Advances in restoration ecology: rising to the challenges of the coming decades

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Abstract. Simultaneous environmental changes challenge biodiversity persistence and human well-being. The science and practice of restoration ecology, in collaboration with other disciplines, can contribute to overcoming these challenges. This endeavor requires a solid conceptual foundation based in empirical research which confronts, tests and influences theoretical developments. We review conceptual developments in restoration ecology over the last 30 years. We frame our review in the context of changing restoration goals which reflect increased societal awareness of the scale of environmental degradation and the recognition that inter-disciplinary approaches are needed to tackle environmental problems. Restoration ecology now encompasses facilitative interactions and network dynamics, trophic cascades, and above- and belowground linkages. It operates in a non-equilibrium, alternative states framework, at the landscape scale, and in response to changing environmental, economic and social conditions. Progress has been marked by conceptual advances in the fields of trait-environment relationships, community assembly, and understanding the links between biodiversity and ecosystem functioning. Conceptual and practical advances have been enhanced by applying evolving technologies, including treatments to increase seed germination and overcome recruitment bottlenecks, high throughput DNA sequencing to elucidate soil community structure and function, and advances in satellite technology and GPS tracking to monitor habitat use. The synthesis of these technologies with systematic reviews of context dependencies in restoration success, model based analyses and consideration of complex socio-ecological systems will allow generalizations to inform evidence based interventions. Ongoing challenges include setting realistic, socially acceptable goals for restoration under changing environmental conditions, and prioritizing actions in an increasingly space-competitive world. Ethical questions also surround the use of genetically modified material, translocations, taxon substitutions, and de-extinction, in restoration ecology. Addressing these issues, as the Ecological Society of America looks to its next century, will require current and future generations of researchers and practitioners, including economists, engineers, philosophers, landscape architects, social scientists and restoration ecologists, to work together with communities and governments to rise to the environmental challenges of the coming decades.

Key words: Anthropocene; community assembly; ecosystem function; ecosystem services; ESA Centennial Paper; faunal restoration; global change; landscape scale; novel ecosystems; resilience; socio-ecological systems; traits; trophic networks.

Received 1 March 2015; revised 7 May 2015; accepted 13 May 2015; published 7 August 2015. Corresponding Editor: D. P. C. Peters.
INTRODUCTION

We are in an unprecedented era of simultaneous global environmental changes, many unperceived at the founding of the Ecological Society of America (ESA) one hundred years ago (Steffen et al. 2011, Barnosky et al. 2012, Steffen et al. 2015). Significant challenges facing humanity include global biodiversity loss, anthropogenic pollution and associated climate change, land allocation, energy generation and coping with a growing global human population (Vitousek et al. 1997, Steffen et al. 2005). However, there are inspiring messages that suggest global environmental change and associated challenges can be tackled (DeFries et al. 2012). One long-term, potentially cost-effective, and optimistic solution is the science of restoration ecology and its applied practice of ecological restoration (Dobson et al. 1997, Nelleman and Corcoran 2010, Suding et al. 2015).

The restoration of ecosystems that have been damaged, degraded or destroyed, through establishing or re-introducing flora and fauna (SERI 2004), provides options to mitigate environmental degradation, especially at large scales (Menz et al. 2013). Ecological restoration has the potential to improve air quality, reverse forest clearance and desertification, slow biodiversity loss, enhance urban environments and perhaps improve human livelihoods and humanity’s relationships within nature. These examples highlight the opportunity for restoration ecology to develop the tools that will allow people to rise to the environmental challenges of the coming decades, finding solutions that meet both social and environmental goals, particularly when coupled with other disciplines. However, rising to these challenges will require clear articulation of restoration goals (Hobbs and Norton 1996) and solid ecological foundations upon which to build restoration practice.

Here, we elucidate the conceptual foundations upon which to build restoration practice, in the context of the plurality of restoration motivations and goals that characterize the current era. We explicitly consider conceptual ecological developments pertinent to restoration since A. D. Bradshaw’s (1983) Presidential Address to the British Ecological Society in 1982, when he stated: “The acid test of our understanding is not whether we can take ecosystems to bits on paper, however scientifically, but whether we can put them together in practice and make them work.” We explore how conceptual developments are being applied to restoration practice and how ecological knowledge is faring against the ‘acid test’.

