REVIEWS AND SYNTHESES

The ecology of restoration: historical links, emerging issues and unexplored realms

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Abstract

Restoration ecology is a young academic field, but one with enough history to judge it against past and current expectations of the science's potential. The practice of ecological restoration has been identified as providing ideal experimental settings for tests of ecological theory; restoration was to be the 'acid test' of our ecological understanding. Over the past decade, restoration science has gained a strong academic foothold, addressing problems faced by restoration practitioners, bringing new focus to existing ecological theory and fostering a handful of novel ecological ideas. In particular, recent advances in plant community ecology have been strongly linked with issues in ecological restoration. Evolving models of succession, assembly and state-transition are at the heart of both community ecology and ecological restoration. Recent research on seed and recruitment limitation, soil processes, and diversity–function relationships also share strong links to restoration. Further opportunities may lie ahead in the ecology of plant ontogeny, and on the effects of contingency, such as year effects and priority effects. Ecology may inform current restoration practice, but there is considerable room for greater integration between academic scientists and restoration practitioners.

Keywords

Alternative stable states, contingency, ontogenetic niche shifts, seed limitation.

Ecology Letters (2005) **8**: 662–673

INTRODUCTION

Ecological restoration is 'intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity and sustainability' SER (2004). Restoration ecology is the field of science associated with ecological restoration. The practice of ecological restoration is many decades old, at least in its more applied forms, such as erosion control, reforestation, and habitat and range improvement. However, it has only been in the last 15 years that the science of restoration ecology has become a strong academic field attracting basic research and being published in indexed peer-reviewed journals (Fig. 1). Associated with this growth has been an increasing desire to define a scientific identity for restoration ecology and its relationship to ecological restoration.

Early on, far-sighted ecologists recognized that the practice of ecological restoration could be an 'acid test' of ecological theory (Bradshaw 1987), and conversely, recognized that the highly manipulative nature of ecological restoration provided an ideal setting for hypothesis generation and testing in ecology (Jordan *et al.* 1987b). One of the first attempts to delineate an ecological discipline centred on restoration was the seminal volume by Jordan *et al.* (1987a). In recent years, there has been considerable discussion of the conceptual bases of restoration ecology (Cairns & Heckman 1996; Hobbs & Norton 1996; Allen *et al.* 1997; Perrow & Davy 2002; Peterson & Lipcius 2003; Temperton *et al.* 2004; van Andel & Grootjans 2005; Aronson & van Andel 2005). There emerge two kinds of questions about the links between conceptual ecology and ecological restoration. First, what set of ecological principles and concepts serve as an essential basis for effective restoration? Second, are there conceptual areas of ecology unique to, or at least uniquely well informed by, ecological restoration?

In this review, we explore conceptual areas of enquiry that have been active in restoration ecology, suggest new or understudied research areas, and ask whether the surge in academic interest has been accompanied by useful information transfer to restoration practitioners. We are not including in this review invasive species biology, which has seen its own explosive growth in the last decade (e.g. Bais *et al.* 2003; Carlton 2003; Callaway & Ridenour 2004; Dukes & Mooney 2004; Rejmanek *et al.* 2005) and is in need
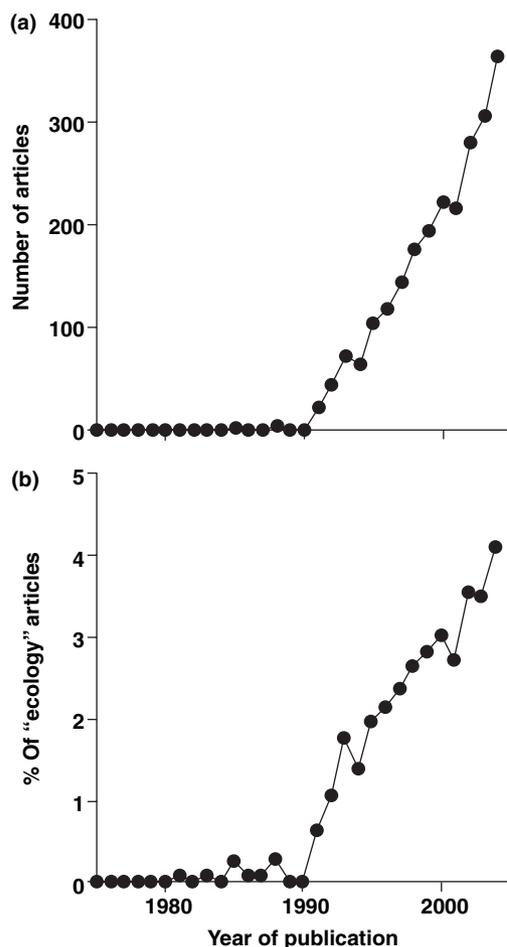
Figure 1 Growth in the field of restoration ecology, based on a keyword search of articles using 'restor* and ecol*' on the Web of Science carried out in January 2005. The * is a truncation symbol. (a) The number of such articles appearing in each year since 1974. (b) Because the absolute number of articles in ecology has also been increasing steadily, this figure shows the relative contribution of the articles in part (a), above, captured by a search for the keyword 'ecol*'. By this estimate, restoration ecology has grown to account for >4% of all ecology papers as of 2004. Web of Science URL: http://isi02.isiknowledge.com/portal.cgi.

