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The restoration of biodiversity: Where has research been and where does it need to go?[1]

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The practice of ecological restoration is a primary option for increasing levels of biodiversity by modifying human-altered ecosystems. The scientific discipline of restoration ecology provides conceptual guidance and tests of restoration strategies, with the ultimate goal of predictive landscape restoration. I construct a conceptual model for restoration of biodiversity, based on site-level (e.g., biotic and abiotic) conditions, landscape (e.g, interpatch connectivity and patch geometry), and historical factors (e.g., species arrival order and land-use legacies). I then ask how well restoration ecology has addressed the various components of this model. During the past decade, restoration research has focused largely on how the restoration of site-level factors promotes species diversity—primarily of plants. Relatively little attention has been paid to how landscape or historical factors interplay with restoration, how restoration influences functional and genetic components of biodiversity, or how a suite of less-studied taxa might be restored. I suggest that the high level of variation seen in restoration outcomes might be explained, at least in part, by the contingencies placed on site-level restoration by landscape and historical factors and then present a number of avenues for future research to address these often ignored linkages in the biodiversity restoration model. Such work will require carefully conducted restoration experiments set across multiple sites and many years. It is my hope that by considering how space and time influence restoration, we might move restoration ecology in a direction of stronger prediction, conducted across landscapes, thus providing feasible restoration strategies that work at scales over which biodiversity conservation occurs.

Key words: conceptual model; historical contingency; landscape ecology; local interactions; regional species pool; restoration ecology.

Ecological restoration—that is, intentional activities that permanently change human-modified ecosystems to possess a range of desirable attributes such as native species composition or ecosystem functions—represents humankind's primary option for increasing levels of biodiversity. Human land use dominates the Earth's ecosystems, and this destruction of habitat is the leading threat to the world's biodiversity (Vitousek et al., 1997; Wilcove et al., 1998; DeFries et al., 2004; Foley et al., 2005; Fischer and Lindenmayer, 2007). Paired with other conservation strategies, restoration ecology—the science of restoration—represents a means for alleviating this biodiversity crisis (Dobson et al., 1997; Young, 2000; Hobbs and Harris, 2001). Our abilities to recreate ecosystems are simply not—and may never be—sufficient to warrant habitat destruction; however, passive protection of habitat remnants alone will not suffice in many landscapes. There is simply not enough suitable habitat remaining for the long-term persistence of many taxa (Rodrigues et al., 2004). Certainly, we should preserve what remains, but the present century must additionally usher in an era of restoration, in which lands that have been transformed by human land use are modified to better support desired biodiversity and functions (Wilson, 1992; Hobbs and Harris, 2001).

The ultimate goal of restoration ecology must be to predictably restore ecosystems at landscape scales—the scales over which biodiversity is managed in most countries (Bestelmeyer et al., 2003). Ecological restoration, however, has been historically dominated by local-scale efforts with notoriously unpredictable outcomes (Hobbs and Norton, 1996). In efforts to rectify this disconnect, the past 15 years have seen major advances in restoration ecology as an academic discipline. The Society for Ecological Restoration International (SER) has helped organize and formalize restoration ecology, providing a central authority and general guidelines for ecological restoration (SER 2004). Restoration ecology has also become an increasingly prominent topic in scientific publications, both in total articles published and as a percentage of all ecology publications (Young et al., 2005; Fig. 1A, B). Restoration-specific journals such as *Restoration Ecology* have blossomed into major scientific outlets, and restoration papers have had an increasing presence in top-tier applied ecology journals (Fig. 1C), including special issues dedicated to restoration in journals of wide readership (e.g., *Journal of Applied Ecology*, 2003; *Science*, 2009). Numerous books that investigate scientific and practical facets of restoration have been published in this period (e.g., Perrow and Davy, 2002a, b; Falk et al., 2006; van Andel and Aronson, 2006; Clewell and Aronson, 2007; Hobbs and Suding, 2009).

Over the course of this 15-year maturation, an influx of basic ecological theory has produced numerous conceptual restoration-ecology frameworks and models (e.g., Hobbs and Norton, 1996; Palmer et al., 1997; Young, 2000; Hobbs and Harris, 2001; Perrow and Davy, 2002a; Suding et al., 2004; Young et al., 2005; Falk et al., 2006; van Andel and Aronson, 2006; Hobbs and Cramer, 2008; Hobbs and Suding, 2009). Such conceptual frameworks help us make sense of complex ecological issues and, hence, predict outcomes of our restoration activities.

