Synthesis

The ecology and economics of restoration: when, what, where, and how to restore ecosystems

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ABSTRACT. Restoration ecology has provided a suite of tools for accelerating the recovery of ecosystems damaged by drivers of global change. We review both the ecological and economic concepts developed in restoration ecology, and offer guidance on when, what, where, and how to restore ecosystems. For when to restore, we highlight the value of pursuing restoration early to prevent ecosystems from crossing tipping points and evaluating whether unassisted natural recovery is more cost-effective than active restoration. For what to restore, we encourage developing a restoration plan with stakeholders that will restore structural, compositional, and functional endpoints, and whose goal is a more resistant and resilient ecosystem. For where to restore, we emphasize developing restoration approaches that can address the impediment of rural poverty in the developing world and identifying and then balancing the ecosystems and regions in most need of restoration and those that are best positioned for restoration success. For the economics of how to restore ecosystems, we review the advantages and disadvantages of market-based strategies, such as environmental insurance bonds and Payment for Ecosystem Services frameworks, for funding, incentivizing, and ensuring restoration. For the ecology of how to restore ecosystems, we discuss the value of taking into account various ecological theories, site history, and landscape and aquascape perspectives, and employing a more inclusive toolbox that holistically considers alterations to propagule pressure, abiotic conditions, and biotic interactions. Finally, we draw attention to the importance of monitoring; adaptive management; stakeholder involvement; collaborations among scientists, managers, and practitioners; formal evaluation throughout the restoration process; and integrating ecological and economic concepts to maximize restoration success. We hope this overview of key ecological and economic concepts in restoration science sheds light on the discipline and facilitates restoring and maintaining the services and products provided by natural capital, thus improving human livelihoods and hope for posterity.

Key Words: *biodiversity offset; climate change; community assembly and disassembly; ecological threshold; ecosystem engineer; ecosystem function and service; monitoring; novel and hybrid community; payment for ecosystem services; translocation and reintroduction*

INTRODUCTION

Restoration ecology has provided a suite of ecological and economic tools and theories for accelerating the recovery of damaged ecosystems that have proven to be incredibly valuable to humans (Palmer et al. 1997, Hobbs and Harris 2001, SER 2004, Young et al. 2005, Hobbs and Suding 2009, Suding 2011). For example, ecosystem service valuations suggest that the economic benefits of restoration can outweigh the costs (Bullock et al. 2011), and meta-analyses of the published literature suggest that ecological restoration can increase the provisioning of biodiversity and ecosystem services (Dodds et al. 2008, Benayas et al. 2009, De Groot et al. 2013). Consequently, despite controversy regarding how often mandated restoration results in measurable improvements (Bernhardt et al. 2007), theory suggests that ecological restoration can offer a crucial complement to conservation efforts in maintaining services provided by natural capital and thus improving human livelihoods (Dobson et al. 1997, Hobbs and Harris 2001).

This potential value to society has propelled ecological restoration to a prominent role in global environmental policy (Bullock et al. 2011). For instance, by 2020, the European Union aims to restore ecosystems "so far as feasible" to cease biodiversity loss and degradation of ecosystem services (https://www.iucn.org/regions/europe/our-work/eu-biodiversity-policy). By this same target date, the international Convention on Biological Diversity has targeted the restoration of ecosystems that provide essential services. And by 2030, countries of the United Nations have committed to restoring 350 million hectares of degraded ecosystems to combat climate change (Suding et al. 2015).

Importantly, there are several international and national laws that hold parties liable for damaging ecosystems, which at least partially fuels the science of restoration (Rohr et al. 2013). Through several acts, such as the *Endangered Species Act* and *Clean Water Act*, the United States holds responsible parties liable for ecological restoration. In the United States, some of this liability is enforced through the Natural Resource Damage Assessment and Restoration Program, which is limited to mandating restoration in the event of oil spills and hazardous substance releases. Other regulatory mechanisms are used to require restoration from other damaging activities, such as anthropogenic flooding or infrastructure development. The European Union has a program similar to the Natural Resource Damage Assessment and Restoration Program that is described in an environmental liability directive (Rohr et al. 2013). Even when damage to natural capital cannot be attributed to a specific organization, governmental and nongovernmental agencies fund ecosystem restoration in many countries, which further promotes restoration science. For instance, the United States and Canada have provided more than 1 billion dollars to fund restoration of the Great Lakes from damage caused by the release of various invasive species and nonpoint-source pollutants (Allan et al. 2013).

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Despite these national and international regulations that mandate ecological restoration, the field of restoration ecology is young, emerging as a separate discipline in ecology only in the 1980s (Jordan and Lubick 2012). Although several books that thoroughly cover the discipline have been published since then (Falk et al. 2006, Clewell and Aronson 2007, Suter, 2007, Hobbs and Suding 2009, Jordan and Lubick 2012), the detail, rigor, and length of books can be daunting to those looking for an initial introduction or overview to a discipline. A review paper on the many ecological and economic concepts that restoration ecology has spawned and accentuated might be less intimidating than a book, but such a publication does not exist (but see SER 2004 for a primer). To address this gap, we review and highlight insights from ecological and economic principles on when, what, where, and how to restore damaged ecosystems, as well as how to assess restoration success. Our goal is to offer introductory but reasonably comprehensive coverage of concepts advanced in restoration ecology. Because our emphasis is on breadth, we acknowledge that depth has been occasionally relinquished, and we are almost certainly not being exhaustive. Consequently, we encourage readers to explore the cited and associated literature when interested.

Importantly, we define restoration ecology as the science associated with returning to society the biodiversity and ecosystem functions of degraded, damaged, or destroyed ecosystems. This is broader than the Society for Ecological Restoration (SER) definition, which is the science of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004). The distinction between the two definitions is that the SER definition defines ecological restoration only as facilitating the recovery of the damaged or degraded ecosystem, whereas our broader definition also includes approaches that restore biodiversity or function at damaged or other sites. Hence, in this review, we cover concepts that are arguably not restoration based on the SER definition, such as mitigation, "off-site restoration," and the creation of novel or hybrid (with novel elements) ecosystems. We chose to broaden the definition because these concepts are so commonly and controversially covered in the restoration literature, and the historical challenges of successful restoration, as well as the rapid pace of global change, have required that restoration practitioners rethink their definitions of restoration success (Bernhardt et al. 2007, Hiers et al. 2016). While synthesizing these concepts, we emphasize five main components of successful restoration: (1) defining correct and meaningful baselines and selecting realistic and appropriate restoration endpoints, (2) balancing restoration where it is needed most with where it will most likely be successful, (3) creating sustainable economic systems to incentivize restoration, (4) understanding and manipulating the correct ecological processes to successfully restore ecosystems, and (5) monitoring to determine restoration success. Finally, we end with a section on tensions and challenges in restoration ecology.