of its own assessment of conceptual bases (see Hastings et al. 2005), beyond mentioning here that this field is of great interest to ecological restoration (Bakker & Wilson 2004). Restoration ecology has been largely a botanical science, perhaps because natural communities are composed largely of plants, and plants are the basis of most ecosystems (Young 2000). This review is reflective of that emphasis.

ESTABLISHED ECOLOGICAL CONCEPTS

Much of basic and applied research in ecological restoration draws from established ecological principles and concepts

(see Table 1). An understanding of the concepts in Table 1 underlies the successful practice of restoration, and most restoration practitioners recognize this. Competition and physiological limits have long been a basis of applied plant science, including agronomy, horticulture and restoration. Other concepts, such as the extent of positive interspecific effects (Callaway & Walker 1997; Bruno et al. 2003), the importance of local ecotypes and local genetic diversity (Knapp & Dyer 1997; Rice & Emery 2003; McKay et al. 2005), and the roles of natural disturbance regimes in the health of many ecosystems (White & Jentsch 2004) have entered the mainstream of practical ecological restoration more recently. Restoration research often addresses aspects of these concepts as they apply to their restoration applications. The concepts in Table 1 are largely self-explanatory, and we offer them here as a reminder of the deep ecological roots of restoration.

EMERGING ECOLOGICAL CONCEPTS

Of particular interest to academic ecologists interested in restoration are opportunities for restoration ecology to address new and unresolved issues in the field of ecology. Whether these concepts are unique to restoration ecology is not the critical issue. Rather, we ask: What emerging concepts in ecology is restoration particularly well equipped to address? In the past few years, several important research areas have emerged that may fulfil this criterion, and are also applicable to the practice of restoration (see also van Andel & Grootjans 2005; Aronson & van Andel 2005).

Models of community development

Much ecological restoration involves the recovery or construction of functional communities, so it is not surprising that restoration ecologists have taken a particular interest in theories about how communities are constructed and how they respond to different forms of manipulation, especially in the context of recovery after disturbance. Successional theory and state-transition models have been a conceptual basis for restoration since its inception, but the recent development of assembly theory and potential importance of alternative stable states has spurred a spate of books and articles (Luken 1990; Packard 1994; Lockwood et al. 1997; Lockwood 1997; Palmer et al. 1997; Pritchett 1997; Weiher & Keddy 1999; Whisenant 1999; Young et al. 2001; Jackson & Bartolome 2002; Walker & del Moral 2003; Suding et al. 2004; Temperton et al. 2004).