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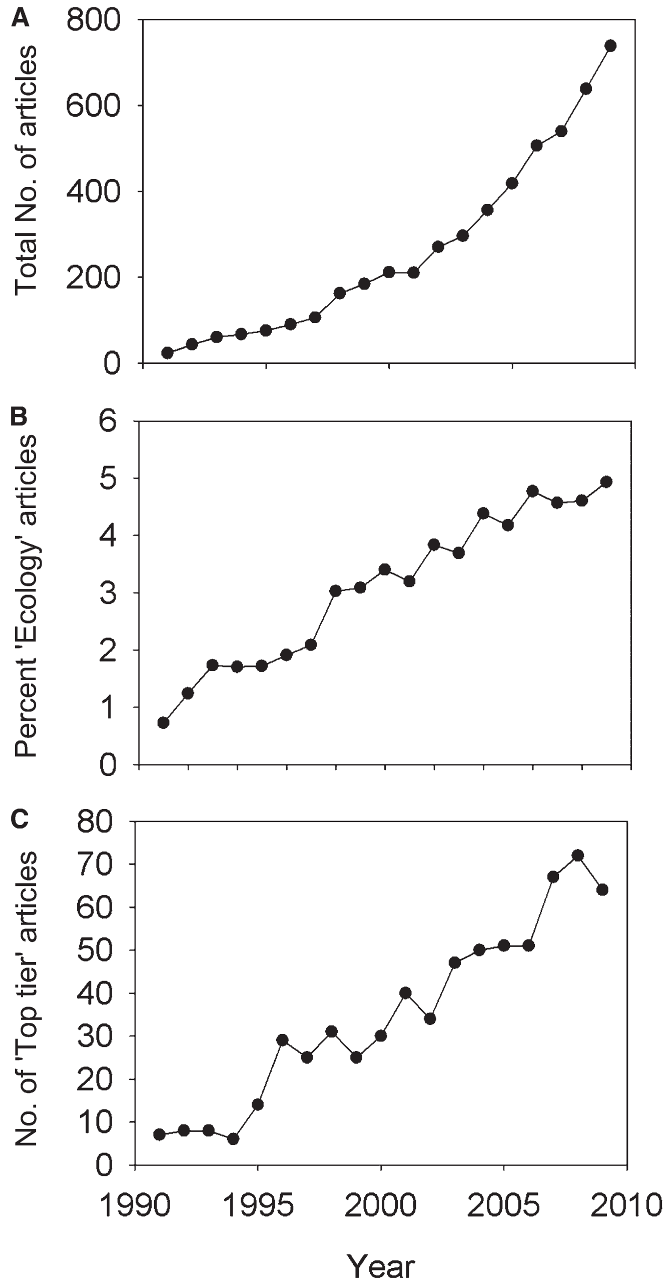

Fig. 1. Publication trends for articles on restoration ecology. All data are from a Web of Science search conducted in July 2010. The past 20 years has seen a steady increase in the total number of restoration ecology articles (A) across all journals (topic = "restor* AND ecol*"), (B) as a percentage of all ecology articles (topic = "restor* AND ecol*"/topic = "ecol*"), and (C) based on representation in top-tier applied ecology journals (search for topic = "restor* AND ecol*", journal name = *Ecological Applications* and *Journal of Applied Ecology*). Panels A and B are after Young et al. (2005), updated to include years 2005–2009.

In doing so, we move beyond restoration as a series of case studies, each of which, through a period of trial and error, may or may not be deemed successful. Further, employing conceptual frameworks in restoration provides opportunities for current advances in ecological theory to influence the direction of restoration science (and vice versa) and, over time, synthesize restoration studies into core restoration theory.

Here, I consider a conceptual model for the restoration of biodiversity, based in part on several past conceptual frameworks (e.g., Hobbs and Norton, 1996; Palmer et al., 1997). I then ask how our research matches this model. Where do its strengths lie, and where is future research needed? Having reviewed the literature of the past decade, I argue that restoration ecology is strong in site-level restoration of species diversity but has prominent weaknesses in the incorporation of landscape and historical factors, in the restoration of a suite of taxa, and in functional and genetic facets of diversity. To help strengthen these weak links, I consider a series of promising future research directions. By providing stronger ties between biodiversity theory and its application to restoration, it is my hope that such work will lead to more predictable restoration outcomes and thus aid landscape-scale biodiversity conservation.

A CONCEPTUAL MODEL FOR THE RESTORATION OF BIODIVERSITY

Biodiversity is among the most commonly assessed outcomes of restoration efforts (Ruiz-Jaen and Aide, 2005), but what factors dictate these biodiversity outcomes? Therein lies the central question behind this conceptual model of biodiversity restoration, but to produce such a model requires understanding how restoration interacts with other major factors in driving patterns of biodiversity (Fig. 2). The regional species pool, or set of species capable of co-occurring at a given site, places bounds on which and how many species might populate a restoration site; however, no site contains all species from this pool (Zobel et al., 1998). Rather, postrestoration biodiversity is a result of a suite of site-level factors, such as abiotic and biotic filters, landscape-level factors (e.g., connectivity between restoration sites and relict source populations), and various historical contingencies (e.g., species arrival order) (Fig. 2). Restoration efforts may seek to modify factors related to sites, landscapes, or historical contingency (bold arrows in Fig. 2). The biodiversity outcomes of restoration, in turn, are dictated by site, landscape, and historical factors (nonbold arrows in Fig. 2), each of which may have some components that are directly influenced