WHEN TO RESTORE
Ecological restoration is often described on a continuum from passive to active restoration. Although this continuum is used somewhat commonly in the literature, passive restoration is an oxymoron because restoration is defined as assisting the recovery of biodiversity and/or ecosystem functions, and by definition,

assistance cannot be passive. Nevertheless, in passive restoration, humans assist by removing, lessening, or ameliorating the factor (s) that are damaging the system, and then monitor the system to ensure that it recovers via natural processes to some previous "healthy" condition. It is often used synonymously with monitored natural recovery. In contrast, remediation refers to the removal of foreign, ecologically deleterious substances without the subsequent monitoring. Hence, with passive restoration or remediation, there is no further assistance after the damaging factor has been removed, though recovery failure may require a more active approach to restoring the ecosystem. Active restoration refers to both removing the factor that is damaging the system and intervening in some additional way to accelerate ecosystem recovery relative to the natural recovery rate (Fig. 1) (Benayas et al. 2009, Rohr et al. 2013).

Fig. 1. Scenarios where human-assisted or active restoration (red line) is (A) and is not (B) more cost-effective than passive restoration (blue line), where the stressor or its adverse effects are removed or mitigated (rectangle) but the system is monitored until it recovers naturally to the mean baseline level of ecosystem services. Also shown is compensatory restoration for the active (green line) and passive restoration (purple line) scenarios. Compensatory restoration, which is required only in some countries, requires the party responsible for the damage to compensate the public for the time and magnitude of the lost ecosystem services. Note how the compensatory restoration is a mirror image (relative to the baseline) of the active and passive restoration but is later in time. Compensatory restoration can begin at any time after the damage has begun (i.e., before or after the active or passive restoration is complete) and often entails improving the services offered by natural resources at ecosystems near the damaged site (off-site restoration). Although the figure is drawn as if the same result will eventually be achieved regardless of the methods, this is not always true.
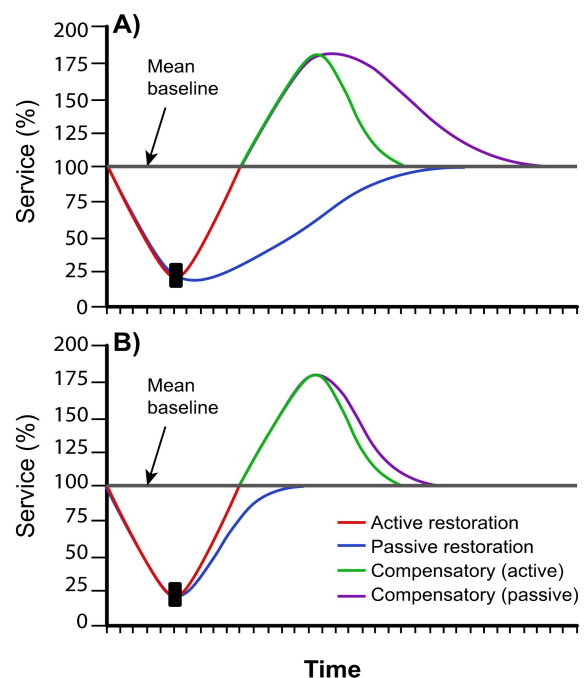
Passive restoration may be a more cost-effective or appropriate course of action, and in some cases, active restoration can even cause more harm than good. For instance, mechanically planting trees can damage naturally resprouting vegetation (Holl and Aide 2011), dredging sediments can resuspend contaminants, making them more bioavailable (Fuchsman et al. 2014), and channel reconfiguration efforts in river restoration can lead to long-term losses of sensitive taxa (Bernhardt and Palmer 2011). Determining whether active or passive restoration is optimal requires knowing the degree of damage; the rate of natural ecosystem recovery, which can be influenced by disturbances and sources of propagules (dispersers); the landscape or aquascape context in which the site is positioned; and the restoration goals, funds, and costs (Dobson et al. 1997, Holl and Aide 2011). For example, the high costs of planting trees made passive restoration more cost-effective than active restoration for a forest restoration project in Latin America (Birch et al. 2010), and a meta-analysis of 240 ecosystems suggested that passive restoration might be more cost-effective because most of these systems recovered naturally from disturbances in ~10 years (Jones and Schmitz 2009), although most ecosystems had relatively minor disturbances. When natural recovery rates are unknown, it can be beneficial to estimate site-specific, unassisted recovery rates for a few years before intervening (Holl and Aide 2011).

Whether passive or active restoration is more cost-effective will depend partly on whether the restoration is occurring in a country that requires compensatory restoration, which compels the responsible party to compensate the public for the lost services during the period before restoration is completed (Fig. 1). Passive restoration tends to be slower than active restoration; thus, the compensatory costs are typically larger for passive restoration, which makes it less cost-effective in countries where compensatory restoration is mandated (Fig. 1), such as in the United States. It is important to keep in mind that even if passive restoration is more cost-effective, in some countries active restoration might still be required by law. In fact, restoration is often policy driven, and the regulatory frameworks and policy instruments often impose rather significant limitations. Finally, it is often useful to consider restoration as early as possible because this can influence the type of remediation that is employed, can ensure that sensitive areas are protected during the remediation process, and can reduce the likelihood that damaged ecosystems transition to adverse alternative stable states (see *Thresholds, alternative states*). Importantly, whether passive or active restoration should be implemented strongly depends on the economic costs and benefits of each; thus, including an ecological economist who has experience in ecological cost-benefit analyses early in restoration planning is critical.

WHAT TO RESTORE: RESTORATION GOALS
What to restore often represents the beginning of the restoration planning process. It should entail establishing measurable goals and benchmarks with significant stakeholder involvement to maximize the chances of obtaining and demonstrating restoration success.

Natural variability and defining baseline conditions
Successful restoration is often measured against a specific set of habitat characteristics that are believed to represent the structure and function of a predisturbance system, often referred to as a baseline. Because the baseline at the site that needs restoration no

longer exists, reference sites are used to approximate this baseline. Selecting reference conditions is a multifaceted problem and might include the use of historical records, paleoecological data, quantitative models, best professional judgment, or extant reference sites (Thorpe and Stanley 2011). Defining reference conditions and the way in which this concept is employed in the literature is remarkably inconsistent (Reynoldson et al. 1997, Stoddard et al. 2006), and can lead to overly restrictive criteria with unintended consequences (Hiers et al. 2016).

Regardless of whether the baseline is characterized by historical properties or the most suitable extant conditions, a single reference site is insufficient to characterize natural spatiotemporal variability (Ruiz-Jaen and Aide 2005). This highlights that ecological restoration should not be focused on a specific numerical value (e.g., number of species) but rather on set goals within a realistic range of values that takes into account the importance of past, legacy, and current disturbances (Brudvig 2011, Hiers et al. 2016). An alternative approach, which integrates both spatial and temporal variation in reference conditions, is to implement a before-after control-impact design, which highlights the importance of considering restoration as a manipulative experiment, with adequate controls and replication.

Finally, whether baseline conditions are stationary around some average condition or changing over time will influence the rate at which apparent recovery is observed (Duarte et al. 2009). For example, if conditions in reference sites are deteriorating as a result of climate change or other long-term directional disturbances, observed recovery might appear to occur sooner relative to reference sites that are not degrading (Fig. 2). In this example, the fact that restored sites appear to achieve similar ecological structure or functioning as the reference sites does not mean that the original objectives were achieved. Not only is the variation and constancy of the baseline important; the trajectory and stability of the ecological responses of the restoration are also important (Fig. 2). Low stability (high variance) of ecological responses in restored sites might indicate successful restoration earlier than more stable sites, but higher stability itself is often a preferable restoration outcome (see *Restoration endpoints*).