Successional theory is often simplified as being the orderly and predictable return after disturbance to a climax community. State-transition community models are similar in supposing a restricted set of community states with some set of limits to transitions between those states (Rietkerk &

Table 1 Established ecological concepts that are generally understood by restoration practitioners. Some of these are deeply embedded in the knowledge base of restorationists (and agronomists); others are in the process of being incorporated into restoration practice

1. Competition: (plant) species compete for resources, and competition increases with decreasing distance between individuals and with decreasing resource abundance (c.f., Fehmi *et al*. 2004; Huddleston & Young 2004).
2. Niches: species have physiological and biotic limits that restrict where they can thrive. Species selection and reference communities need to match local conditions. See also the 'Ecology of ontogeny' section in the text.
3. Succession: in many ecosystems, communities tend to recover naturally from natural and anthropogenic disturbances following the removal of these disturbances (see also text). Restoration often consists of assisting or accelerating this process (Luken 1990). In some cases, restoration activities may need to repair underlying damage (soils) before secondary succession can begin (Whisenant 1999).
4. Recruitment limitation: the limiting stage for the establishment of individuals of many species is often early in life, and assistance at this stage (such as irrigation or protection from competitors and herbivores) can greatly increase the success of planted individuals (Whisenant 1999; Holl *et al*. 2000), but again, see the 'Ecology of ontogeny' section.
5. Facilitation: the presence of some plant species (guilds) enhances natural regeneration. These include N-fixers and overstorey plants, including shade plantings and brush piles (see Parrotta *et al*. 1997; Gomez-Aparicio *et al*. 2004; for conceptual reviews, see Callaway & Walker 1997; Lamb 1998; Bruno *et al*. 2003).
6. Mutualisms: mycorrhizae, seed dispersers and pollinators are understood to have useful and even critical roles in plant regeneration (e.g. Bakker *et al*. 1996; Wunderle 1997; Holl *et al*. 2000).
7. Herbivory/predation: seed predators and herbivores often limit regeneration of natural and planted populations (Holl *et al*. 2000; Howe & Lane 2004).
8. Disturbance: disturbance at a variety of spatial and temporal scales is a natural, and even essential, component of many communities (Cramer & Hobbs 2002; Poff *et al*. 2003; White & Jentsch 2004). The restoration of disturbance regimes may be critical.
9. Island biogeography: larger and more connected reserves maintain more species, and facilitate colonizations, including invasions (Naveh 1994; Lamb *et al*. 1997; Bossuyt *et al*. 2003; Holl & Crone 2004; Hastings *et al*. 2005).
10. Ecosystem function: nutrient and energy fluxes are essential components of ecosystem function and stability at a range of spatial and temporal scales (Ehrenfeld & Toth 1997; Aronson *et al*. 1998; Bedford 1999; Peterson & Lipcius 2003).
11. Ecotypes: populations are adapted to local conditions, at a variety of spatial and temporal scales. Matching ecotypes to local conditions increases restoration success (Knapp & Dyer 1997; Montalvo *et al*. 1997; McKay *et al*. 2005).
12. Genetic diversity: all else being equal, populations with more genetic diversity should have greater evolutionary potential and long-term prospects than genetically depauperate populations (Rice & Emery 2003; McKay *et al*. 2005).

van de Koppel 1997; Allen-Diaz & Bartolome 1998; Whisenant 1999; Bestelmeyer *et al*. 2004). State-transition models are an example of a conceptual framework in ecology that is directly attributable to scientists interested in land management and restoration. Succession and state-transition models have appealed to restoration scientists and practitioners because both suggest that a pathway to the desired state exists, even if candidate sites for restoration sometimes appear to be 'stuck' in a degraded or alternative state (Bakker & Berendse 1999). Some ecologists suggest moving away from these approaches in favour of alternative theories, especially those associated with assembly (see below). For others, the succession/assembly debate is an opportunity to revisit classical succession theory and rediscover its richness, including its ability to analyse alternative stable states (Young *et al*. 2001; White & Jentsch 2004). In fact, some early successional theory (Gleason 1926, p. 20; Egler 1954) remarkably foreshadowed assembly theory (Young *et al*. 2001).