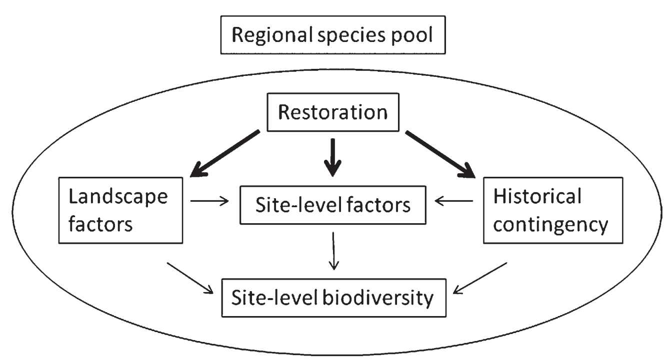

Fig. 2. Conceptual model of biodiversity restoration. Biodiversity at a restored site is a function of site-level, landscape, and historical filters imposed on the regional species pool, which describes all potential members of a given site. Biodiversity can be defined at the species, functional, or genetic level. Restoration might directly manipulate local, landscape, or historical factors (bold arrows). Biodiversity, in turn, may be affected by local, landscape, or historical factors that may or may not be directly influenced by restoration (nonbold arrows).

by restoration and others that are independent of restoration. Below, I explore the facets of this model in more detail.

The regional species pool—Of overarching importance for the biodiversity that develops at a restored site is the composition and size of the regional species pool (Zobel et al., 1998). Its composition dictates which species might colonize a restored site and which species we might consider actively reintroducing during restoration (Brudvig and Mabry, 2008). Furthermore, restored sites in more diverse regions can sample from a larger regional species pool and potentially contain higher levels of biodiversity than restored sites in less diverse regions (Cornell and Lawton, 1992). Thus, the regional species pool places bounds on the levels and composition of biodiversity at restored sites.

Site-level factors—Site-level conditions create a series of filters that facilitate or impede membership of plants and animals during restoration. Not surprisingly, manipulation of a site to make it suitable for a target community is key in ecological restoration (Hobbs and Norton, 1996; Palmer et al., 1997; Perrow and Davy, 2002a, b; van Andel and Aronson, 2006; Clewell and Aronson, 2007; Fig. 2). In practice, efforts are dictated by the level of prior human-induced modification. At highly modified sites, restoration may begin by reinstating basic abiotic and structural conditions. Past work has taken a wide variety of approaches, ranging from replacing topsoil on former mine sites (Bradshaw, 1997), to bank stabilization and channel reconstruction during river restoration (Bernhardt et al., 2005), to reduction of overstory tree density during savanna restoration for bird habitat (e.g., Brawn, 2006; Mabry et al., 2010). Once abiotic and structural conditions have been restored, it may be important to restore a disturbance regime. In systems historically characterized by frequent disturbances such as fire or flooding, restoration may seek to promote disturbance frequency (e.g., Brown et al., 2004). Alternatively, restoration may attempt to suppress disturbance in systems that have been altered by unusually high levels of disturbance, such as frequently burned tropical forests (e.g., Aide and Cavelier, 1994; Cochrane, 2003). Simply creating a suitable site will not, however, guarantee restoration success, and many restoration efforts that adopted an "if you build it, they will come" approach have ultimately failed to support desired community members. Thus, biotic conditions may need to be actively reinstated, and, in many instances, the simple act of reintroducing individuals can dramatically influence postrestoration biodiversity levels (e.g., Pywell et al., 2002). Planting seedlings or introducing seeds is the most common approach with plants; however, a passive restoration approach, in which species are assumed to disperse to a site without human assistance, may be appropriate in some situations and is more common in the restoration of animal communities (Ruiz-Jaen and Aide, 2005). Reintroduction of focal species may not succeed without consideration of species interactions. With the example of plants, successful restoration may be contingent upon not only reintroducing plant propagules, but also promoting or controlling a suite of interacting species, including mycorrhizae, pollinators, seed dispersers, consumers, and competing plant species (e.g., Nelson and Allen, 1993; Sweeney et al., 2002; Bakker et al., 2003). The effects of (native or exotic) invasive species on native biodiversity during restoration may be particularly important (D'Antonio and Meyerson, 2002). Considerations range from the properties of ecosystems that confer invasion resistance, to direct and indirect effects (mediated by changes in ecosystem properties) of invasive species on native biodiversity, to the promotion of exotic species by disturbances related to restoration, to the role of invasive species in forming alternative stable states that may be resistant to restoration efforts (e.g., Zavaleta et al., 2001; Suding et al., 2004; Funk et al., 2008; Nelson et al., 2008). Restoration approaches may range from eradication of invasive species, to utilization of invasive species as tools during restoration, to management of highly invaded ecosystems as novel entities, with goals related to ecosystem functions and services, rather than native species composition (e.g., Zavaleta et al., 2001; Ewel and Putz, 2004; Hobbs et al., 2006; Seastedt et al., 2008). Finally, it is important to recognize that site-level factors not directly manipulated by restoration may also have bearing on the biodiversity outcomes of restoration (Fig. 2).

