



When and where to actively restore ecosystems?

K.D. Holl^{a,*}, T.M. Aide^b

^a Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA

^b Department of Biology, University of Puerto Rico-Rio Piedras, P.O. Box 23360, San Juan, PR 00931-3360, USA

ARTICLE INFO

Article history:

Received 7 April 2010

Received in revised form 24 June 2010

Accepted 3 July 2010

Available online 25 August 2010

Keywords:

Active restoration

Forest recovery

Passive restoration

Succession

Tropical forest

ABSTRACT

Given the extent of land use and land cover change by humans on a global scale, conservation efforts have increasingly focused on restoring degraded ecosystems to provide ecosystem services and biodiversity. Many examples in the tropics and elsewhere, however, show that some ecosystems recover rapidly without human intervention which begs the question of in which cases and to what extent humans should actively work to facilitate ecosystem recovery. We recommend that all land managers consider a suite of ecological and human factors before selecting a restoration approach. Land managers should first consider what the likely outcome of a passive restoration (natural regeneration) approach would be based on the natural ecosystem resilience, past land-use history, and the surrounding landscape matrix. They should also identify the specific goals of the project and assess the resources available. Conducting these analyses prior to selecting restoration approaches should result in a more efficient use of restoration resources both within and among projects and should maximize the success of restoration efforts.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Conservation efforts have traditionally focused on protecting areas where the land cover has not been heavily altered by humans and such efforts must remain a priority. Given the extent of land use and land cover change by humans on a global scale, conservation efforts have increasingly focused on natural recovery and active restoration of degraded ecosystems in order to restore both ecosystem services and biodiversity (Aronson et al., 2007; Chazdon, 2008b; Rey Benayas et al., 2008). These restoration efforts range from removing human disturbances (e.g. fire, grazing, water removal from rivers) in order to allow for natural or unassisted recovery ("passive restoration" sensu DellaSala et al., 2003; Rey Benayas et al., 2008) to humans actively intervening in an effort to accelerate and influence the successional trajectory of recovery ("active restoration").

Given that natural recovery in many ecosystems can take decades, there is often considerable social pressure to intervene to accelerate this process, particularly in urban settings where degraded areas are highly visible. Active restoration projects are becoming increasingly common, often at a cost of considerable time and labor. In these projects, land managers intervene in a range of ways to facilitate recovery, including restoring pre-disturbance topography (in terrestrial and wetland systems) or river channel patterns; reintroducing propagules of plants or animals;

and actively manipulating disturbance regimes such as fire and flooding (Perrow and Davy, 2002; Van Andel and Aronson, 2006).

There is considerable debate, however, regarding whether active restoration is always necessary (Prach and Hobbs, 2008; Clewell and McDonald, 2009; Rey Benayas et al., 2009), given the numerous examples of ecosystems recovering over a period of decades without human intervention (Jones and Schmitz, 2009). For example, the vast majority of forest in the eastern United States was logged approximately a century ago and is now second growth forest, which has recovered the structure and much of the pre-disturbance species composition of the original forest (Duffy and Meier, 1992; McLachlan and Bazely, 2001). Similar patterns of forest recovery have been documented in some tropical ecosystems (Guariguata et al., 1997; Finegan and Delgado, 2000; Letcher and Chazdon, 2009), although rates of tropical forest recovery are highly variable (Holl, 2007; Chazdon, 2008a) for several reasons that are discussed in more detail later. One of the most dramatic examples of extensive forest recovery is Puerto Rico, where by the end of the 1930s forest covered less than 10% of the island. The subsequent decline of the agriculture sector has facilitated natural forest regeneration, and by the year 2000, forest cover increased to more than 40% (Helmer, 2004; Páres-Ramos et al., 2008). Forest biomass and species richness in these secondary forests is similar to mature forests after 30–40 years of recovery (Aide et al., 2000).

In some cases restoration efforts may actually slow ecosystem recovery or have a strong influence on the direction of the successional trajectory. For instance, *Alnus acuminata* (Andean alder) is often planted with the goal of accelerating forest recovery in the Andes, but after 30 years of regeneration these areas have lower

* Corresponding author. Tel.: +1 831 459 3668; fax: +1 831 459 4015.
E-mail address: kholl@ucsc.edu (K.D. Holl).