Early assembly theory related to the observation that spatially isolated communities had different compositions of species, but similar guild structure – the 'rule' of guild proportionality (Wilson & Roxburgh 1994) or forbidden combinations (Diamond 1975). It was hypothesized that random differences in colonization and establishment, coupled with strong priority effects, might explain these alternative community states. Work in aquatic microcosms and mesocosms and with simulation models sometimes demonstrated alternative states (e.g. Samuels & Drake 1997; Petraitis & Latham 1999), and sought to explore the details of how they were produced (Chase 2003b; Warren *et al*. 2003; see review in Young *et al*. 2001). Simulations in particular have raised the spectre of virtually unlimited alternative stable states; including the oft-cited 'Humpty-Dumpty' effect (Pimm 1991; Luh & Pimm 1993; Samuels & Drake 1997). More recently, assembly theorists have moved beyond colonization and priority effects to ask about additional forces that can push community trajectories in different directions (Suding *et al*. 2004; Temperton *et al*. 2004; Tilman 2004). For example, 'nexus species' have been proposed as species that may be transient in community development but whose presence or absence has profound long-term effects (Drake *et al*. 1996; Lockwood & Samuels 2004).

More extensive broadening of the meaning of 'assembly theory' has also taken place. In a recent volume on assembly and restoration that addresses a wealth of conceptual and practical issues in restoration (Temperton *et al*. 2004), the

majority of authors agree with definitions of assembly theory as 'the explicit constraints that limit how assemblages are selected from a larger species pool' (Weiher & Keddy 1999), or 'ecological restriction on the observed patterns of species presence or abundance' (Wilson & Gitay 1995). The major disagreement among them is whether these filters are strictly biotic, or can be abiotic as well. When thus broadly defined, assembly theory encompasses virtually all of modern ecology (Young 2005), including all of the entries in Table 1, and is reminiscent of Krebs' (1972) definition of ecology (citing Andrewartha's 1961 definition of population ecology) as 'the scientific study of interactions that determine the distribution and abundance of organisms'. What is being proposed is that assembly theory is a framework that can unify virtually all of (community) ecology under a single conceptual umbrella. Independent of that ambitious goal, assembly theory's contribution in the context of restoration ecology may be its explicit focus on the full range of mechanisms at work in community formation. The array of these mechanisms has sometimes been referred to as 'assembly rules'. These rules are rarely explicitly stated (Young 2005), but would include the core concepts of guild proportionality and priority effects. The existence of strict rules is itself debated (Weiher & Keddy 1999).

The conceptual frameworks of succession and assembly (*sensu stricto*) can have very different predictions (Young *et al.* 2001), some of which can be tested in restoration settings (Wilson *et al.* 2000). However, few experimental restoration studies have been published that were explicitly designed to distinguish between them (Pywell *et al.* 2002), or even to test the concept of priority itself (Lulow 2004), although temporary reductions in weeds during restoration plantings are essentially priority experiments. Given the modernity of this debate within restoration ecology, this research shortfall is not surprising, and we may expect more publications in the near future. The restoration and creation of vernal pools (Collinge 2003) and prairie potholes (Keddy 1999; Seabloom & van der Valk 2003) may be ideally suited to this kind of research, because of their discrete nature and potential for multiple independent replicates.

We still do not know the relative strengths of divergence and convergence in most natural or restored communities, or as McCune & Allen (1985) asked: Will similar communities develop on similar sites? (Chase 2003a). Under what conditions do convergent (successional) tendencies overcome initial conditions at a site, or fail to (Marrs *et al.* 2000; Wilkins *et al.* 2003)? If alternative stable states are pervasive, they may represent either a challenge to restoration, or an opportunity (Luken 1990; Young & Chan 1998; de Blois *et al.* 2004). Sometimes lost in this discussion is the reality that many ecosystems do recover after disturbance (e.g. Haeussler *et al.* 2004; Voigt & Perner 2004; see also

Table 1) and that management techniques that fight successional trends are far less likely to succeed than those that work with them (e.g. Marrs *et al.* 2000; Cox & Anderson 2004; but see de Blois *et al.* 2004).

Diversity/function relationships

The study of diversity/stability relationships that began in the 1970s has broadened to include questions about the relationships between species diversity and a variety of ecosystem functions (Waide *et al.* 1999; Schwartz *et al.* 2000; Tilman *et al.* 2001; Cardinale *et al.* 2004; Hooper *et al.* 2005). What mechanisms drive these relationships? How many species are sufficient for a particular function? These questions are of central interest to restoration, and restoration experiments may provide an ideal setting for testing them. Initial results from a variety of diversity studies (reviewed in Lawler *et al.* 2001; Loreau *et al.* 2002; Hooper *et al.* 2005) suggest that (i) full or nearly full function is often achieved with 10–15 species (Fargione *et al.* 2003) or even fewer (Wardle 2002; Tracy & Sanderson 2004), and (ii) the presence of different functional groups is often an important driver of ecosystem function (Hooper & Vitousek 1998; Fargione *et al.* 2003). This latter result is referent to the guild proportionality of assembly theory (see above). Both these results have clear implications for restoration, but as yet have rarely been the subject of formal study in restoration settings (Callaway *et al.* 2003; Gondard *et al.* 2003; Aronson & van Andel 2005).