Landscape factors—Landscape-scale factors can influence the site-level biodiversity outcomes of restoration efforts in a number of ways (Fig. 2), and this has been explored conceptually in some detail (e.g., Naveh, 1994; Hobbs and Norton, 1996; Bell et al., 1997; Palmer et al., 1997; Hobbs, 2002; Holl et al., 2003; Young et al., 2005; Maschinski, 2006). Of central importance is the fact that restored habitat patches are frequently too small to provide for self-sustaining populations (Kuussaari et al., 2009). The consequence of this is that restored patches are indeed patches within larger landscapes, and landscape-scale factors that affect patch-level population dynamics and interpatch movement may influence restoration outcomes (Fig. 2). In practice, the site-level biodiversity outcomes of restoration may be influenced by the composition of the surrounding landscape (e.g., Matthews et al., 2009; Mabry et al., 2010), by connectivity between patches of restored habitat and remnants or other restored habitats (e.g., Damschen et al., 2008), or through the influence of patch geometry—the size or shape of patches undergoing restoration (e.g., Damschen et al., 2008; Morrison et al., 2010). In turn, restoration may seek to modify landscape-scale effects. Landscape restoration strategies include construction of new habitat patches in specific locations that maximize biodiversity benefits (Huxel and Hastings, 1999), construction of landscape elements—such as corridors or stepping stones—to connect restored patches of habitat with each other or with remnants (Crooks and Sanjayan, 2006; Damschen et al., 2008), or restoration of matrix habitat separating focal remnant or restored patches, to facilitate interpatch movement (Prugh et al., 2008) or promote biodiversity in the matrix itself through spillover effects (Brudvig et al., 2009). It is through the melding of restoration and such elements of landscape ecology that restoration implementation might move from its current focus on individual patches to landscape-scale restoration (Naveh, 1994; Hobbs and Norton, 1996; Bell et al., 1997; Hobbs, 2002; Holl et al., 2003).

Historical contingency—Although mitigating the effects of historical land use is of central importance to restoration, only recently have the intricacies of history on restoration outcomes been explored (e.g., Young et al., 2001, 2005; Temperton et al., 2004). This followed increasing acknowledgment of the unpredictability of restoration outcomes, which suggested that the classical views of succession that dominated early restoration thinking may not always be appropriate (Young et al., 2001, 2005; Hobbs and Suding, 2009). Indeed, historical contingency—factors related to restoration timing and prerestoration legacies—has been central to a number of theories recently applied to restoration, including alternative states (Suding et al., 2004), novel ecosystems (Hobbs et al., 2009), assembly rules (Temperton et al., 2004), and threshold models (Suding and Hobbs, 2009). Some elements of historical contingency can be directly manipulated by restoration, such as species arrival order or initial species composition, which can lead to priority effects, with demonstrated or theorized effects on community composition (Young et al., 2001; Chase, 2003; Temperton and Zirr, 2004; Fukami et al., 2005; Fig. 2). In turn, other facets of history can have strong sway on restoration outcomes while remaining outside the scope of restoration manipulation (Fig. 2). Examples include year effects (interannual variation in biotic and abiotic conditions; e.g., Bakker et al., 2003; Vaughn and Young, 2010), variation in the type or intensity of past disturbance (resulting in land-use legacies, such as destruction of soil seed banks or persistent exotic vegetation; Bakker et al., 1996; Stromberg and Griffin, 1996), or historical landscape effects, including levels of historical connectivity, which may be drivers of present-day patterns of biodiversity (e.g., Lindborg and Eriksson, 2004; Brudvig and Damschen, in press).

Defining and measuring biodiversity—While promoting biodiversity is a major focus in restoration (SER, 2004; Ruiz-Jaen and Aide, 2005), it is important to recognize the multifaceted nature of biodiversity and the variety of ways in which we might define or measure it during restoration (Naeem, 2006). This includes the many taxa that we might seek to restore or measure during restoration evaluations (Young, 2000; Ruiz-Jaen and Aide, 2005), the consideration of functional diversity and how this relates to ecosystem function following restoration (e.g., Ehrenfeld and Toth, 1997; Naeem, 2006; Wright et al., 2009), and genetic considerations during restoration, including evaluation of genetic diversity as a biodiversity measure (Hufford and Mazer, 2003; McKay et al., 2005; Falk et al., 2006).

EVALUATING THE BIODIVERSITY RESTORATION MODEL

How well has restoration science addressed this conceptual model for the restoration of biodiversity? Have the various local, landscape, and historical factors that dictate restoration outcomes been adequately investigated? Do weak links exist? To answer these questions, I populated a set of restoration ecology articles and then scored each for how it addressed the biodiversity-restoration conceptual model.

On 12 July 2010, I conducted an ISI Web of Science search with topic = 'restor* OR rehabilit* OR recreat* OR re-creat*' AND publication name: 'restoration ecology OR ecological applications OR journal of applied ecology', with publication years 2000–2010. Inclusion of '*' results in a search for all articles containing this string of letters (e.g., 'restore', 'restoration', 'rehabilitated', 'recreating') within the title, abstract, or key words. I constrained the search to these years to make a fair assessment of how research has addressed conceptual restoration frameworks, virtually all of which have been published in the past 10 to 15 years (e.g., Hobbs and Norton, 1996; Palmer et al., 1997; Young, 2000; Hobbs and Harris, 2001; Perrow and Davy, 2002a; Suding et al., 2004; Young et al., 2005; Falk et al., 2006; van Andel and Aronson, 2006; Hobbs and Cramer, 2008; Hobbs and Suding, 2009). I focused on these journals in an effort to maximize the number of studies that specifically focused on restoration ecology, spanning a wide variety of ecosystems and taxa. Although restoration studies are published in numerous journals, focus on this subset was supported by an initial search of all journals for the above topic words AND 'ecol*', which resulted in >5400 articles published in >460 journals. The above three were the most common resulting journals that did not have a taxonomic or system-specific focus (*Restoration Ecology*, no. 1; *Ecological Applications*, no. 4; *Journal of Applied Ecology*, no. 8; vs., e.g., *Forest Ecology and Management*, no. 2) and that frequently publish studies specifically about restoration ecology (e.g., I chose not to include *Biological Conservation* or *Conservation Biology*). One other journal, *Ecological Restoration*, would have been a suitable fourth source of articles, but it is not referenced on Web of Science.