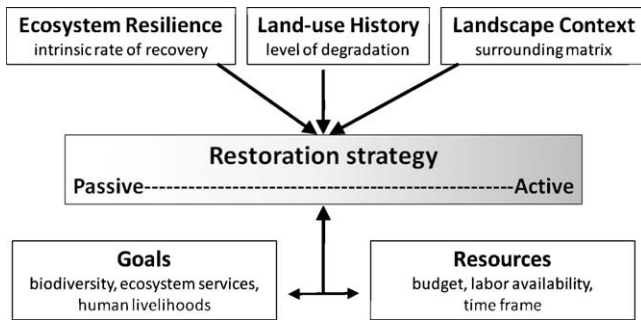


Fig. 1. Factors that should be considered when planning the management strategies for recovering/restoring degraded lands.

alpha and beta diversity in comparison with secondary forests of the same age (Murcia, 1997). Similarly, mechanically planting trees to restore the density and diversity of tropical dry forest trees in central Brazil causes damage to naturally resprouting species, resulting in no net gain in tree establishment (Sampaio et al., 2007).

These examples beg the question of when and where humans should intervene to actively restore ecosystems vs. simply allowing the ecosystems to passively recovery. Here we provide a conceptual framework for deciding whether and to what extent humans should intervene to facilitate forest recovery. These decisions are critically important given the limited resources available for restoration. We focus the majority of our examples on tropical forests, in keeping with the special issue, although the framework applies broadly to a range of ecosystems.

Tropical forests provide an excellent ecosystem in which to explore these ideas since over half the tropical moist forest cover worldwide has been reduced to less than 50% tree cover (Asner et al., 2009), which has contributed to extensive loss of biodiversity and greater than 12% of global carbon dioxide emissions (van der Werf et al., 2009). Although deforestation has been the dominant process in tropical forest, during the last 20 years there has been a substantial increase in tropical secondary forest due to primarily passive restoration (i.e. natural regeneration), but also to active restoration (Lamb et al., 2005; Wright and Muller-Landau, 2006; Chazdon, 2008b).

2. Conceptual framework

The decision of which restoration strategy should be employed in a degraded system depends on the natural rate of recovery and the desired endpoint for the ecosystem (Fig. 1). The rate of recovery is affected by the intrinsic ecosystem resilience (defined as the degree and pace with which an ecosystem recovers the initial structure and function following disturbance, sensu Westman, 1978), the level of human degradation, and the characteristics of the landscape around the focal area (Fig. 1). Information on these factors will help to decide on the type and degree of intervention that will be necessary. Equally important are the goals and the resources available for a project, which will help to determine the scale and timeframe of the project. A balanced evaluation of both these factors should be the first step in developing a restoration strategy.

2.1. Ecosystem resilience

Ecosystems vary greatly in the rate at which they are able to recover naturally from human disturbance. For example, a survey of 240 studies showed that aquatic systems take approximately 10 years to recover a range of ecosystem and community variables, whereas most forest systems take greater than 40 years (Jones and Schmitz, 2009). In tropical forests, the rate of recovery is strongly influenced by the types of disturbances with which these

systems have evolved and varies along abiotic gradients, including rainfall, temperature, and soil type (Holl, 2007). In general, natural resilience tends to be higher in drier tropical forest, in part because dry tropical forests have a much higher percentage of wind-dispersed seeds (Ewel, 1977; Vesk and Westoby, 2004; Vieira and Scariot, 2006), which leads to a lower degree of dispersal limitation. Moreover, resprouting is more common in tropical dry forests (Vesk and Westoby, 2004; Vieira and Scariot, 2006). This combination of characteristics, plus removing cattle grazing and reducing the frequency of fire, has permitted the recovery of extensive areas of tropical dry forest in northwestern Costa Rica within a matter of decades (Janzen, 2002).

Large-scale temperature gradients can also affect the rate of recovery particularly across elevation gradients with recovery being faster in relatively warmer areas which generally favor more rapid growth (Ewel, 1980; Zarin et al., 2001). Finally, soils in the tropics range from oxisols and ultisols which have low nutrient levels and high acidity to areas with more fertile, volcanic soils, such as andisols and inceptisols. Differences in availability of nutrients that are needed for growth, as well as concentrations of potentially toxic elements (e.g. Fe, Al), can have strong influences on growth rates (Herrera and Finegan, 1997; Moran et al., 2000; Zarin et al., 2001). For example, canopy height in forest regenerating on alfisols is twice as tall after 20 years as forests regenerating on other soil types in the Amazon Basin (Moran et al., 2000).

One would expect that systems with fewer numbers of species of plants and animals, and more generalist plant–animal interactions, such as eastern hardwood forests in the United States or less diverse tropical forest types, would be more resilient than more diverse systems. However, there are examples of highly diverse systems in which the vast majority of species have recovered over a few decades (Aide et al., 2000; Letcher and Chazdon, 2009) and less diverse systems where rarer species have not recovered (McLachlan and Bazely, 2001). Moreover, it is impossible to systematically compare the effect of diversity on recovery given the many other confounding factors.