Seed limitation and restoration

Seed limitation is an emerging focus of studies examining factors governing plant community structure and mechanisms of species coexistence, and a primary concern in restoration. It is not clear to what extent lack of seeds limits recruitment in natural plant populations, and its importance relative to other factors (Crawley 1990). However, sowing additional seeds on even undisturbed sites frequently does increase the number of established individuals of seeded species, indicating that there are more safe sites than seeds to fill them for some species in many communities (e.g. Tilman 1997; Turnbull *et al.* 2000; Zobel *et al.* 2000; Foster & Tilman 2003). These results suggest that likelihood of seed arrival does influence community structure in some communities, and more specifically support lottery-type models of species coexistence (McEuen & Curran 2004).

In restoration settings, dispersal limitation and missing seed banks can result in depauperate species assemblages, especially in fragmented landscapes (Stampfli & Zeiter 1999; Seabloom & van der Valk 2003, see also Fig. 2). Introduction of propagules for desired species is then appropriate as a way of manipulating or accelerating vegetation change
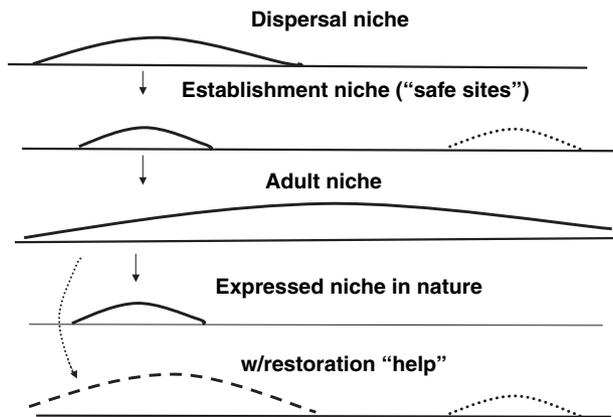
Dispersal niche

Establishment niche ("safe sites")

Adult niche

Expressed niche in nature

w/restoration "help"

Figure 2 One scenario of ontogenetic niche space, and the possible effects of restoration activities. The *x*-axis is a gradient of whatever environmental parameters define or restrict niche space, be they abiotic, biotic or temporal. For a fuller explanation, see text and Table 2. For simplicity, the 'reproductive niche' of Table 2 is not shown here. In nature, these niche spaces will differ in various ways for each species, and through time.

(Whisenant 1999, p. 122; Palmer *et al.* 1997). On less disturbed sites, seed addition to reinforce or re-introduce lost or threatened native species also may be worth trying (e.g. Seabloom *et al.* 2003a,b).

Some unanswered questions about seed limitation are of special interest to restoration ecology. For example, do positive results from seed addition represent only 'transient coexistence' (Foster & Tilman 2003), or do they cause permanent changes to community structure? Some seed addition studies have shown a dramatic drop in sown species presence between seedling and adult stages (Turnbull *et al.* 2000), while others have shown persistence for as long as 8 years (Foster & Tilman 2003). In addition, do higher rates of seeding, or seeding in multiple years (Collinge 2003) lead to longer persistence of seeded individuals or species, and, consequently, greater change in community structure? Seed addition rates for grassland species have ranged from <200 m^{-2} (e.g. Seabloom *et al.* 2003a) to more than 20 000 m^{-2} (e.g. Zobel *et al.* 2000). For us, one of the most interesting aspects of seeding studies is the implication that some natural populations are fecundity limited.