Restoration endpoints
A fundamental component of any successful restoration activity is to identify restoration goals and objectives (Palmer et al. 2005, Hobbs 2007). While most restoration ecologists would agree that successful restoration should maximize or emulate baseline attributes, including genetic diversity, community structure and function, and the services provided by ecosystems, there is a lack of consensus about how many attributes to measure and which features should be prioritized. Pereira et al. (2013) developed a list of essential biodiversity variables for biodiversity conservation, which include genetic composition of species of interest, species' abundance, community composition, and ecosystem function, and we believe that a similar list of essential restoration values (ERVs) should be used as restoration endpoints in monitoring plans (Table 1). Although it is unlikely that all restoration programs would include all of the ERVs, this list highlights the fundamental characteristics of ecosystems that might need to be restored and maintained to ensure long-term success. Regardless of which ERVs are used, evaluating restoration projects across multiple ERVs should increase restoration success.

Table 1. Examples of essential restoration values for restoration of degraded and disturbed ecosystems that align with ecological and conservation priorities (modified from Pereira et al. 2013).

Essential restoration values	Examples	Rationale
Genetic diversity	Genotypic variation of restored populations or threatened or endangered species	Maximize chance of including individuals that optimally perform in local conditions. Preserve intraspecifc diversity. Maximize ecosystem function.
Individual fitness	Survival, growth, and reproductive rate of restored populations	To project long-term population growth and persistence.
Population abundance	Density of keystone species or apex predators; health of threatened or endangered species	Allow for threatened species assessments. Simple sampling protocol for population health and persistence.
Species traits	Multitrait community functional diversity; key traits that affect specific ecosystem services	Alternative measure of community diversity that does not depend on species identity. Allows assessment of whether restored sites are as functionally diverse as reference sites. Maximize ecosystem function.
Evolutionary diversity	Measures of total and differences in evolutionary diversity; spatial turnover in evolutionary history	Alternative measure of community diversity that does not depend on species identity. Measure of functional diversity when traits are unknown. Maximize ecosystem function.
Community structure and composition	Species richness and diversity; compositional turnover	Straightforward measures, relatively easy to quantify and compare. Most commonly collected data; makes broad spatial and temporal comparisons possible. Maximize ecosystem function.
Ecosystem function	Carbon sequestration and net primary production; nutrient cycling	Measures ecosystem health. Maximize return on restoration efforts.
Resistance and resilience	Magnitude of response to, and rate of, recovery from natural disturbances	Directly measure ecosystem robustness. Informs long-term restoration success.
Ecosystem services	Pollination; reduced stormwater flow	Quantify economic benefits of restoration. Maximize return on restoration efforts. Aligns with economic and policy priorities.

Fig. 2. The influence of baseline conditions on apparent rates of recovery in damaged ecosystems. The figure shows situations where baseline conditions (+/- SD) are consistent (upper panel) and degrading (lower panel) over time. Solid black lines indicate the ecological trajectory of restored sites and end where there is no statistical difference between restored and baseline conditions. Perceived recovery occurs much more rapidly under low stability or because of degrading baseline conditions.
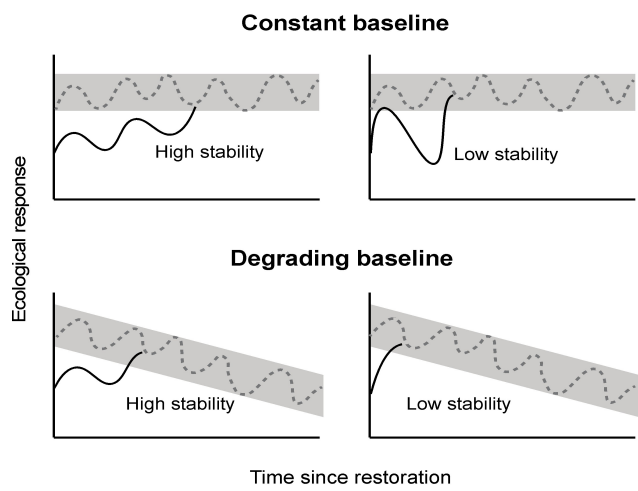
Many of the proposed ERVs in Table 1 are already considered regularly in restoration ecology (e.g., genetic diversity, species richness, and ecosystem function), whereas other measures, such as the analysis of species traits or the evolutionary (phylogenetic) distances separating species, are employed more rarely. The diversity of traits or evolutionary lineages in a local system have been recommended as useful alternatives to traditional measures of community composition because they can be linked to the delivery and stability of ecosystem functions and services (Cadotte et al. 2011, Cadotte 2013). Restoration activities that select for greater trait diversity create species assemblages that occupy more niches, which often convert more of the local resources into measurable functions, such as greater community biomass production (Cadotte et al. 2011).

Beyond traits, species' functional and trophic roles are critical to understanding the functions of natural communities. Apex predators play a disproportionate role in regulating the structure and function of ecosystems, and the losses of trophic cascades that they drive have resulted in unanticipated ecological effects, such as increases in invasive species and diseases, changes in fire frequencies, reductions in carbon sequestration, and alterations in biogeochemical cycles (Ripple et al. 2014). Reestablishing these large consumers and the critical services they offer should be a priority in ecological restoration (Ripple et al. 2014).

Importantly, restoration scientists must remember that threatened, endangered, or rare species might be lost if the restoration targets are ecosystem functions, services, resistance,

or resilience; similarly, ecosystem functions and services might be diminished if the restoration target is species richness or threatened species. Hence, to enhance the likelihood that both rare species and services are restored, where possible, we encourage that restoration targets include structural (habitat structure and disturbance regimes), compositional (biodiversity), and functional endpoints of the ecosystem before damage. However, in reality, this is challenging, and practitioners often must consider trade-offs among structural, compositional, and functional endpoints.

Thresholds, alternative states, and what to restore
The theoretical concepts of ecological thresholds, resistance, and resilience have important practical applications for restoration (Suding and Hobbs 2009). Ecological thresholds are defined as abrupt, nonlinear changes in composition or function of communities in response to disturbance. Although their frequency in nature is controversial (Capon et al. 2015), they have been reported in lake, coral reef, pelagic, and desert communities (Bellwood et al. 2004, Scheffer et al. 2009). As illustrated in Fig. 3, natural communities that are resistant (ability to maintain equilibrium conditions following disturbance) and exhibit resiliency (ability to return to predisturbance conditions after disturbance) to disturbances have deep basins of attraction that slow the transition to an alternative state. In contrast, communities exposed to chronic or extreme stressors are much more likely to undergo state transitions. Depending on the type, duration, extent, and level of the stressor, these alternative states may remain stable long after stressors are removed, resulting in a novel community that is unlikely to return to the original baseline or reference condition (Scheffer et al. 2009, Suding and Hobbs 2009).