2.2. Land-use history

Just as different forest types inherently differ in their resilience, the rate and direction of forest recovery are also influenced by the past land-use history (Fig. 1, Jones and Schmitz, 2009). The intensity of past land uses, which can range from selective logging and hunting to grazing to small-scale or industrial agriculture, affects many site-specific factors that influence the rate of recovery (reviewed in Holl, 2007). For example, both the intensity and duration of past land use affect the availability of propagules within a site (i.e. seed bank, resprouts, and existing seedlings); lands used for selective logging or shifting agriculture are more likely to retain a seed bank of forest species than those used for extended grazing or monoculture crop production (Meli, 2003; Holl, 2007). Past land-use practices also influence the remnant vegetation in a particular site, which in turn may affect the rate of recovery. For example, when grazing animals are removed from pastures, aggressive exotic grasses often arrest succession (reviewed in Holl and Cairns, 2002). Past and ongoing hunting of large animals can strongly limit seed dispersal and alter patterns of seed predation and herbivory, which in turn influence the rate and trajectory of recovery (Stoner et al., 2007; Wright et al., 2007). In more extreme cases, land-use practices that cause severe soil degradation (Aide and Cavelier, 1994) or change the hydrology (Zimmerman et al., 2007) can degrade a site to a point where restoration is difficult. For example, Moran et al. (2000) found that canopy height in former shifting agriculture sites increased at three times the rate of sites prepared with mechanical cultivation in the Amazon Basin.

Even within a given land-use type the frequency and intensity of disturbance can vary, and this will affect the rate of recovery and the species composition of the recovering habitat. For example, the number of clearing cycles of shifting agriculture is negatively related with the biomass accumulation rate (Lawrence et al., 2010). Species composition in areas that have been selectively logged and abandoned should not change much, but if there has been a history of repeated clearing, grazing, burning, or hunting spanning decades to centuries, the species pool is likely to be dominated by a subset of species that can tolerate these disturbances.

Many authors have highlighted the importance of the extent of degradation in determining the degree of intervention required to restore a specific site, and the possibility that extensive degradation will cause the ecosystem to cross a threshold where active restoration is impossible or extremely expensive (Hobbs and Norton, 1996; Whisenant, 1999; Lamb et al., 2005; Chazdon, 2008b; Jackson and Hobbs, 2009; Suding and Hobbs, 2009). Clearly, as the level of degradation becomes more intense, more active restoration will be necessary to achieve a state similar to predisturbance condition.

2.3. Landscape context

In addition to the intrinsic site conditions, the surrounding land-use matrix affects recovery because it serves as an important source of propagules, as well as potential disturbances. If restoration is to occur in an area previously used for large-scale industrial agriculture, such as sugar cane in southeastern Brazil or pasture in northeastern Australia, it may be several kilometers to the nearest sources of forest seeds, which can greatly limit the potential for passive restoration (White et al., 2004; Rodrigues et al., 2009). In contrast, in much of Central America there are commonly small patches of forest, riparian vegetation, living fences, and remnant trees within the agricultural land-use matrix that serve as sources of seeds, enhance the mobility of seed-dispersing fauna (Harvey et al., 2006; Chazdon et al., 2009), and in turn facilitate the recovery process. Moreover, disturbances from surrounding land uses, such as movement of agricultural chemicals, invasive species, or fire can impede recovery. Therefore, the spatial scale of human disturbance will strongly influence the ability of the system to recover.

Although a detailed GIS analysis of land-use patterns in the matrix around a focal site can provide useful information during the design phase of a study, this can be expensive and time consuming. Alternatively, Google Earth provides free access to high resolution aerial images for many regions of the world and basic analytical tools, which can greatly improve the understanding of the landscape context of a project without an extensive budget or technical expertise.

2.4. Goals

Historically, restoration efforts have focused on restoring the predisturbance species composition and a range of ecosystem functions (Bradshaw, 1984). Increasingly, however, there is recognition that the endpoint of ecosystem succession is necessarily dynamic given the inherent variability of ecosystems and both natural and human-induced climatic changes over time (Choi et al., 2008; Jackson and Hobbs, 2009), which makes it challenging to select an endpoint for restoration. Within the broad goal of “restoring tropical forest” there are often conflicting endpoints. Is the goal to maximize carbon sequestration, restore a mature forest plant composition, conserve a threatened primate, or balance conservation with providing for human livelihoods? Is restoring tree cover sufficient or is the goal to restore the full complement of species? Is a primary goal to create employment or educational opportunities rather than a specific ecological endpoint?