This search resulted in 1314 articles (754 in *Restoration Ecology*, 296 in *Ecological Applications*, and 264 in *Journal of Applied Ecology*). From this set, I randomly selected 300 articles, for which I scored attributes relevant to the conceptual model: site-level factors, landscape factors, and historical contingency (Table 1). For each article, I noted whether attributes were evaluated (regardless of whether they were the focus of restoration activities) and, when restoration was performed, which attributes were manipulated by these activities. In addition, I noted the focal ecosystem, focal taxon or taxa, and level(s) of biodiversity measured (if any): species, functional, genetic.

Of the 300 randomly selected articles, 276 pertained to some facet of restoration. Of these, 215 were empirical studies, among which 173 conducted some form of active restoration (including an explicit "do-nothing" approach), 17 constructed mathematical models with a restoration focus, 28 were conceptual, presenting new ideas, and 15 were reviews of past published work. Below, I focus on the 173 empirical active restoration studies and 17 modeling studies to assess strong and weak links in the "biodiversity restoration" conceptual model (Appendix S1; see online file at http://www.amjbot.org/cgi/content/full/ajb.1000285/DC1). I include modeling studies because of their utility for assessing processes important to restoration, like landscape connectivity or change over long periods, which may be difficult to actively manipulate.

STRONG AND WEAK LINKAGES IN THE RESTORATION OF BIODIVERSITY

Strong restoration linkages—The major focus of restoration ecology during the past decade has been the restoration of site-level conditions and the subsequent effects on biodiversity. The vast majority (97%) of studies investigated restoration of site-level factors (Fig. 3). Of these, most restored biotic conditions; however, restoration of abiotic and structural conditions and of disturbance regime were all reasonably well investigated (Fig. 3). Biodiversity was a frequently assessed restoration outcome and, perhaps not surprisingly given this focus on site-level restoration, 78% of studies found biodiversity to be a function of site-level conditions (Fig. 3).

Weak restoration links—Landscape-level factors and factors related to historical contingency remain underexplored in restoration ecology. Weak links exist in the conceptual model of biodiversity restoration, in terms of both restoring landscape (e.g., interpatch connectivity) and historical factors (e.g., species arrival order) and investigating how landscape and historical

TABLE 1. Attributes for which restoration ecology articles in the literature review were scored. Articles were first evaluated for appropriateness—empirical or modeling restoration studies—and then scored for which attributes were evaluated and which attributes were specifically manipulated by restoration.

Attribute category	Attribute	Description
Site-level factors		
	Abiotic	Was the abiotic environment measured/manipulated (e.g., hydrology, soils, water quality/chemistry)?
	Structure	Was habitat structure measured/manipulated (e.g., stream channel configuration, tree density)?
	Biotic	Were biotic factors evaluated/manipulated (e.g., competitors, seed dispersers)?
	Disturbance	Was disturbance regime quantified/manipulated (e.g., fire, flooding)?
Landscape factors		
	Patch attributes	Were patch area or geometry evaluated/manipulated?
	Connectivity	Was connectivity to remnants or other restoration patches evaluated/manipulated?
	Surrounding landscape	Was composition of present-day landscape surrounding focal patch quantified (e.g., percent forest vs. agricultural field)?
Historical contingency		
	Land-use legacies	Were residual effects of past land uses (e.g., agriculture, silviculture) specifically considered?
	Historical landscape	Were historical landscape variables evaluated (e.g., historical patch size, historical connectivity)?
	Species arrival order	Was the order of species (re) introduction considered/manipulated?
	Year effects	Were impacts of interannual variation in biotic and abioitc conditions considered?

factors affect biodiversity during restoration (e.g., effects of surrounding landscape or land-use legacies on patch-scale restoration; Fig. 3). Although landscape factors have received relatively more attention than historical factors, only 11% of papers tested how landscape effects influenced site-level factors, and most of these considered biotic conditions. Most facets of historical contingency remain very poorly explored, with most existing tests focused on land-use legacies (4%; Fig. 3). No papers dealt with year or historical landscape effects, and only one considered species arrival order (Fig. 3). Virtually every paper that investigated landscape or historical factors found effects on biodiversity (Fig. 3).

Focal systems, taxa, and level of biodiversity—Most restoration studies have been conducted in terrestrial systems (64%) and with plants (63%; Fig. 4). Relatively less well studied have been wetlands (15%) and freshwater aquatic systems (lakes, rivers, streams; 12%), with coastal (2%) and marine (0%) systems having received little or no investigation (Fig. 4). Less well studied focal taxa include arthropods (13%), birds (6%), other vertebrates (6%), fishes (4%), other invertebrates (3%), plankton (0.5%), and soil microbes (0.5%), the latter two represented by single papers (Fig. 4).