Fig. 3. Threshold responses of communities to levels of stress (upper panel) and the effects of stressors on the transition of communities to an alternative stable state. Stressor exposure is hypothesized to reduce the depth of attraction basins, making it more likely that the community will undergo a regime shift. Greater effort is needed to restore ecosystems after regime shifts, and some systems that experienced a regime shift might not be restorable.
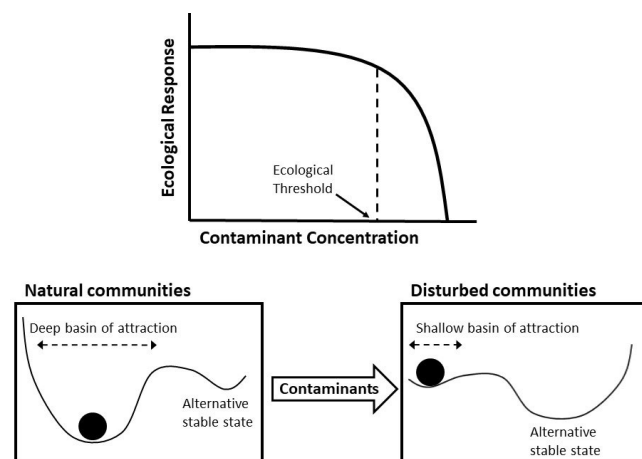
Assuming that threshold responses and alternative stable states are common, there are three important upshots of these critical transitions. First, alternative stable states emphasize the importance of preventing levels of stressors from exceeding critical thresholds, which highlights the importance of starting restoration early to prevent these transitions (Rohr et al. 2016). Second, if regime shifts have occurred, some restoration scientists have argued that the only viable option is to "restore" with a novel or hybrid community, which returns ecosystem functions but with a different species composition (Hilderbrand et al. 2005, Seastedt et al. 2008, Suding and Hobbs 2009, Higgs et al. 2014, Hobbs et al. 2014). Not surprisingly, novel and hybrid targets are controversial, with some researchers questioning the notion that historical communities cannot be restored, as well as whether novel or hybrid targets are restored at all (Murcia et al. 2014). Third, given the rapidly changing world that humans have created, some restoration ecologists have postulated that novel or hybrid communities might be defensible even if historical communities can be restored. They have argued that few ecosystems have escaped the widespread effects of anthropogenic disturbances, such as climate and land use changes, species invasions, or globally distributed contaminants, which makes it challenging to determine what the restoration target should be, and that novel or hybrid communities could be designed to offer more ecosystem services and be more resistant and resilient to anthropogenic change than historical ecosystems (Choi 2007, Seastedt et al. 2008, Jackson and Hobbs 2009, Thorpe and Stanley 2011, Rohr et al. 2013, Hobbs et al. 2014). As mentioned in the *Introduction*, this would be inconsistent with many definitions of restoration; thus, the trade-offs of various restoration targets must be considered. Wagner et al. (2016) offer a decision support tool for determining when the goal of management of a damaged ecosystem should be remediation, restoration to historical conditions, or a hybrid or novel ecosystem. Given the uncertainties regarding when critical transitions will occur, whether they can be reversed, and the costs and benefits of their prevention and reversal, they pose serious challenges to economists and decision-makers who are attempting to weigh various restoration options.

WHERE TO RESTORE
Based on our broad definition of restoration, returning lost biodiversity and ecosystem functions to society can be done at the location where damage occurred or elsewhere, referred to as on-site restoration and "off-site restoration," respectively. Off-site restoration is intentionally in quotes because it does not meet the definition of restoration proposed by the SER (SER 2004) because it does not assist with the recovery of the damaged or degraded ecosystem. Off-site restoration is often used synonymously with mitigation or biodiversity offsets, the latter of which provides a mechanism for maintaining or enhancing natural capital and ecosystem services in situations where development is being planned, despite detrimental environmental impacts (Ives and Bekessy 2015).

Although on-site restoration is usually preferable to off-site restoration, there are instances where off-site restoration might be more desirable or even required. First, off-site restoration might be compulsory in countries where compensatory restoration is mandated, which can entail improving natural resources at sites other than the one being restored to compensate the public for lost resources at the altered site (Fig. 1). Second,

off-site restoration might be required or preferred in scenarios where the stressor realistically cannot be removed, where removal is not practical, or where any damage is irreversible. This occurs commonly with some invasive species and contaminants that cannot be removed without causing extensive damage or where remediation is impractical because of continuous inputs from the surrounding landscape or aquascape. Third, off-site restoration might be defensible when the benefits of development or resource extraction far exceed the local loss of ecosystem services. However, there are serious ethical and economic issues to offsetting, such as the local human population not being compensated for damages to their natural capital and ecosystem service debts associated with offsetting (Ives and Bekessy 2015). Finally, off-site restoration might be justified if conditions are expected to deteriorate with a high likelihood of threatening local biodiversity. As an example, some restoration ecologists have recommended reestablishing communities poleward in anticipation of climate change (Choi 2007). However, others have expressed concerns about this approach because although climate change can enhance damage caused by some stressors (Moe et al. 2013), it might ameliorate the effects of other stressors (Rohr et al. 2011), which makes reliable economic cost-benefit analyses difficult. Additionally, off-site restoration in anticipation of climate change can be challenging because of uncertainties regarding the magnitude and effects of climate change (Harris et al. 2006, Choi 2007, Rohr et al. 2013).

Importantly, success of landscape- and aquascape-scale restoration will be more likely in some ecosystems and parts of the world than in others (Menz et al. 2013). Nevertheless, most restoration occurs in developed countries rather than in the developing world where the need for restoration is most acute (Aronson et al. 2010). Two of the biggest challenges to restoration science will be to develop approaches that can address the restoration impediment of rural poverty in the developing world (Lamb et al. 2005), and to identify and then balance the ecosystems and regions in most need of restoration and those that are best positioned for restoration success (Menz et al. 2013).

HOW TO RESTORE: THE ECONOMIC CONCEPTS

Before restoration can occur, funds are needed to implement restoration; thus, economic principles that facilitate providing adequate capital are a crucial component of how to restore biodiversity and ecosystem functions (Holl and Howarth 2000). Although there are several laws and associated litigation that financially support some restoration (Rohr et al. 2013), most restoration projects are small and rarely have funds for considering landscape or aquascape contexts or for monitoring to determine restoration success (Holl et al. 2003, Bernhardt et al. 2007, Lake et al. 2007, Rohr et al. 2007, Brudvig 2011, Rohr et al. 2013). Additionally, economic valuations of ecosystem services shortchange their value to posterity because their future value is habitually externalized and discounted, often exponentially declining into the future (Bullock et al. 2011, Rohr et al. 2013). Hence, financial needs for restoration typically exceed available resources, even where solid planning is in place; thus, the success of future restoration projects will undoubtedly depend on economic efficiencies and adequate capital (Holl and Howarth 2000, Bernhardt et al. 2007). "Social cost-benefit analyses" have been a useful tool applied to restoration because they seek to address this intergenerational inequity associated with over-

discounting the future value of ecosystem services, as well as intragenerational inequities associated with a dollar being worth more to a poor person than a rich person (MacLeod and Johnston 1990).

Although there is a lack of adequate attention to costs in the restoration literature (Holl and Howarth 2000), several economic studies show that there are substantial efficiency gains when the spatiotemporal distribution of costs is formally considered at the outset of conservation and restoration planning processes (Naidoo et al. 2006). The magnitude of these gains depends on the spatiotemporal correlation between, and the relative variability of, the costs and benefits of various restoration scenarios. Hence, it is often better to incorporate costs, including those for monitoring, at the outset of restoration planning rather than incur the higher costs of a less efficient restoration plan (Naidoo et al. 2006).