The numerous, potentially conflicting, ecological and social goals of even a single restoration project, highlight the importance of clearly identifying goals at the outset, ideally in consultation with all stakeholders. Although this may seem obvious, a surprising number of restoration projects lack clear goals (Lockwood and Pimm, 1999; Holl and Cairns, 2002; Bernhardt et al., 2005), which are critical for selecting a restoration approach. For example, if the goal of tropical forest restoration is to maximize carbon sequestration then densely planting a few rapid-growing tree species may be advisable, whereas if the goal is to increase biodiversity, planting several species of trees in some areas and allowing for natural recovery in other areas is more likely to maximize habitat heterogeneity for colonizing species. Restoration projects also may aim to achieve a range of social goals, such as providing income for local communities (Mesquita et al., 2010), offering educational opportunities (Cruz and Segura, 2010), or serving to reconnect people with natural systems (Clewett and Aronson, 2006).

2.5. Resources

Even when a restoration project has been designed around a strong understanding of the biological component and clear goals, limited funding will often constrain which restoration options are feasible. In these cases, it is fortunate that many tropical sites will recover through passive restoration. In other cases, projects that require minor intervention (e.g. one time planting or fire control during the first few years of recovery) may be achieved with a limited budget. But, if a site requires active restoration, substantial funding will be needed for at least a 5–10-year period to ensure the success of the project. Unfortunately, there is a strong temporal mismatch between the temporal scale of human decision-making (i.e. funding) and that of ecosystem recovery. In other words, humans want to see change immediately, but most ecosystems take decades to years to recover from disturbance naturally. Clearly, most funding will be needed in the initial phases of the project, but it is critical that a project also have funds for long-term monitoring and future interventions (Holl and Cairns, 2002; Tischew et al., 2010).

The common case of limited funding for tropical forest restoration highlights the need to consider whether passive recovery is an option and how to most strategically use the available resources to achieve the project goals. For example, planting islands of trees may increase habitat heterogeneity at a substantially lower cost than planting large areas with trees (Holl et al., *in press*). Another possibility is to utilize an agro-successional restoration approach (Vieira et al., 2009) and incorporate agroforestry approaches as a transition phase in restoration, which can help to simultaneously provide for human livelihoods, reduce management costs, and facilitate forest recovery.

3. Applying the framework to restoration decisions

In order to apply our framework to decision-making we recommend that managers begin by clearly identifying the goals of the restoration project, assessing the resources available, and answering the three questions we discuss below. This process will certainly be iterative, as the goals may need to be modified to fit the available resources.

3.1. If we take a passive restoration approach, what results do we expect?

A critical first step of any restoration project is to understand the ecology of the system and, in particular, document the rate of natural recovery before intervening. This sounds like common sense, but large amounts of money have been spent on ill-planned

restoration projects that are not necessarily beneficial for the environment (DellaSala et al., 2003). For example, Gardener et al. (2010) reported that 64% of the money spent on exotic plant eradication in the Galapagos Islands went to projects that were not completed. These examples have been best documented in reviews of compensatory restoration projects (NRC, 2001; Matthews and Endress, 2008; Tischew et al., 2010), which consistently report that only a small fraction of sites restored as mitigation for habitat destruction succeed in replacing the lost ecological communities and functions. There are many anecdotal cases of other types of failed restoration projects, but often projects are not monitored to determine the degree to which they achieve the original goals (NRC, 2001; Bernhardt et al., 2005), and information on failed outcomes are rarely published (Zedler, 2007).

It is human nature when viewing a degraded area to think that something must be done. But, as noted in the introduction, there are many examples where active restoration can slow or redirect recovery, and many examples where passive restoration can be effective over large areas. To assess the rate of natural recovery, it may be possible to gain information from other sites in the region that have been abandoned previously, either through site visits, talking to other land managers, or from the published literature. It is often wise to wait a few years to observe the rate of natural regeneration in the target area before intervening, given that site conditions vary greatly even over small spatial scales (Holl et al., *in press*). It is also important to identify the barrier(s) that if removed, would allow a system to recovery without further intervention.

