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OPINION ARTICLE

Arrival ≠ Survival

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Abstract

Seed dispersal is commonly a limiting process in ecosystem recovery, and several recent studies have proposed novel methods for overcoming this important biological barrier, particularly in tropical pastures. Multiple experiments in various regions have shown that bird perches attract birds and increase seed dispersal but not seedling recruitment in degraded habitats. New bat-focused restoration applications, such as roost boxes and fruit oils, have proven capable of attracting animals and augmenting seed dispersal, but these applications have yet to be vetted by seedling establishment data. Seeds and seedlings in pastures have low probability of survival, attributable to predation, dessication, rot, and competition with ruderal vegetation. As such, these novel applications are unlikely to have the desired effect of accelerating tropical forest succession. Given that seed dispersal is meaningless if arriving seeds cannot survive, and that seedling recruitment measurements are not prohibitively difficult to take, we suggest that studies of novel seed dispersal techniques should include a measure of seedling recruitment. Without this information, it cannot be assumed that such applications accelerate forest recovery.

Key words: abandoned pasture, bat roost, bird perch, essential oils, faunal restoration, seed dispersal, seedling recruitment, tropical forest.

Lack of seed dispersal limits recovery in a range of ecosystems. This is particularly a concern in tropical pastures (Aide & Cavelier 1994; Holl 1999; Zimmerman et al. 2000; Cubiña & Aide 2001; Hooper et al. 2005), where agriculture rapidly depletes seed banks of later successional species (Meli 2003). Most trees in the humid tropics are dispersed by animals (Howe & Smallwood 1982), so new seed input is contingent upon frugivorous animals carrying seeds into pasture—a habitat with stressful microclimate, high predation risk, and low resource availability for diurnal animals (Daily & Ehrlich 1996). Over the past two decades, several novel applications have been tested to attract frugivorous animals into degraded pastures, with the expectation that they will deposit seeds which will grow into shrubs and trees.

Bird perching structures represent one such application. Pastures are structurally simplistic seas of grass with few natural places for birds to perch. Because frugivorous birds typically defecate while perched rather than in flight (Charles-Dominique 1986), a lack of structure contributes to low bird-mediated seed dispersal. Numerous experiments in many regions have demonstrated that perching structures attract birds and increase seed dispersal in the surrounding area (McClanahan & Wolfe 1993; Aide & Cavelier 1994; Sarmiento 1997; Holl 1998; Miriti 1998; Shiels & Walker 2003; Zanini & Ganade 2005; Heelemann et al. 2012; Graham & Page 2012). Although many of these authors measured seedling recruitment in addition to seed dispersal, none found that bird perches increase seedling abundance or diversity in tropical pastures.

Perch experiments, along with many studies of tree demography, demonstrate that tree recruitment is a function of both arrival and survival in a particular habitat (Schupp et al. 1989). Whereas perches may increase seed dispersal, seeds in tropical pastures have a low probability of surviving. One study in montane Costa Rica, for example, found that animal-dispersed seeds arriving into abandoned pastures had a 0.1% probability of establishing and surviving over an 18-month period (Holl 2002). Causes of seed mortality include predation, dessication, and rot (Cole 2009). Seeds that persist long enough to germinate soon face stiff competition with exotic pasture grasses (Holl et al. 2000) and predation from a variety of herbivores (Nepstad et al. 1990). Given these odds, it would seem that seeds dispersed below bird perches have passed out of the cloaca and into the frying pan. Seedling survival thus represents a second and no less important barrier to tropical forest recovery.

Recently, experiments to attract fauna and enhance seed dispersal have gone over to the dark side. Frugivorous bats are important seed dispersers in early tropical succession (Fleming 1988; Whittaker & Jones 1994; Stoner et al. 2007), and they disperse a different suite of species than sympatric birds (Galindo-González et al. 2000). To attract fruit bats into a forest pasture mosaic, Kelm et al. (2008) used artificial roost boxes—hollow concrete structures with netting on the ceiling for bats to hang from. Within weeks, the roosts were colonized by multiple bat species, and seed dispersal increased in the

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surrounding area. Another research team in Brazil developed a method for attracting bats into pastures using essential oils of bat-dispersed fruits, such as *Piper* and *Ficus* (Bianconi et al. 2007; Bianconi et al. 2012). When these oils were placed in pastures and agriculture fields, bat activity increased significantly. Captured bats defecated viable seeds, suggesting that essential oils could increase seed dispersal by bats in degraded habitats. In both cases, the authors emphasize that their method is promising for restoring degraded pasture.

Unfortunately, neither of these novel bat applications has been vetted through an assessment of seedling recruitment, and two decades of experimentation with bird perches suggest that augmenting bat-mediated seed dispersal is unlikely to accelerate forest succession. In pollination biology, pollen deposition observations have to be supported by seed set data to prove that pollination increases fecundity. Likewise, restoration techniques for increasing seed dispersal must demonstrate increased seedling recruitment before they can be considered effective. Monitoring seedling recruitment requires less time and effort than seed dispersal. Whereas seed traps must be emptied on a regular basis over a long period of time to take into account fruiting seasonality, seedlings may be measured as little as twice—once at the outset of an experiment and once at the conclusion.