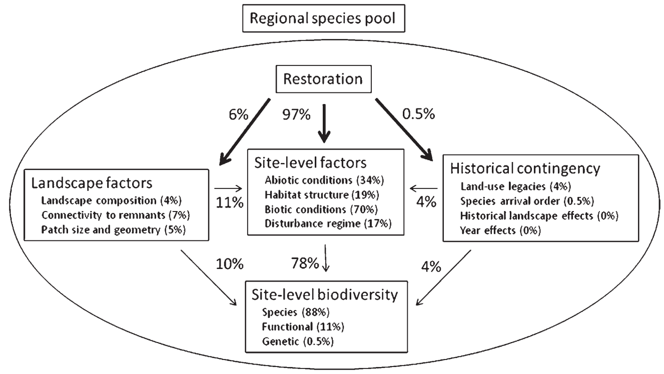

Fig. 3. Results of a literature review (percentage of 190 articles evaluated) that assessed how past research has addressed the conceptual model of biodiversity restoration. Past work has been overwhelmingly focused on site-level restoration, with assessment at the species-level of biodiversity. Relatively little effort has been directed toward understanding links between restoration and landscape processes or factors that determine historical contingency, nor has biodiversity been frequently assessed at the functional or genetic biodiversity levels. (Note: tallies may exceed 100% because of studies that investigated multiple links.)

Biodiversity is a major focus of restoration studies: 88% of the papers in this review assessed biodiversity in some way, and all but one of these assessed species-level biodiversity (Fig. 3). In addition to species diversity, 11% of papers also assessed some facet of functional diversity—generally based on plant life-form group (e.g., graminoid, forb, shrub). A single paper investigated an element of genetic diversity.

FUTURE RESEARCH NEEDS

Restoration ecology research holds both areas of clear focus (restoring site-level factors, effects on species diversity) and marked weaknesses (understanding the roles of landscape factors and historical contingency, effects on functional and genetic diversity) (Fig. 3). To produce a predictive restoration science that promotes biodiversity at landscape scales, these weaknesses need to be addressed by future research. Below, I provide a series of future research directions to help with such efforts.

Landscape factors—"Large-scale, landscape-level restoration actions are widely implemented but receive little attention from academic ecologists" (Holl et al., 2003). Now, nearly 10 years later, my analysis suggests that we have much work left to do on this front. We might move forward in a number of ways, ranging from models, to small-scale restoration experiments set across multiple sites with varying landscape attributes, to large-scale experiments that encompass or restore landscape elements, to use of statistical techniques for assessing outcomes of actual landscape restoration efforts, which may be unreplicated and leave much to be desired in terms of experimental control (Holl et al., 2003). I echo Holl et al. (2003) in concluding that we must move forward on all these fronts, and likely on many others, if we are to understand and implement landscape restoration. Indeed, numerous questions at the interface of restoration and landscape ecology remain (Simberloff and Cox, 1987; Bell et al., 1997; Huxel and Hastings, 1999; Holl et al., 2003; Crooks and Sanjayan, 2006). For example,

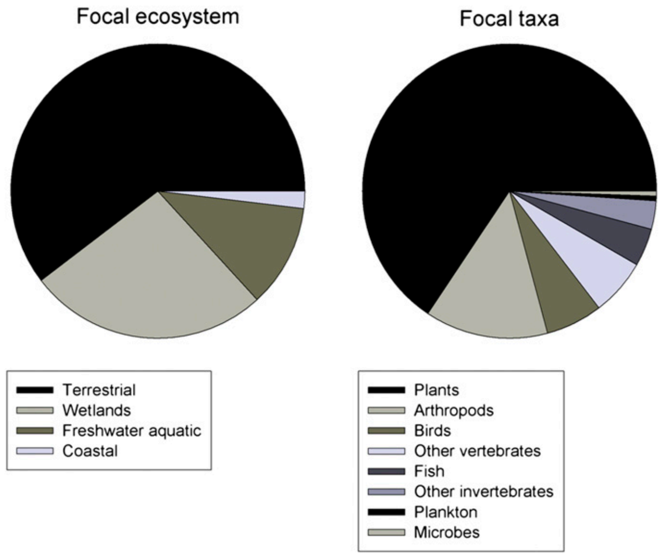

Fig. 4. Focal system and taxa in a review of 190 restoration studies published in the journals *Ecological Applications*, *Journal of Applied Ecology*, and *Restoration Ecology* during the past decade. The majority of restoration studies were focused on plants in terrestrial systems.

should landscape restoration efforts focus on enlarging existing remnant patches, building new patches, or connecting existing patches? When and for which species can landscape connectivity promote "passive restoration" and when must we actively reintroduce species? Will restoring landscape connectivity prove detrimental to target species by facilitating movement of negative agents, such as disease, predators, or disturbance (and if so, under which environmental conditions will detrimental effects occur)? How can we best use restoration to facilitate species migration during climate change?