3.2. *If intervention is necessary, how and when should we intervene to achieve the project goals?*

Again, the answer to this question should be based on the ecology of the system, the goals of the project, and the amount of resources available. In some cases, minor interventions (e.g. eliminating grazing, controlling fires) can be sufficient to initiate or accelerate the natural regeneration process (Janzen, 2002). In other cases, fast-growing woody species may establish quickly, whereas large-seeded, mature-forest species are likely to colonize over a time period of decades, if at all (Martínez-Garza and Howe, 2003). Many studies suggest that both passive and active restoration efforts often serve to restore the more common species, but that rarer species often do not recover, resulting forests with a subset of the original species (e.g., McLachlan and Bazely, 2001; Holl, 2002a; Martínez-Garza and Howe, 2003; Grimbacher and Catterall, 2007; Bonilla-Moheno, 2008). In such cases, enrichment planting or seeding of these less common, often later successional, species after a canopy has established is a promising restoration strategy to maximize diversity at a much lower cost than propagating and planting tree seedlings over a large area (Martínez-Garza and Howe, 2003; Lamb et al., 2005; Bonilla-Moheno and Holl, *in press*; Cole et al., 2011). In sites that are highly degraded or where the goal is to maximize short-term biomass it may be necessary to plant seedlings. It also is advisable to tailor restoration efforts to different conditions within a site. For example, if regeneration is faster near remnant forest patches then introducing propagules in areas distant from source populations will be the best expenditure of effort. Another high impact intervention would be to restore vegetation on steep slopes with high erosion. This approach would be particularly beneficial if the project goals include improving water quality or reducing sedimentation.

3.3. *At a landscape or regional scale, how can restoration resources be used most efficiently?*

Ideally, rather than deciding whether or not to invest resources in restoration on individual sites, the relative merits of several

projects should be compared at a regional scale. This approach is most appropriate where the funding for restoration is provided by general funds such as taxpayer dollars, international aid funds, or grants from private foundations. We recognize that some restoration resources, such as funds tied to individual sites (e.g. restoration required by specific mining or agricultural firms) or labor from volunteers motivated by a commitment to specific local project, are not fungible. An increasing amount of funds, however, are available for forest restoration through payment for environmental service programs, which usually focus on providing ecosystem services such as carbon sequestration and erosion reduction (Wunder, 2007), and such programs should consider cost effectiveness at a regional scale.

Resources should preferentially be allocated to sites where ecosystems are sufficiently resilient, but where degradation or the landscape context is inhibiting natural recovery, rather than sites which are likely to recover with no or minimal intervention. A difficult problem is what to do with sites where resilience is low and degradation is high, meaning that restoration is likely to be extremely expensive and the outcome uncertain (Hobbs et al., 2009). For example, in some severely degraded ecosystems, such as mines, it may be critical to intervene to minimize short-term acute threats to human health, such as revegetating highly disturbed areas to minimize toxic runoff to water supplies. Investing resources in such restoration projects may be deemed necessary from a human health and ethical standpoint, but they will draw scarce resources away from efforts that are more likely to succeed. A more cost effective approach in such cases may be to try to re-established 'novel' ecosystems that help to minimize off site impacts of concern, rather than trying to restore a semblance of the predisturbance conditions (Hobbs et al., 2009).

4. Conclusions

Our framework does not provide thresholds where there is a clear yes or no answer to land managers about when and how to intervene to facilitate recovery. While this vagueness is frustrating, we argue that yes/no answers do not reflect the ecological and social realities of most degraded sites. We advocate that if managers consider the questions we have outlined both during the planning process, as well as over time, monitoring results and using this information to implement an adaptive management approach, it will result in more efficient use of restoration resources both within and among projects. It will also maximize the degree to which restoration projects succeed in achieving their goals. An excellent example of this type of approach being applied at a regional scale is planning efforts to restore the Atlantic Forest biome in Brazil (Rodrigues et al., 2011). They have categorized nearly 500,000 ha in this biome along a gradient of lands ranging from those that have low potential for recovery and will need extensive planting to those that have pioneer establishment and will need enrichment planting to those that naturally recovery and do not need intervention.

There is a strong temporal mismatch between the temporal scale of human decision-making and that of ecosystem recovery. In other words, humans want to see change immediately but most ecosystems take decades to years to recover from disturbance naturally. In most cases a bit more patience to allow systems to follow the natural recovery process is needed. By waiting for at least few years, it is possible to assess whether intervention is necessary and if so how to best allocate efforts. To date, most direct comparisons of recovery in actively restored vs. passively restored tropical forests have been less than 5 years (Holl, 2002b), which means that it is often impossible to know how much the forest in sites restored using different approaches will differ a couple to several decades from now. As more long-term data sets on the effectiveness of

active tropical forest restoration efforts become available, those data will help in evaluating when and where to restore.

Acknowledgements

We thank the Holl lab group, Martha Bonilla, and an anonymous reviewer for their comments on previous versions of this manuscript.

