, D. (1999). The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology, 7*(3), 288–297. https://doi.org/10.1046/j.1526-100X.1999.72022.x
[38] Pizo, M. A., & dos Santos, B. T. P. (2011). Frugivory, post-feeding flights of frugivorous birds and the movement of seeds in a Brazilian fragmented landscape. *Biotropica, 43*(3), 335–342. https://doi.org/10.1111/j.1744-7429.2010.00695.x
[39] Béllo Carvalho, R., Alves, K. J. F., & Pizo, M. A. (2023). Spillover of avian seed dispersers between secondary forests and degraded areas in a tropical island. *Acta Oecologica, 121*, Article 103959. https://doi.org/10.1016/j.actao.2023.103959
[40] Barrantes, G., & Pereira, A. (2002). Seed dissemination by frugivorous birds from forest fragments to adjacent pastures on the western slope of Volcán Barva, Costa Rica. *Revista de Biología Tropical, 50*(2), 569–575. https://www.scielo.sa.cr/scielo.php?script=sci_arttext&pid=S0034-77442002000200016

DOI: 10.54254/2753-8818/2027.36965

[41] Matula, R., Šrámek, M., Kvasnica, J., Uherková, B., Slepička, J., Matoušková, M., Kutchartt, E., & Svátek, M. (2019). Pre-disturbance tree size, sprouting vigour and competition drive the survival and growth of resprouting trees. *Forest Ecology and Management, 446*, 71–79. https://doi.org/10.1016/j.foreco.2019.05.012
[42] Aussenac, G. (2000). Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. *Annals of Forest Science, 57*(3), 287–301. https://doi.org/10.1051/forest:2000119
[43] Xue, Y., Zhang, W., Ma, C., Ma, L., & Zhou, J. (2014). Relative importance of various regeneration mechanisms in different restoration stages of Quercus variabilis forest after selective logging. *Forest Systems, 23*(2), 199–208. https://doi.org/10.5424/fs/2014232-03263
[44] Pietras, J., Stojanović, M., Knott, R., & Pokorný, R. (2016). Oak sprouts grow better than seedlings under drought stress. *iForest - Biogeosciences and Forestry, 9*(4), 529–535. https://doi.org/10.3832/ifor1823-009
[45] Caldwell, M. M., & Richards, J. H. (1989). Hydraulic lift: Water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia, 79*(1), 1–5. https://doi.org/10.1007/BF00378231