It is also important to realize that costs and benefits of restoration are often nonlinear functions of effort and time (Naidoo et al. 2006). If a system has passed a threshold, the shape of the benefit relationship can be concave because an enormous amount of effort might be needed to shift it back to an alternative state, whereas subsequent changes within this returned state might be easier than the initial effort. In contrast, the relationship can also be convex or asymptotic, where initial gains cost the least and there are diminishing returns with subsequent efforts. In this latter case, agreeing on what constitutes successful restoration up front will be crucial because of these diminishing returns. Importantly, these nonlinearities must be reasonably well characterized to accurately assess the cost-benefit ratios of various restoration options through time, and might dictate whether historical, hybrid, or novel communities are the restoration targets.

Cost multipliers and restoration insurance can be beneficial to cope with the enormous intangibles and cost uncertainties of restoration. Increasing the best estimate of costs by two to three fold should help address cost uncertainties. Such cost multipliers are already common in U.S. environmental law, such as with the *Environmental Protection Act* Superfund program and *Oil Pollution Act* (Holl and Howarth 2000). Additionally, restoration insurance, which would cover restoration costs in the case of unexpected ecological conditions, such as extreme weather events that are becoming more common with climate change, might also be judicious and cost-effective (Holl and Howarth 2000). Statutes requiring restoration insurance would help maintain ecosystem services for posterity.

Several unconventional but promising funding strategies have been developed to facilitate raising adequate capital for restoration, such as environmental assurance bonding and Payment for Ecosystem Services (PES) frameworks (Bullock et al. 2011). With environmental assurance bonding, parties responsible for environmental damage post bonds that can be used to pay restoration costs if they default on their commitment to return an ecosystem to some specified condition (Costanza and Perrings 1990). For example, a company might post a bond before surface mining, and the money would be released only after the site has been sufficiently restored.

Payment for Ecosystem Services programs provide another progressive approach to funding restoration. These frameworks

offer financial credits to parties for actions that maintain or increase the provisioning of ecosystem functions. These credits can then be purchased, sold, or traded. Several successful PES programs could serve as models for restoration, such as in-lieu fee programs and wetland mitigation banking in the United States, the Grain to Green Project that is paying farmers to convert steeply sloping cropland to forest and pasture in China, and REDD1—Reducing Emissions from Deforestation and Forest Degradation, internationally (Bullock et al. 2011). Similarly, carbon emissions trading or cap and trade are market-based systems similar to PES programs that are proposed to mitigate the adverse effects of climate change.

Payment for Ecosystem Services programs can produce more funds for restoration than many present approaches. Importantly, credits can be combined to pursue larger scale restoration projects than are often currently considered. Large-scale restorations projects have the value of enhancing the recovery of apex predators that often require considerable tracts of land or water (Ritchie et al. 2012). Additionally, given that the cost of dealing with regulatory issues and negotiating and executing contracts has to be paid for each restoration project, large-scale coordinated restoration could produce considerable administrative cost savings (Bullock et al. 2011). Indeed, a one-time pulse investment for large-scale river restoration was determined to be up to 10 times more efficient than annual allocations totaling the same amount (Neeson et al. 2015).

There are, however, obstacles to successful implementation of environmental assurance bonding and PES programs. For instance, there are concerns about the long-term sustainability of PES programs because there is little disincentive to allowing the ecosystem to degrade after payments cease (Bullock et al. 2011). Payment for Ecosystem Services programs can also result in an accumulation of ecosystem service debts if the level of services provided as offsets does not match the true losses (Palmer and Filoso 2009, Maron et al. 2012, Curran et al. 2014) or if the bond is not large enough to create an ample disincentive to default on the restoration commitment (Costanza and Perrings 1990, Holl and Howarth 2000). Ecosystem service debts might be expected given that services are often not accurately valued, future services are regularly discounted, and restored ecosystems rarely match the services of the same ecosystems before damage (Benayas et al. 2009). Additionally, in many cases, administrative and institutional frameworks would need to be developed to determine and track bond payments and the purchasing, selling, and trading of ecosystem service credits. Nevertheless, environmental assurance bonds and PES strategies could increase both the frequency and success of ecological restoration if these hurdles can be surmounted and local and regional institutional frameworks can manage their complexities.

HOW TO RESTORE: THE ECOLOGICAL CONCEPTS
While adequate funds are being obtained for restoration, it is important to consider how the ecosystem will be restored. There are numerous ecological theories that have contributed to improving restoration success, several of which we review here.

How to successfully reintroduce and translocate
Many active restoration projects restore biodiversity by translocating (moving from elsewhere) or reintroducing (taking a local stock, replicating it in "captivity," and introducing it where it was found) plants and animals. Most translocation or reintroduction efforts in the 1970s and 1980s were unsuccessful, which resulted in failed restoration, but these failures and successes have subsequently allowed scientists and practitioners to identify strategies that are more successful than others (Seddon et al. 2007, 2014), many of which are summarized by the Association of Zoos & Aquariums Guidelines for Reintroduction of Animals Born or Held in Captivity (AZA 1992). For example, when restoring any species, a population viability analysis should be conducted to estimate (1) the minimum number of individuals to release for restoration success, and (2) the impact of the release on the captive or wildlife source population. Once these data are collected, an economic cost-benefit analysis should show that reintroduction is the most cost-effective recovery strategy for the available funds, which again emphasizes the importance of including an ecological economist early in restoration planning.

In addition to the recommendations in the previous paragraph, there are several important factors that must be considered separately for animal and plant reintroductions or translocations. For animals bred in captivity, there might be value in artificially selecting for tolerance of the stressor of concern before any reintroduction occurs (Venesky et al. 2012). Over successive generations in captivity, animals can lose vital traits for survival in the wild, such as predator and food recognition; thus, retraining these animals can improve restoration success (Seddon et al. 2007, Christie et al. 2012). For both captively bred and wild animals, soft reintroductions, where animals are held in enclosures at the release site for acclimatization to local environmental conditions or establishment of social and reproductive bonds, can improve restoration success relative to hard reintroductions where no acclimatization occurs (AZA 1992, Seddon et al. 2007, Seddon et al. 2014). For example, one of the best known examples of where a soft reintroduction was employed successfully was in restoring wolves to Yellowstone National Park, USA (Seddon et al. 2014).

For plants, the selection of the life stage to introduce is particularly important. Seeds are easy to obtain in large numbers and are less expensive than older plants, but the rate of recovery to the pre-injury condition is slower and the risk of introducing undesired and even invasive plants is greater for seeds than other life stages. Hence, the economic costs of restoration using seeds might outweigh the benefits, especially when compensatory restoration is required. However, planting trees sometimes requires large equipment that can compact soils, kill understory plants, and increase erosion. Regardless of which life stage is optimal for a given restoration, in many cases, laws might mandate that trees rather than seeds be planted to restore damaged lands.