The importance of soil microbial communities

Restoration ecology has helped elevate soil microbial communities – and the processes they mediate – to a more prominent position in ecology, building on knowledge accumulated in soil and agronomic sciences (e.g. Wardle 2002; Bais *et al.* 2003; Reynolds *et al.* 2003). We now recognize, in the context of restoration, the central role of

soil microbes for the success of higher plants and for overall ecosystem health. Plants with nitrogen-fixing symbioses have been employed throughout the history of restoration. Mycorrhizal associations have also been long explored in restoration settings, where their benefits have been repeatedly demonstrated (Smith & Read 1997), although the necessity of active mycorrhizal introduction is less clear (Renker *et al.* 2004).

Some soil organisms have the ability to reduce available soil nitrogen, especially when provided with excess carbon. In sites degraded by high levels of nitrogen, restoration practitioners have explored various forms of carbon addition to reduce soil nitrogen. These techniques can work in the short run, but often have limited long-term effects (reviewed in Corbin *et al.* 2004; see also Blumenthal *et al.* 2003; Baer *et al.* 2004; Huddleston & Young 2005). Curiously, such studies have rarely directly measured microbial responses to carbon addition (Corbin & D'Antonio 2004), but instead their inferred effects on soil nutrient conditions. Manipulations of soil microbial communities may also facilitate restoration of sites with high levels of salts or toxic metals (Kernaghan *et al.* 2002). The importance of soil aggregates, and their reliance on soil microbes, has also recently caught the attention of restoration ecologists (Jastrow *et al.* 1998; Requena *et al.* 2001; Rillig *et al.* 2003).

Research on microbial and allelo-chemical soil ecology (Bais *et al.* 2003; Callaway & Ridenour 2004) sheds light on relatively unexplored ecological processes of enormous scope, and directly responds to a need in restoration practice for practical and economical methods for site amelioration. Continued research into the ecology of soil microbes may reveal new potential for increasing restoration success, and may provide missing pieces in our understanding of community development. For example, studies of assembly and diversity and function in soil communities (Wardle 2002; Walker *et al.* 2004) have traditionally been overlooked in ecology, and restoration theory and practice is helping to fill in the gaps (Gros *et al.* 2004).

FUTURE ECOLOGICAL CONCEPTS

There are a number of areas of ecology and conservation biology that we suspect will increasingly inform and be informed by restoration (see also Aronson & van Andel 2005). Not discussed further here, but understudied in the context of restoration, are Allee effects, population viability analyses, trophic ecology (including indirect effects), gap analysis (Lee *et al.* 2002; Linke & Norris 2003), metapopulation dynamics and metacommunities (Leibold *et al.* 2004). There is also increasing interest in the unique issues of restoration at the landscape and ecosystem levels (Holl *et al.* 2003; Aronson & van Andel 2005). In addition, there are two areas where we see particularly appropriate

opportunities to link emerging conceptual ecology to restoration.

Ecology of ontogeny

In a landmark paper, Grubb (1977) proposed that for many plants, the life stage that defined the species niche was the period from germination to establishment, and that this created niche separation among species (see Ribbens *et al.* 1994). He suggested this was often hidden from the observer who only noticed that adults seemed to share considerable niche space. Grubb's hypothesis was that adults of different species did indeed share niche space – that looking at adults would tell us little about species coexistence and individual species distributions (see Davis 1991). Implicit in this discussion was the concept that many species can exist as adults in far broader niche space than that into which they can successfully recruit. Grubb gives several examples of established plants persisting in circumstances unfavourable for recruitment.

This is an example of 'ontogenetic niche shifts', which recently have been much explored for animals (e.g. Post 2003; Takimoto 2003), but rarely for plants (Eriksson 2002), perhaps because plants are sedentary. Ontogenetic niche shifts are both conceptually interesting and a useful context for looking at the effects of restoration practices (Table 2). Figure 2 is an illustration of one possible pattern of ontogenetic niches. Environmental factors defining niche space may include temperature, moisture, soil conditions and biotic interactions. The expressed niche will be the union of all the ontogenetic niches. A narrowing of niche space through ontogeny can be considered the equivalent of a 'filter' in assembly (see above). Seeds often disperse to more sites than are suitable for establishment. Conversely, dispersal barriers can keep seeds from reaching some suitable sites. Restoration activities may broaden the recruitment niche through assisted establishment (dashed lines) or the dispersal niche through translocation of propagules (dotted lines). If the recruitment or dispersal stages are indeed niche bottlenecks (filters), then restoration efforts designed to maximize success at these limiting stages run the risk of artificially extending the local range of species (lowermost figure).