References

- Aide, T.M., Cavelier, J., 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. *Restoration Ecology* 2, 219–229.
- Aide, T.M., Zimmerman, J.K., Pascarella, J.B., Rivera, L., Marcano-Vega, H., 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. *Restoration Ecology* 8, 328–338.
- Aronson, J., Milton, S.J., Blignaut, J.N. (Eds.), 2007. *Restoring Natural Capital*. Island Press, Washington, DC.
- Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., Emerson, R., 2009. A contemporary assessment of change in humid tropical forests. *Conservation Biology* 23, 1386–1395.
- Bernhardt, E.S., Palmer, M.A., Allan, J.D., Alexander, G., Barnas, K., Brooks, S., Carr, J., Clayton, S., Dahm, C., Follstad-Shah, J., Galat, D., Gloss, S., Goodwin, P., Hart, D., Hassett, B., Jenkinson, R., Katz, S., Kondolf, G.M., Lake, P.S., Lave, R., Meyer, J.L., O'Donnell, T.K., Pagano, L., Powell, B., Sudduth, E., 2005. Ecology—synthesizing US river restoration efforts. *Science* 308, 636–637.
- Bonilla-Moheno, M., 2008. *Forest Recovery and Management in the Yucatan Peninsula*. Mexico. University of California, Santa Cruz.
- Bonilla-Moheno, M., Holl, K.D., in press. Direct seeding to restore tropical mature-forest species in areas of slash-and-burn agriculture. *Restoration Ecology*, doi:10.1111/j.1526-100X.2009.00580.x.
- Bradshaw, A.D., 1984. Land restoration: now and in the future. *Proceedings of the Royal Society of London B* 223, 1–23.
- Chazdon, R., 2008a. Chance and determinism in tropical forest succession. In: Carson, W.P., Schnitzer, S.A. (Eds.), *Tropical Forest Community Ecology*. Wiley-Blackwell, Oxford, pp. 384–408.
- Chazdon, R., Harvey, C.A., Komar, O., Van Breugel, M., Ferguson, B.G., Griffith, D.M., Martinez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Philpott, S., 2009. Beyond reserves: a research agenda for conserving biodiversity in tropical cultural landscapes. *Biotropica* 41, 141–153.
- Chazdon, R.L., 2008b. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320, 1458–1460.
- Choi, Y.D., Temperton, V.M., Allen, E.B., Grootjans, A.P., Halassy, M., Hobbs, R.J., Naeth, M.A., Torok, K., 2008. Ecological restoration for future sustainability in a changing environment. *Ecoscience* 15, 53–64.
- Clewett, A., McDonald, T., 2009. Relevance of natural recovery to ecological restoration. *Ecological Restoration* 27, 122–124.
- Clewett, A.F., Aronson, J., 2006. Motivations for the restoration of ecosystems. *Conservation Biology* 20, 420–428.
- Cole, R.J., Keene, C.L., Zahawi, R.A., Holl, K.D., 2011. Direct seeding of late successional trees to restore tropical montane forest. *Forest Ecology and Management* 261, 1590–1597.
- Cruz, R.E., Segura, R.B., 2010. Developing the bioliteracy of school children for 24 years: a fundamental tool for ecological restoration and conservation in perpetuity of the Area de Conservación Guanacaste, Costa Rica. *Ecological Restoration* 28, 193–198.
- DellaSala, D.A., Martin, A., Spivak, R., Schulke, T., Bird, B., Criley, M., Van Daalen, C., Kreilick, J., Brown, R., Aplet, G., 2003. A citizen's call for ecological forest restoration: forest restoration principles and criteria. *Ecological Restoration* 21, 14–23.
- Duffy, D.C., Meier, A.J., 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology* 6, 196–201.
- Ewel, J., 1980. Tropical succession: manifold routes to maturity. *Biotropica* 12, 2–7.
- Ewel, J.J., 1977. Differences between wet and dry successional tropical ecosystems. *Geo-Eco-Trop* 1, 103–117.
- Finegan, B., Delgado, D., 2000. Structural and floristic heterogeneity in a 30-year-old Costa Rican rain forest restored on pasture through natural secondary succession. *Restoration Ecology* 8, 380–393.
- Gardener, M.R., Atkinson, R., Renteria, J.L., 2010. Eradications and people: lessons from the plant eradication program in Galapagos. *Restoration Ecology* 18, 20–29.
- Grimbacher, P.S., Catterall, C.P., 2007. How much do site age, habitat structure and spatial isolation influence the restoration of rainforest beetle species assemblages? *Biological Conservation* 135, 107–118.
- Guariguata, M.R., Chazdon, R.L., Denslow, J.S., Dupuy, J.M., Anderson, L., 1997. Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. *Plant Ecology* 132, 107–120.
- Harvey, C.A., Medina, A., Sanchez, D.M., Vilchez, S., Hernandez, B., Saenz, J.C., Maes, J.M., Casanoves, F., Sinclair, F.L., 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecological Applications* 16, 1986–1999.
- Helmer, E.H., 2004. Forest conservation and land development in Puerto Rico. *Landscape Ecology* 19, 29–40.
- Herrera, B., Finegan, B., 1997. Substrate conditions, foliar nutrients and the distributions of two canopy tree species in a Costa Rican secondary rain forest. *Plant and Soil* 191, 259–267.
- Hobbs, R.J., Higgs, E., Harris, J.A., 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24, 599–605.
- Hobbs, R.J., Norton, D.A., 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4, 93–110.