Can ecosystem engineers facilitate restoration?
Ecosystem engineers—organisms that can create, significantly modify, maintain, or destroy a habitat—can be important tools for restoration (Byers et al. 2006). Ecosystem engineers are well-known causative agents driving the transition of ecosystems across basin boundaries from one stable state to another (Fig. 2). In fact, Byers et al.(2006) suggest that because ecosystem engineers reduce the threshold of human effort needed to attain desired states and often represent self-sustaining solutions, they might be cheap, easy, fast, sustainable, and in some cases, the only feasible option for restoring damaged ecosystems. Hence, ecosystem engineers can make restoration more economical.

Fig. 4. Restored habitats are subject to ecological assembly mechanisms. These mechanisms control which species can colonize, and their performance, the outcomes of species interactions, and the resulting diversity of the assemblage. Boxes in bold indicate assembly processes that can be manipulated by restoration activities.
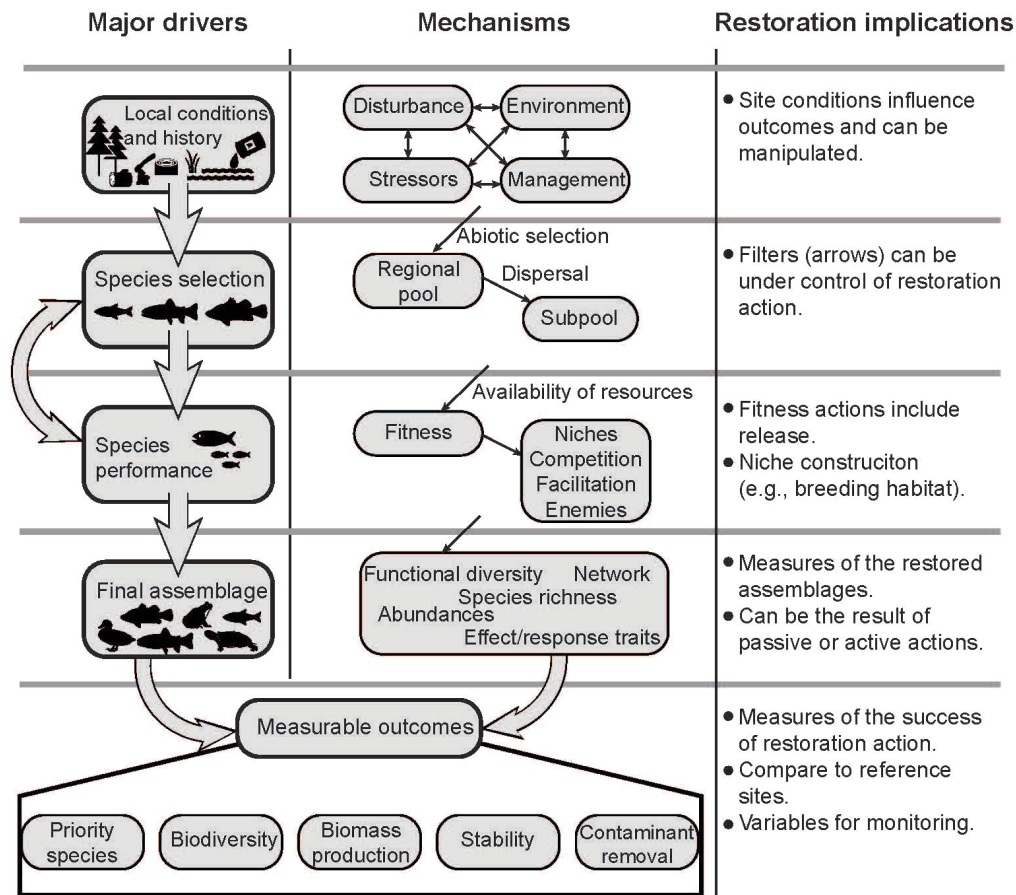
There are several examples where ecosystem engineers have been useful to ecological restoration. For instance, phytoremediation, or the use of plants to remove and concentrate contaminants from soil, sediments, or water, has been used to clean up sites contaminated with heavy metals and certain organic compounds, which has facilitated natural recovery (Weis and Weis 2004). In fact, it has been estimated that harvesting 1 ha of *Thlaspi*, a plant that can concentrate metals, might yield US$1000 in recoverable metals, thereby providing a potential economic incentive to restoration and the commercial development of phytoremediation techniques (Dobson et al. 1997). In many cases, the historical community can be restored after plants used for phytoremediation are harvested. Similar to phytoremediation, microbial remediation, or the use of microbes to accelerate contaminant breakdown, has also been a valuable use of ecosystem engineers for restoration purposes (Dobson et al. 1997, Kang 2014). Other examples include beavers that have been reintroduced to restore historical flow regimes of lotic systems (Burchsted et al. 2010), and manipulations of key members of lake food webs to help restore eutrophic lakes that have shifted to undesirable alternative stable states (Fig. 2)(Scheffer et al. 1993). Despite these examples,

phyto- and microbial remediation and the use of other ecosystem engineers is not occurring commonly in restoration practice.

How community assembly and disassembly theory can facilitate restoration success
Theories about community assembly and change have been the objects of ecological research for more than 100 years (Connell and Slatyer 1977, Pickett and McDonnell 1989), and these theories have direct relevance for restoration (Palmer et al. 1997, Temperton et al. 2004, Young et al. 2005, Funk et al. 2008). Community assembly theory is predicated on the fact that the species composition of communities is influenced by three primary drivers: (1) local site conditions or history, (2) availability or selection of species, and (3) performance of those species within the community (Fig. 4) (Pickett and McDonnell 1989, Cohen et al. 2016). Importantly, while these assembly drivers are not necessarily independent of one another (Cadotte and Tucker 2017), each of these assembly drivers can be manipulated to attain desired restoration outcomes.

The first assembly driver is local site conditions and history. They are important because they can affect restoration by affecting the

Fig. 5. The influence of fitness and niche differences on species coexistence based on Chesson's (2000) coexistence theory. Target species interact with nontarget competitors (including exotic species), and the outcome of their interactions will influence restoration success. Restoration actions can directly influence competitive interactions by influencing either species fitness or niche opportunities (adapted from Adler et al. 2007, MacDougall et al. 2009).
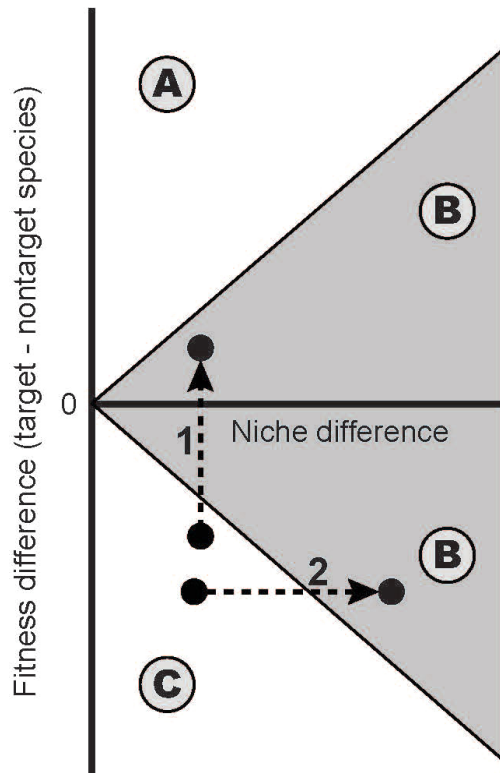
Regions of coexistence

A. Target species outcompetes nontarget species: no additional restoration action needed.

B. Target species coexists with nontarget species: no additional restoration action needed unless removal of nontarget species is a priority.