Humans can temporarily or permanently alter the expressed niche in several ways. First, we may eliminate the reproductive, dispersal or recruitment niches by altering the environment or by eliminating obligate pollinators or seed dispersers. In short-lived species, this results in rapid population extinction. In longer-lived species, this results in 'living dead' (Janzen 2001) or 'relict populations' (Eriksson 1996, 2000) temporarily persisting as non-recruiting adults. In such situations, restoration may require restoring the lost links in the recruitment chain.

Second, we may extend the dispersal niche by overcoming dispersal barriers or limitations. Although this can be useful in re-introducing locally extinct populations, overcoming dispersal barriers can also result in the invasion of new habitats and may produce viable persistent populations where that species had not previously existed. In restoration, imprecise species lists or misidentification of or disregard for subspecies can result in this kind of range extension, and, in addition, can pollute local genotypes (Montalvo & Ellstrand 2001; McKay *et al.* 2005).

Third, we can create non-recruiting populations by bypassing limits set by recruitment niches and actively planting individuals in sites where saplings and adults can thrive and grow but where their seeds are not able to successfully germinate and establish. Foresters and horticulturalists often explicitly plant individuals where 'natural recruitment' does not occur, but restoration practitioners run the risk of doing so inadvertently.

In many restoration and mitigation projects, the measure of success is growth and survival, with less concern, or even no concern, for intergenerational persistence, especially in the case of longer-lived plants such as woody species and bunchgrasses. Assisting plantings through the early stages of

Table 2 A suggested typology of different kinds of ontogenetic niches as they relate to the distribution of plant species (See Fig. 2)

Reproductive niche: The set of environmental parameters that allows adults to produce flowers, engage in successful fertilization, and rear seeds up to the dispersal stage. There is some evidence that the reproductive niche is narrower than the persistence niche. For example, individuals at the edge of species ranges are less likely to engage in successful reproduction (Maycock & Fahselt 1992). In a related pattern, male plants of dioecious species are often found in more severe sites than female plants (e.g. Bertiller *et al.* 2002).

Dispersal niche: The set of environmental parameters that determines where seeds arrive. This can be related to dispersal barriers as well as local dispersal limitations.

Recruitment (establishment) niche: The set of environmental parameters that allows seeds to germinate and become established (safe sites). This is similar to Grubb's (1977) regeneration niche, which may also combine reproductive, dispersal and recruitment niches.

Adult niche: The set of environmental parameters that allows established plants to survive and grow. This is likely to be broader than other ontogenetic niches, both ecologically and biogeographically. Grubb (1977), p. 119) calls this the 'habitat niche'.

Expressed niche: The set of environmental parameters in which plant is actually found. In nature, this would be the niche space shared by the dispersal, recruitment and adult niches.

recruitment is commonplace in restoration, because it is these stages that are the most vulnerable to loss. However, if such assisted individuals are inadvertently established in sites or microsites where natural recruitment is not possible, then (local) artificial range extensions are possible. Conversely, if recruitment opportunities are simply rare or episodic, restoration assistance might be appropriate. These situations may not be easily distinguishable. We urge restoration researchers to address these issues.

The broad adult niche may operate similarly along successional gradients. Mid-seral species, once established, may persist for an entire generation, even if the conditions for establishment have long passed (Young *et al.* 2001). When such species are long-lived, as is the case with many clonal species, this can result in arrested succession (Schnitzer *et al.* 2000; Griscom & Ashton 2003; Mallik 2003; Slocum *et al.* 2004), and an alternative (quasi-)stable state. Von Holle *et al.* (2003) point out that communities dominated by long-lived species may be resistant to invasion by exotic species, at least for the life span of the residents.

CONTINGENCY AND YEAR EFFECTS

Ecology studies contingent systems and processes. Historical and stochastic effects create patterns not fully explicable with simple deterministic models. Several types of contingency are critical drivers of community structure in ecological systems, and are not only theoretically interesting, but also have strong implications for ecological restoration (Bakker *et al.* 2003; Wilson *et al.* 2004). For example, the presence or absence of herbivores can have profound effects on community development and structure (see Howe & Lane 2004). Nexus species and contingent arrival times (priority effects) were discussed above.