- Holl, K.D., 2002a. Long-term vegetation recovery on reclaimed coal surface mines in the eastern USA. *Journal of Applied Ecology* 39, 960–970.
- Holl, K.D., 2002b. Tropical moist forest. In: Perrow, M.R., Davy, A.J. (Eds.), *Handbook of Ecological Restoration*. Cambridge University Press, Cambridge, UK, pp. 539–558.
- Holl, K.D., 2007. Old field vegetation succession in the neotropics. In: Hobbs, R.J., Cramer, V.A. (Eds.), *Old Fields*. Island Press, Washington, DC, pp. 93–117.
- Holl, K.D., Cairns Jr., J., 2002. Monitoring and appraisal. In: Perrow, M.R., Davy, A.J. (Eds.), *Handbook of Ecological Restoration*, vol. 1, pp. 411–432.
- Holl, K.D., Zahawi, R.A., Cole, R.J., Ostertag, R., Cordell, S., in press. Planting seedlings in plantations versus tree islands as a large-scale tropical forest restoration strategy. *Restoration Ecology*, doi:10.1111/j.1526-100X.2010.00674.x.
- Jackson, S.T., Hobbs, R.J., 2009. Ecological restoration in the light of ecological history. *Science* 325, 567–569.
- Janzen, D.H., 2002. Tropical dry forest: area de Conservación Guanacaste, north-western Costa Rica. In: Perrow, M.R., Davy, A.J. (Eds.), *Handbook of Ecological Restoration*. Cambridge University Press, Cambridge, UK, pp. 559–583.
- Jones, H.P., Schmitz, O.J., 2009. Rapid recovery of damaged ecosystems. *PLoS One* 4, e5653.
- Lamb, D., Erskine, P.D., Parrotta, J.D., 2005. Restoration of degraded tropical forest landscapes. *Science* 310, 1628–1632.
- Lawrence, D., Radel, C., Tully, K., Schmoor, B., Schneider, L., 2010. Untangling a decline in tropical forest resilience: constraints on the sustainability of shifting cultivation across the globe. *Biotropica* 42, 21–30.
- Letcher, S.G., Chazdon, R.L., 2009. Rapid recovery of biomass, species richness, and species composition in a forest chronosequence in northeastern Costa Rica. *Biotropica* 41, 608–617.
- Lockwood, J.L., Pimm, S.L., 1999. When does restoration succeed? In: Weiher, E., Keddy, P. (Eds.), *Ecological Assembly Rules*. Cambridge University Press, Cambridge, pp. 363–392.
- Martinez-Garza, C., Howe, H.F., 2003. Restoring tropical diversity: beating the time tax on species loss. *Journal of Applied Ecology* 40, 423–429.
- Matthews, J.W., Endress, A.G., 2008. Performance criteria, compliance success, and vegetation development in compensatory mitigation wetlands. *Environmental Management* 41, 130–141.
- McLachlan, S.M., Bazely, D.R., 2001. Recovery patterns of understory herbs and their use as indicators of deciduous forest regeneration. *Conservation Biology* 15, 98–110.
- Meli, P., 2003. Tropical forest restoration. Twenty years of academic research. *Inter-ciencia* 28, 581–589.
- Mesquita, C.A.B., Holvorcem, C.G.D., Lyrio, C.H., de Menezes, P.D., da Silva Dias, J.D., Azevedo Jr., J.F., 2010. COOPLANTAR: a Brazilian initiative to integrate forest restoration with job and income generation in rural areas. *Ecological Restoration* 28, 199–207.
- Moran, E.F., Brondizio, E.S., Tucker, J.M., Da Silva-Forsberg, M.C., McCracken, S., Falesi, I., 2000. Effects of soil fertility and land-use on forest succession in Amazonia. *Forest Ecology and Management* 139, 93–108.
- Murcia, C., 1997. Evaluation of Andean alder as a catalyst for the recovery of tropical cloud forests in Colombia. *Forest Ecology and Management* 99, 163–170.
- National Research Council, 2001. *Compensating for wetland losses under the Clean Water Act*. National Academy Press, Washington, D.C.
- Páres-Ramos, I.K., Gould, W.A., Aide, T.M., 2008. Agricultural abandonment, sub-urban growth, and forest expansion in Puerto Rico between 1991 and 2000. *Ecology and Society*, 13.
- Perrow, M.R., Davy, A.J., 2002. *Handbook of Ecological Restoration*. Cambridge, UK.
- Prach, K., Hobbs, R.J., 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology* 16, 363–366.
- Rey Benayas, J.M., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. *Frontiers in Ecology and Environment* 6, 329–336.
- Rey Benayas, J.M., Newton, A.C., Diaz, A., Bullock, J.M., 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325, 1121–1124.
- Rodrigues, R.R., Lima, R.A.F., Gandolfi, S., Nave, A.G., 2009. On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation* 142, 1242–1251.
- Rodrigues, R.R., Gandolfi, S., Nave, A.G., Aronson, J., Barreto, T.E., Vidal, C.Y., Brancalion, P.H.S., 2011. Large-scale ecological restoration of high diversity tropical forests in SE Brazil. *Forest Ecology and Management* 261, 1605–1613.
- Sampaio, A.B., Holl, K.D., Scariot, A., 2007. Does restoration enhance regeneration of seasonal deciduous forests in pastures in central Brazil? *Restoration Ecology* 15, 462–471.
- Stoner, K.E., Vulinec, K., Wright, S.J., Peres, C.A., 2007. Hunting and plant community dynamics in tropical forests: a synthesis and future directions. *Biotropica* 39, 385–392.
- Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology & Evolution* 24, 271–279.