Experimental landscape restoration research will likely be costly by ecology research standards, requiring substantial spatial and temporal scope. For example, to understand landscape effects during restoration one might propose to replicate a plant community-assembly experiment in forest patches situated in different types of landscapes (e.g., urban, forested, agricultural). Even modestly replicated (e.g., $N = 6$), such an experiment could require 18 sites and sizeable funding spread over 5 to 10 years. Although standard 3- to 5-year grants may not be well tailored to this type of proposal, the development of funds for research like this would undoubtedly prove beneficial to the field of restoration ecology.

In the meantime, I suggest one key question that we must answer now: how important are site-level conditions versus landscape effects during restoration? The answer will tell us whether we are justified in the current patch-level restoration paradigm (Fig. 3). Should landscape effects prove weak, we might continue with our focus on restoring a maximum number of individual patches, though hopefully with the ultimate goal of connecting patches to one another (Crooks and Sanjaya, 2006). Alternatively, should landscape effects prove strong, we may be conducting restoration with blinders on—enabling a clear view of the patches we are focused on, but blind to the effects of the landscapes that surround them. Thus, landscape effects may prove to be major reasons for the level of site-to-site variation in restoration outcomes—such as the level or composition of biodiversity—that currently impedes prediction. We are poised to begin answering this question, by analyzing factors such as patch geometry and landscape composition around existing restoration sites with geographic information systems. Several studies have employed such an approach, with mixed results. For example, Mabry et al. (2010) found an interaction between surrounding landscape composition and site-level savanna restoration, so that only restored sites in open-country landscapes supported characteristic savanna birds. Matthews et al. (2009) found that variation in restored wetland plant-community composition was explained equally by site- and landscape-level factors. Holl and Crone (2004) found support for local, but not landscape, factors (surrounding landscape composition, connectivity, patch geometry) determining patterns of understory plants in restored riparian forests. Clearly, this is not a large sample size, and (although this is also not a comprehensive literature review) much more work is needed. Ultimately, this must take the form of well-crafted experiments if we are to understand the predictable role of landscape effects on restoration. However, the near-ubiquitous influence of landscape effects on site-level biodiversity in my literature review suggests their widespread importance during restoration (Fig. 3), and such observational approaches are worthy first efforts.

Historical contingency—Relationships between historical contingency and restoration are among the most poorly investigated links in biodiversity restoration (Fig. 3), in spite of the high level of theoretical interest that restoration ecologists have shown. At this point, theoretical and conceptual work has markedly outstripped the number of strong experimental tests of these ideas (e.g., Young et al., 2001, 2005; Lockwood and Samuels, 2004; Suding and Hobbs, 2009). To be fair, theories on historical contingency and community assembly have been relatively recent arrivals to restoration ecology, introduced primarily during the past decade (e.g., Young et al., 2001, 2005; Chase, 2003; Suding et al., 2004; Temperton et al., 2004; Young et al., 2005; Suding and Hobbs, 2009), in contrast to the older tenure of other weak links in the biodiversity restoration model, such as landscape effects (Naveh, 1994). Given the high level of academic interest in historical contingency and the utility of restoration for testing these ideas, it seems likely that this link will strengthen with time; however, this work needs to be prioritized, because related concepts, such as threshold models, are currently being applied to restoration efforts without full understanding of their relevance (Suding and Hobbs, 2009).

At this point, most work that has addressed historical contingency in restoration has been demonstrational, largely providing support for the influence of history on restoration outcomes. For example, Bakker et al. (2003) showed the importance of year effects for native grass establishment during restoration, via interannual variation in precipitation. Fukami et al. (2005) demonstrated the importance of priority effects—initial species composition—in experimental grassland plots for ensuing plant colonization and community assembly. Brudvig and Damschen (2010) provide evidence for the influence of historical connectivity with woodland remnants on understory community composition, during restoration of postagricultural woodlands. Further, every study in my review that evaluated historical contingency found that it influenced biodiversity-restoration outcomes (Fig. 3).

Little, if any, work has tested the predictions of when history should matter to restoration (Chase, 2003). For example, history should matter least—and, thus, restoration outcomes should be most predictable—in highly connected, frequently disturbed, low-productivity systems with small regional species pools. Conversely, history, such as species arrival order or initial species composition, should matter most—and, thus, restoration outcomes should be most variable—in poorly connected, infrequently disturbed, high-productively systems with large regional species pools. The utility of restoration for testing these basic theoretical predictions is outstanding, and such experimental tests are strongly needed to aid in predicting restoration outcomes.

The less-studied facets of biodiversity—Restoration has focused almost exclusively on the species level of biodiversity, with emphasis on only a few taxanomic groups—primarily plants, but also, to lesser degrees, arthropods and vertebrates (Fig. 4). In some ways this focus makes perfect sense. We have sampled the facets of biodiversity that are most easily and inexpensively measured, requiring only botanical knowledge (for plants, at least) and survey time. In light of how rare monitoring is during restoration (Bernhardt et al., 2005), perhaps this approach is justified—it allows for assessment of a maximum number of restoration sites, economizing both time and money. We now need to understand the impacts of restoration on the less-studied facets of biodiversity (Fig. 3). Do plants function as an umbrella taxon, or species as an umbrella diversity level, during restoration? In other words, do restoration activities that promote plant biodiversity also promote diversity of other taxa, like nonarthropod invertebrates, soil microbes, and plankton? Does restoration of species diversity also result in restoration of functional and genetic diversity?