Given the importance of seedling recruitment for restoration of nearly all terrestrial ecosystems, all evaluations of restoration applications for increasing seed dispersal to accelerate ecosystem recovery should incorporate a measure of seedling recruitment. Likewise, editors should not publish articles that expound on the utility of methods not supported by such data. Sexy applications like bat roosts lend themselves to rapid adoption by conservation groups (Reid & Casallas-Pabón 2012). Without adequate field validation, practitioners run a risk of wasting limited resources on techniques that ultimately may be useless.

Implications for Practice

- Novel restoration treatments such as bird perches, bat roosts, and essential oils are not likely to increase seedling establishment in degraded tropical pastures unless other barriers to tree recruitment are addressed.
- Researchers should provide evidence of seedling establishment, not just seed dispersal, before making recommendations to practitioners about the efficacy of restoration techniques.

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LITERATURE CITED

Aide, T. M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecolology **2:**219–229.

Bianconi, G. V., S. B. Mikich, S. D. Teixeira, and B. Maia. 2007. Attraction of fruit-eating bats with essential oils of fruits: a potential tool for forest restoration. Biotropica **39:**136–140.

Bianconi, G. V., U. M. S. Suckow, A. P. Cruz-Neto, and S. B. Mikich. 2012. Use of fruit essential oils to assist forest regeneration by bats. Restoration Ecology **20:**211–217.

Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds, and bats in French Guyana. Pages 119–135 in A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. Dr W Junk Publishers, Dordrecht, Netherlands.

Cole, R. J. 2009. Postdispersal seed fate of tropical montane trees in an agricultural landscape, southern Costa Rica. Biotropica **41:**319–327.

Cubiña, A., and T. M. Aide. 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. Biotropica **33:**260–267.

Daily, G. C., and P. R. Ehrlich. 1996. Nocturnality and species survival. Proceedings of the National Academy of Sciences of the United States of America **93:**11709–11712.

Fleming, T. H. 1988. The short-tailed fruit bat: a study in plant-animal interactions. University of Chicago Press, Chicago, Illinois.

Galindo-González, J., S. Guevara, and V. J. Sosa. 2000. Bird- and bat-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology **14:**1693–1703.

Graham, L. L. B., and S. E. Page. 2012. Artificial bird perches for the regeneration of degraded tropical peat swamp forest: a restoration tool with limited potential. Restoration Ecology **20**:631–637.

Heelemann, S., C. B. Krug, K. J. Esler, C. Reisch, and P. Poschlod. 2012. Pioneers and perches—promising restoration methods for degraded renosterveld habitats? Restoration Ecology **20:**18–23.

Holl, K. D. 1998. Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? Restoration Ecology **6:**253–261.

Holl, K. D. 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica **31:**229–242.

Holl, K. D. 2002. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. Journal of Ecology **90:**179–187.

Holl, K. D., M. E. Loik, E. H. V. Lin, and I. A. Samuels. 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restoration Ecology **8:**339–349.

Hooper, E., P. Legendre, and R. Condit. 2005. Barriers to forest regeneration of deforested and abandoned land in Panama. Journal of Applied Ecology **42:**1165–1174.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13:**201–228.

Kelm, D. H., K. R. Wiesner, and O. von Helversen. 2008. Effects of artificial roosts for frugivorous bats on seed dispersal in a neotropical forest pasture mosaic. Conservation Biology **22:**733–741.

McClanahan, T. R., and R. W. Wolfe. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biology **7:**279–288.

Meli, P. 2003. Tropical forest restoration: twenty years of academic research. Interciencia **28:**581–589.

Miriti, M. N. 1998. Regeneracão florestal em pastagens abandonas na Amazônia central: competicão, predacão, e disperso de sementes. Pages 191–197 in C. Garson and P. Moutinho, editors. Floresta Amazônica: dimica, regeneracâo e manejo. Instituto Nacional de Pesquisa da Amazônia, Manaus, Brazil.

Nepstad, D. C., C. Uhl, and E. A. Serrao. 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Pará, Brazil. Pages 215–229 in A. B. Anderson, editor. Alternatives to deforestation: steps toward sustainable use of the Amazon rainforest. Columbia University, New York.

Reid, J. L., and D. Casallas-Pabón. 2012. Designing homes for tropical bats: scientists explore artificial roosts for rebuilding forest. BATS **30**:7–9.

Sarmiento, F. O. 1997. Arrested succession in pastures hinders regeneration of Tropandean forests and shreds mountain landscapes. Environmental Conservation **24:**14–23.

Schupp, E. W., H. F. Howe, C. K. Augspurger, and D. J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology **70:**562–564.

Shiels, A. B., and L. R. Walker. 2003. Bird perches increase forest seeds on Puerto Rican landslides. Restoration Ecology **11:**457–465.

Stoner, K. E., P. Riba-Hernandez, K. Vulinec, and J. E. Lambert. 2007. The role of mammals in creating and modifying seedshadows in tropical forests and some possible consequences of their elimination. Biotropica **39:**316–327.

Whittaker, R. J., and S. H. Jones. 1994. The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. Journal of Biogeography **21:**245–258.

Zanini, L., and G. Ganade. 2005. Restoration of Araucaria forest: the role of perches, pioneer vegetation, and soil fertility. Restoration Ecology **13:**507–514.

Zimmerman, J. K., J. B. Pascarella, and T. M. Aide. 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology **8:**350–360.