C. Nontarget species outcompetes target species: additional restoration action needed.

Example management action

1. Stressor impacting target species fitness is removed. Target species can now coexist with nontarget species.

2. Local niche heterogeneity is increased, allowing coexistence of target and nontarget species.

types of species that can persist at a given site (Fig. 4) (Jackson and Hobbs 2009). For example, the outcomes of forest understory (Brunet 2007), prairie (Grman et al. 2013), and salt marsh (Crain et al. 2008) plant restorations have all been shown to depend on the historical legacies of past anthropogenic influences. Although restoration ecologists cannot change the past, it is not uncommon for them to manipulate current environmental conditions to favor specific restoration goals, such as altering soil nutrients to aid target plant establishment (Blumenthal et al. 2003) or recreating natural channel structure in channelized streams (Poff et al. 1997, Palmer et al. 2010). By manipulating abiotic conditions, practitioners can filter out or favor dispersers from the regional species pool—the second assembly process, which is called species selection (Fig. 4) (Zobel et al. 1998). Some species from the regional pool are filtered out because of their limited dispersal abilities, which is often overcome in restoration by intentionally introducing individuals or propagules to a local site; in some cases, these introductions might be of species that are particularly tolerant of the stressors that caused the initial damage (Rohr et al. 2016). The important consequences of dispersal limitation is that the more isolated a site is, the fewer dispersers it will receive

and the more essential active restoration will be, which emphasizes the imperative of considering a landscape and aquascape perspective (Brudvig 2011).

The third assembly driver is species performance associated with local species interactions (Fig. 4). Harnessing biotic interactions and the knowledge of species coexistence theory (Chesson 2000, Adler et al. 2007) can be a useful tool to facilitate restoration. For instance, Silliman et al. (2015) suggest that 96% of restoration organizations release plant propagules in dispersed arrangements in an effort to reduce competition, but they revealed in their study that clumping plant species that facilitate one another can greatly improve restoration at no additional cost, thereby highlighting the importance of facilitative interactions to restoration success. Habitat simplification can often be an impediment to restoration because homogeneous sites have less niche space than heterogeneous sites, which will increase niche overlap that can reduce biodiversity (Fig. 5) (Chesson 2000, Adler et al. 2007). Thus, increasing structural complexity in a manner that matches the niches of desired species can occasionally enhance biodiversity and restoration by reducing competitive exclusion (Palmer et al. 2010).

Priority effects, the notion that the species that get to a location first can out-compete others and prevent their establishment, are common in nature; thus, it is often important to ensure that desired species arrive early in ecosystem recovery (Young et al. 2005, Fukami 2015). Indeed, recent work suggests that there is a narrow range of parameters that allows for desirable species to eliminate or coexist with undesirable species once they have established (Crandall and Knight 2015). An important potential consequence of approaches that relax species filters in an effort to increase niche space and biodiversity is that they could also facilitate colonization of undesirable species, such as invasives. One approach for impeding invasive species and thus enhancing the likelihood of restoration success is to increase the chances that the niche requirements of the invasives are already occupied in the focal ecosystem by maximizing the trait diversity of desired species or matching the traits of introduced desired species to potential invaders (Pokorny et al. 2005, Funk et al. 2008, Laughlin 2014). An important caveat regarding invasive species, however, is that not all are necessarily problematic. For instance, some invasive plants can be more effective at removing pollutants or reducing their bioavailability than can native plants, which makes them useful ecosystem engineers for remediation (Windham et al. 2003).

Although restoration practitioners regularly manipulate propagule pressure by introducing species and removing abiotic factors that are distressing ecosystems, they seem to less frequently intentionally manipulate species interactions, such as predation, competition, or facilitation. We believe that restoration success could be improved by more directly considering species coexistence and community assembly theories and employing a more inclusive toolbox that holistically considers alterations to propagule pressure, abiotic conditions, and biotic interactions, especially when challenged with restoring systems that are facing multiple stressors, such as climate change, invasive species, and contaminants (Rohr et al. 2004, Rohr and Palmer 2013). A more inclusive toolbox also increases flexibility by offering more restoration strategies, which in turn can facilitate the identification of approaches that are the most economically efficient (Naidoo et al. 2006).

MONITORING AND RESTORATION SUCCESS
Without monitoring restoration endpoints and reference conditions, restoration science cannot assess restoration progress, which limits the ability to analyze restoration outcomes and provide guidance to future projects (Hilderbrand et al. 2005, Bernhardt et al. 2007). To ensure that restoration is not doomed to repeat past mistakes, the journal *Restoration Ecology* includes the section "Set-backs and Surprises," which provides anecdotes that could be incorporated into further restoration design or analyses, and highlights the importance of publishing both successes and failures. Additionally, recent efforts for global capacity building, streamlining knowledge dissemination, and linking technology, innovation, and science, such as the Global Restoration Network and Future Earth, forebode accelerated improvements to restoration science. Nevertheless, effective monitoring of restoration projects is not guaranteed, often because funds are lacking; thus, not surprisingly, restoration goals often remain unassessed or unattained (Bernhardt et al. 2007, Hering et al. 2010, Suding 2011). Moreover, monitoring often occurs for only a small number of species (Rohr et al. 2007), which raises uncertainties about success. However, metagenomic and

barcoding technologies hold great promise for enhancing monitoring because they are taxonomically more comprehensive, many times quicker, and less reliant on taxonomic expertise than more standard monitoring approaches (Ji et al. 2013, Perring et al. 2015). Additionally, metatranscriptomic techniques can even provide a window to species functions and responses to stress, thereby offering opportunities to more thoroughly link community structure to function and stability in future assessments of restoration success. Hence, new molecular techniques hold promise of reducing the expense of monitoring.

Of the restoration projects with adequate monitoring, shifts in species distributions, legacies of past land use, and regional shifts in species pools and climate have been identified as potential impediments to success (Suding 2011). The most successful restoration projects have been those that have had significant community and stakeholder involvement; an advisory committee; collaborations among scientists, managers, and practitioners; solid restoration planning that considers the importance of legacy, past, and current disturbances; and evaluation of progress, not only after completion but during the planning and implementation phases of restoration (Bernhardt et al. 2007, Nilsson et al. 2016). Employing an adaptive management approach, an iterative process whereby information obtained from previous restoration activities can inform future decision-making, can enhance restoration success by ensuring that opportunities exist to make corrections should the restoration falter or move off course (Hilderbrand et al. 2005, Seastedt et al. 2008).

TENSIONS AND CHALLENGES IN RESTORATION ECOLOGY
Restoration ecology faces many tensions and challenges. We have covered several of these challenges because they clearly fit in one of the "when," "what," "where," or "how" to restore subheadings. There are also several struggles that do not readily fit within these subheadings, which we would be remiss if we did not discuss.