The controlled perturbations that accompany restoration may prove particularly useful for understanding linkages between species, functional, and genetic levels of biodiversity. Concepts from biodiversity–ecosystem functioning research are of fundamental interest to restoration ecology, and the linkages between these two disciplines have been explored in some detail (Young et al., 2005; Naeem, 2006; Wright et al., 2009). Rarely, however, are functional aspects of biodiversity assessed during restoration studies (Fig. 3). This can be accomplished through measurement of species traits relevant to ecosystem functioning (Petchey and Gaston, 2002). In addition to providing useful insight into ecosystem functioning during restoration, trait-based approaches might elucidate the strength of ecological filters and assembly rules (Fukami et al., 2005) and common community responses across sites and systems during restoration (McGill et al., 2006).

Linkages between species and genetic diversity are less well developed and remain largely theoretical (Vellend and Gerber, 2005). Species and genetic diversity may be highly correlated because similar processes control both, such as area, isolation, and environmental heterogeneity (Vellend and Gerber, 2005). By providing manipulations of—or at least variation in—these processes, restoration sites may prove useful for empirical tests of species/genetic diversity linkages.

Multitaxon assessments during restoration present opportunities to evaluate multispecies interactions, which may elucidate nonintuitive patterns of community development (Strauss and Irwin, 2004). Restoration has focused on some pairwise species interactions, such as plant–plant (Gómez-Aparicio, 2009), plant–mycorrhizae (Ruiz-Jaen and Aide, 2005), and plant–herbivore interactions (e.g., Sweeney et al., 2002), whereas others remain relatively poorly investigated, such as plant–pollinator interactions (Dixon, 2009; though see Forup and Memmott, 2005; Forup et al., 2008). Multispecies interactions remain very poorly considered in restoration, in spite of evidence that they may help to explain nonintuitive outcomes. For example, apparent competition—a plant × plant × consumer interaction—might contribute to the nonintuitive inability of competitively superior native perennial grass species to reestablish in California grasslands, which have been invaded by competitively inferior annual grasses (Seabloom et al., 2003; Orrock et al., 2008; Orrock and Witter, 2010).

Meta-analysis—It is time for meta-analysis in restoration ecology. Meta-analysis presents tools for drawing general conclusions from the results of multiple studies (Gurevitch and Hedges, 2001). My literature review resulted in an estimated ~750 papers in which restoration of some form was conducted, published in just three journals during the past 10 years. Herein lies a rich data set, from which we might ask a variety of questions. For example, a recent meta-analysis found that restoration of a variety of ecosystems increased biodiversity and ecosystem services; however, levels remained lower than at reference sites (Benayas et al., 2009). Further, a second recent meta-analysis harnessed the manipulative nature of restoration studies to investigate questions about the roles of competition and facilitation during plant establishment, demonstrating the utility of this approach for addressing basic concepts in ecology (Gómez-Aparicio, 2009). Although few other examples of restoration meta-analysis exist, the potential is clearly present for addressing a wide variety of basic and applied issues in ecology and, at the same time, asking questions about the generalities of restoration outcomes (or lack thereof). The latter may be of particular importance, should restoration ecology remain focused on site-level phenomena, independent of landscape and historical context. Rather than addressing the roles of landscape and historical contingency in single studies, we might harness variation across studies to understand these issues.

Conclusions—Guided by restoration ecology, ecological restoration represents a primary tool for reversing the world's biodiversity crisis. However, to uphold this promise and enable predictable biodiversity restoration at landscape scales, restoration ecology must strengthen weak links in its conceptual model. At present, restoration research is highly focused on promoting species diversity—primarily of plants—within individual restoration patches. Far less is known about a variety of less-investigated taxa (e.g., soil microbes and plankton) and levels of biodiversity (functional and genetic) or about how landscape factors and historical contingency contribute to restoration outcomes. More research attention must be directed toward these less-investigated links, particularly landscape and historical effects, which may be major factors behind the site-to-site variation and nonintuitive restoration outcomes that inhibit prediction in restoration ecology. Such work might be accomplished through individual studies working across multiple sites or through meta-analysis working across multiple studies. Although we may make some progress through the study of existing restoration efforts, our ability to understand contingency in restoration will ultimately necessitate well-crafted experiments, manipulating the factors of interest and controlling for the variation in sites and restoration approaches that otherwise limit the utility of observational studies. With this comes the need for research funding and, in particular, restoration-specific funding to allow for the expense of working across multiple sites and many years. Restoration ecology has seen immense development during the past 10 to 15 years, and these are key research directions for further growth and strengthening as an academic discipline. At the same time, ties to practice—ecological restoration—must remain strong, and the influx of ecological theory into restoration ecology must be translated into feasible restoration strategies that work well. It is ecological restoration that most proximally will reverse biodiversity declines; however, it is restoration ecology that must illuminate the way forward (Hobbs and Norton, 1996; Falk et al., 2006; Giardina et al., 2007).

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