- Tischew, S., Baasch, A., Conrad, M.K., Kirmer, A., 2010. Evaluating restoration success of frequently implemented compensation measures: results and demands for control procedures. *Restoration Ecology* 18, 467–480.
- van der Werf, G.R., Morton, D.C., DeFries, R.S., Olivier, J.G.J., Kasibhatla, P.S., Jackson, R.B., Collatz, G.J., Randerson, J.T., 2009. CO₂ emissions from forest loss. *Nature Geoscience* 2, 737–738.
- Van Andel, J., Aronson, J. (Eds.), 2006. *Restoration Ecology: The New Frontier*. Blackwell Publishing, Malden, MA.
- Vesk, P.A., Westoby, M., 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* 92, 310–320.
- Vieira, D.L.M., Holl, K.D., Peneireiro, F.M., 2009. Agro-successional restoration as a strategy to facilitate tropical forest recovery. *Restoration Ecology* 17, 451–459.
- Vieira, D.L.M., Scariot, A., 2006. Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecology* 14, 11–20.
- Westman, W.E., 1978. Measuring the inertia and resilience of ecosystems. *Bioscience* 28, 705–710.
- Whisenant, S.G., 1999. *Repairing Damaged Wildlands: A Process-oriented, Landscape-approach*. Cambridge University Press, Cambridge.
- White, E., Tucker, N., Meyers, N., Wilson, J., 2004. Seed dispersal to revegetated isolated rainforest patches in North Queensland. *Forest Ecology and Management*, 409–426.
- Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. *Biotropica* 38, 287–301.
- Wright, S.J., Stoner, K.E., Beckman, N., Corlett, R.T., Dirzo, R., Muller-Landau, H.C., Nunez-Iturri, G., Peres, C.A., Wang, B.C., 2007. The plight of large animals in tropical forests and the consequences for plant regeneration. *Biotropica* 39, 289–291.
- Wunder, S., 2007. The efficiency of payments for environmental services in tropical conservation. *Conservation Biology* 21, 48–58.
- Zarin, D.J., Ducey, M.J., Tucker, J.M., Salas, W.A., 2001. Potential biomass accumulation in Amazonian regrowth forests. *Ecosystems* 4, 658–668.
- Zedler, J.B., 2007. Success: an unclear, subjective descriptor of restoration outcomes. *Ecological Restoration* 25, 162–168.
- Zimmerman, J.K., Aide, T.M., Lugo, A.E., 2007. Implications of land use history for natural forest regeneration and restoration strategies in Puerto Rico. In: Hobbs, R.J., Cramer, V.A. (Eds.), *Old Fields*. Island Press, Washington, DC, pp. 51–74.