Interannual variations in establishment success (Bartha *et al.* 2003), also known as 'year effects', have been a persistent problem for ecological restoration practitioners, who often have only a single planting year to achieve their project goals. Episodic recruitment, so common in nature (Crawley 1990), is a bane to restoration practitioners. If we could recognize the particular conditions most favourable to successful restoration efforts, we could enhance the success of restoration efforts, either through more effective timing of restoration plantings or through more cost-effective use of expensive management practices, such as irrigation. This is particularly true as we increase our ability to make long-term forecasts and predict major climatic events like El Nino and La Nina. Even post-establishment, a number of restoration studies have shown that management treatments, such as grazing and burning, can be highly contingent upon year effects (e.g. Sarr 2002; Bartolome *et al.* 2004; Foster & Dickson 2004). Here we discuss two

additional kinds of year effects that are also particularly relevant to restoration.

First, it is well known that a number of species exhibit considerable interannual variation in seed production, and an ongoing goal of ecological research is to explain mast years of high production (c.f. Piovesan & Adams 2001; Abrahamson & Layne 2003; Kerkhoff & Ballantyne 2003; Koenig *et al.* 2003). Of even greater interest to restoration, however, especially when seed must be gathered from natural populations, are years of total reproductive failure, compared with 'normal' years of merely low reproductive output (Hobbs & Young 2001). In other words, ecological restoration is at least as interested in the unexplored troughs of seed production (expressed on a log scale to reveal relative variation at low levels) as in the peaks.

Second, interannual variation in the relative success of herb layer functional groups appears to result in 'grass years' and 'forb years' associated with different rainfall patterns within sites, at least in California grasslands (Pitt & Heady 1978; Evans & Young 1989, see also Rabotnov 1974). However, this earlier research did not tease apart direct year effects from indirect effects related to grass–forb competition. Results from restoration settings, where these confounding influences can be controlled, appear to show that these differences are directly related to interannual difference in the abiotic environment, probably the timing of rainfall (Lulow 2004). Levine & Rees (2004) suggest that interannual variability itself may determine species coexistence in this system (see also Grubb 1977, pp. 111–112). Restoration settings are an ideal backdrop for testing all of these ecological concepts relating to contingency, and it is time for restoration research to take advantage of this.

CONCLUSION

What land and resource managers want most from ecologists is practical guidance in achieving restoration goals effectively (Cairns 1993; Clewell & Rieger 1997), and this remains one of the main foci of research in restoration ecology (Table 2). There is evidence that restoration practitioners are listening to at least some of what restoration ecologists are saying; the greater emphasis on appropriate genetic choices in restoration is a good example. Conversely, how well has restoration ecology bridged the divide between an emerging applied science and the more general themes of ecological theory? In several of the areas discussed here we think it has, and is continuing to do so. Plant community ecology in particular has been invigorated by the rise of restoration ecology as a field and by the challenges provided by ecological restoration.

Nonetheless, ecological restoration has been more of an acid test of horticultural and agronomic skills than of ecological understanding. A useful comparison for the state

of restoration ecology is with that of its sister science, conservation biology, which predates restoration ecology as an academic field by a decade or so (Young 2000). Conservation biologists also have gone through a period of academic soul-searching, trying to discover and develop conceptual bases for their emerging science, but having a limited impact on field conservation (Harcourt 2000). A similar self-evaluation is occurring within restoration. The restoration practitioner's need to construct ecological communities, often from scratch, means that even the most basic questions about community functioning and structure cannot be taken for granted. Nevertheless, our image of theory-driven restoration research may partly be an artefact of the kinds of studies accepted for publication or by dissertation committees, while much real-world restoration takes place largely independent of interchange with the academic field of restoration ecology. In both restoration and conservation, tension between academic research and typical on-the-ground, time- and resource-limited implementation is probably unavoidable, and even healthy. If the recent past is any guide, we will continue to see growth in the science of restoration ecology, and continued interest by academic scientists in the opportunities that restoration provides for the examination of historical and emerging ecological theories.

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