Ecological restoration is inherently context-dependent; thus, there are important differences in approaches to restoring different types of ecosystems, such as aquatic and terrestrial systems. Therefore, any imposed "one-size-fits-all" approach to restoration can create tension (Wright et al. 2009). For example, ecosystem properties of most lotic ecosystems (streams and rivers) seem to be driven predominantly by abiotic forces, such as hydrology, geomorphology, bathymetry, channelization, flow rates, and sediment grain size, whereas ecosystem properties and functions of many terrestrial systems seem to be driven more so by biodiversity. Thus, in terrestrial ecosystems, where vegetation itself provides much of the physical structure of the environment on which other organisms depend, it is easy to see how planting diverse native species assemblages could effectively "restore" not only an ecosystem function (portion of productivity) but also key components of ecosystem structure (e.g., canopy architecture) (Wright et al. 2009). In contrast, seeding streams with the appropriate algae and macroinvertebrates is no guarantee that those organisms will establish because these dominant taxa in lotic systems are easily dispersed, short-lived, and small, and abiotic structure plays such a predominant role in species establishment (Wright et al. 2009). Aquatic restoration efforts tend to focus on restoring stream channel structure or wetland or river hydrology, with the assumption (not supported by empirical

data) that biodiversity will recover if physical structure and physical processes are restored (Bernhardt and Palmer 2011, Palmer et al. 2014).

Much like the type of ecosystem being restored can cause tension, so too can the type of restoration project. Restoration projects can be selected or mandated. Selected projects are supported mostly by "bottom-up" forces, such as philanthropic efforts or taxes. Mandated restoration is often enforced from "top-down" regulation associated with holding parties responsible for some form of damage to the environment. Flexibility and willingness to "do the right thing" are often traits of bottom-up driven restoration, whereas mandated restoration efforts often focus on fulfilling a limited set of regulatory obligations. Additionally, mandated restoration often involves negotiations associated with litigation that can compromise monitoring and restoration success (Palmer and Hondula 2014).

Finally, emphasis on restoration success has encouraged practitioners to have very specific restoration targets and outcomes, but these good intentions can lead to homogenization and simplification of restoration habitats and a greater cost than required to support healthy populations (Hiers et al. 2016). These problems can be particularly acute when overly precise prescriptions are enacted at broad policy or regulatory scales because they leave managers little discretion in interpretation of restoration outcomes or application of restoration strategies (Lave 2009). Narrow goals uniformly applied across jurisdictions simplify management, resonate with cultural expectations of scientific precision, and provide safeguards against controversy and litigation, but they also have the potential to hinder the ability of practitioners to actually achieve the broader goals of restoration when they cause a net loss of suitable habitat and biological diversity by homogenizing restored areas (Hiers et al. 2016). This loss of variability can hamper adaptation to environmental change, such as climate change. Thus, restoration and conservation success could be improved with a better balance between policies that assist in restoring species and ecosystems and policies that promote variability and resilience of natural systems (Hiers et al. 2016).

SUMMARY AND CONCLUSIONS

When to Restore: Human-assisted (active) restoration is often but not always more cost-effective than monitored natural recovery (passive restoration); thus, it is wise to evaluate whether active restoration is necessary. Pursuing restoration as early as possible will help prevent ecosystems from transitioning to undesired alternative stable states, and including ecological economists early in restoration will help identify the most cost-effective approach to restoration.

What to Restore: The process of developing a restoration plan with involvement of stakeholders should determine whether the restoration goal should be remediation, restoration to historical conditions, or restoration to a hybrid or novel ecosystem. Subsequently, the plan should entail establishing measurable goals and benchmarks within a realistic range of values; selecting a combination of structural, compositional, and functional restoration endpoints; and identifying multiple reference sites that reflect the range of natural variation. If the goal is a hybrid or novel ecosystem, then ideally this ecosystem should be designed to deliver more services and be more resistance and resilient than the historical ecosystem.

Where to Restore: On-site restoration is often more desirable than off-site restoration, but off-site restoration might be necessary where compensatory restoration is required or where conditions cannot be improved in the long-term to support the targeted biodiversity and functions. Two of the biggest challenges to restoration science will be to develop restoration approaches that can address the impediment of rural poverty in the developing world, and to identify and then balance the ecosystems and regions in most need of restoration and those that are best positioned for restoration success.

How to Restore - Economics: Market-based strategies have been developed to meet the challenge of funding restoration, such as environmental insurance bonds and Payment for Ecosystem Services frameworks where ecosystem service credits can be bought and sold. Payment for Ecosystem Services systems are promising because they incentivize restoration and can produce considerable administrative cost savings, and credits can be combined to pursue larger scale restoration that can facilitate the return of apex predators.

How to Restore - Ecology: Because ecosystem engineers reduce the threshold of human effort needed to attain desired states and they often represent self-sustaining solutions, ecosystem engineers might be inexpensive, easy, fast, sustainable, and in some cases, the only feasible restoration option. Restoration success could be improved by employing proven methods for animal and plant reintroductions; more thoroughly considering site history, landscape and aquascape perspectives, species coexistence and community assembly theories; and employing a more inclusive toolbox that holistically considers alterations to propagule pressure, abiotic conditions, and biotic interactions. A more inclusive toolbox could also improve the cost-effectiveness of restoration.

Assessing Restoration Success: Monitoring restoration endpoints and reference conditions are essential to evaluating restoration progress and success. Of the restoration projects with adequate monitoring, the most successful ones have employed adaptive management; have had significant community and stakeholder involvement, an advisory committee, collaborations among scientists, managers, and practitioners; and have had formal evaluation throughout the restoration process. Overly precise restoration prescriptions enacted at broad policy or regulatory scales can often reduce success by homogenizing restored areas, thus reducing the resilience of ecosystems to environmental change. Future assessments of success should consider measuring links between composition and ecosystem functions and incorporating metagenomic and metatranscriptomic approaches for a more complete assessment of biodiversity and functions.

Conclusion: E. O. Wilson suggested that ecological restoration "is the means to end the great extinction spasm" and that "the next century will…be the era of restoration in ecology" (Wilson 1999), emphasizing the future value and prominence of restoration ecology. We hope that this overview of many of the key ecological and economic concepts in restoration ecology will help clarify the discipline. Most importantly, we are optimistic that the recommendations provided here will facilitate restoring and maintaining the services and products provided by natural capital, and thus improve human livelihoods and hope for the future of humanity.

Box 1: OUTSTANDING QUESTIONS IN RESTORATION SCIENCE

When to Restore

- Is active or passive restoration more cost-effective, and what is the best approach for determining this?

What to Restore

- What combination of restoration endpoints can most reliably and cost-effectively assess restoration success?

- What do we gain or lose when restoration targets are novel or hybrid ecosystems, and how do they respond to various perturbations and stressors?

Where to Restore

- What ecosystems and regions are in the most need of restoration versus the most well positioned for restoration success?

- How do restoration practitioners reliably decide whether on-site or off-site restoration is preferable?

How to Restore: Economics

- How do we build rigorous economic valuation systems that prevent ecosystem service debts and global market incentives (e.g., Payment for Ecosystem Services) for the conservation and restoration of ecosystem services?

- How can restoration science reconcile the dire need for restoration in the developing world with widespread rural poverty there that impedes it?

How to Restore: Ecology

- Which and how can ecological theories inform and enhance restoration?

Assessing Success

- Can we identify the traits of restoration successes and failures to shift restoration ecology to a globally and reliably predictive science?

Responses to this article can be read online at:
http://www.ecologyandsociety.org/issues/responses.php/9876

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