We were motivated to provide this review in acknowledgement of the ESA’s Centenary and given the fact that restoration ecology has become an important discipline within the broad corpus of ecological knowledge since Bradshaw’s address. We aim to build on earlier reviews (e.g., Young et al. 2005, Brudvig 2011, Suding 2011) and present evidence for a coherent conceptual framework that represents the development and contemporary state of restoration ecology (see also Figs. 1 and 2). This framework synthesizes the development and incorporation of important ecological concepts in restoration ecology, as it moved beyond traditional foci of plant communities and single functional goals within a patch (Young 2000). Contemporary practice considers organisms beyond plant communities and multiple functional, as well as compositional, goals. It applies concepts with a landscape scale, anthro-ecological perspective that is required to address environmental issues in the current and future human-influenced biosphere (Ellis 2015).

Ecological restoration provides an ideal setting for hypothesis generation and testing in ecology (Jordan et al. 1987 in Young et al. 2005, Laughlin 2014) but the full potential of this opportunity has yet to be realized. Our review highlights the need for practical tests of the concepts we present while discussing the challenges associated with this call. We further highlight how conceptual and practical developments may be aided by
technological advancement (see also Table 1). We mainly focus on terrestrial ecosystems and examples. However, environmental changes in the marine biosphere (Halpern et al. 2008) also demand restorative action. Many of the ecological concepts we discuss apply to marine areas as well and can inform marine restoration programs into the future and those that are already underway (e.g., Elliott et al. 2007, Bastyan and Cambridge 2008, Campbell et al. 2014).

Fig. 1. Framing conceptual and technological advances in restoration. (a) The development of restoration ecology: Restoration traditionally focused either on a functional goal (e.g., reinstating soil processes, productivity) or, in conservation settings, achieving desired (plant) species composition that was assumed to lead to desired (ecosystem) function, with an ecological worldview that tended to think in terms of equilibrium in an unchanging environment. Over time, non-equilibrium dynamics, simultaneous environmental changes, and widespread persistent degradation of the global environment including the presence of thresholds in ecosystem dynamics became more apparent. This necessitated a rethinking of restoration goals and has led to a plurality of motivations and goals for contemporary restoration across scales. (b) Contemporary restoration ecology: Contemporary restoration ecology sits at the nexus between ecological and social systems and is therefore influenced by changes within each of these dimensions and interactions between them. Contemporary restoration uses trait frameworks and new understanding of trophic networks to achieve dynamic, process-based functional and compositional goals in an era of socio-environmental change. Increasingly, restoration aims to deliver functions such as ecosystem services and resilience, across scales, and has taken far greater account of the human dimension, in terms of our capacity to achieve goals and what form these goals should take. Table 1 and the main text use this framing of contemporary restoration ecology to review conceptual and technological advances that will allow ecological restoration to rise to the environmental challenges of the coming decades.
We conclude by presenting important challenges and opportunities that remain for restoration ecology, especially the necessity to develop mechanisms to test the conceptual ideas presented at the required scale. Robust testing will identify context dependency and the appropriateness of various concepts in different restoration efforts. Our overarching goal is to show how concepts in restoration ecology have the potential to allow ecological restoration to rise to the challenges of the coming decades. The challenge for restoration ecologists, in conjunction with practitioners, colleagues from disciplines such as landscape architecture and economics, and stakeholders, is to reach this potential.

**RESTORATION MOTIVATIONS AND GOALS**

The practice of ecological restoration has varied motivations (Wiens and Hobbs 2015). Some projects are undertaken primarily to address environmental problems (e.g., environmental plantings for carbon sequestration; revegetation to tackle loss of productive capacity through salinity or soil erosion) while others are motivated by legislative requirements for reparation following development or mining (e.g., Carrick et al. 2015). Other projects are focused on

Fig. 2. Achieving functional and compositional goals among flora, fauna and soil. Recent conceptual advances highlight the interactions between flora, fauna and soil in restoration ecology. Developments in plant establishment (technological advances in brown) and soil resource supply have been complemented by a focus on fauna from the outset of projects, the potential for aboveground-belowground linkages to influence restoration success and the use of trait-environment frameworks to integrate across ecosystem properties to achieve restoration success. Although in this schematic the circles are of equal size, it is neither the case that all restorative actions are influenced by each sphere equally, nor do they occur on the same spatial and temporal scales. For instance, it is not possible to restore some soil properties over short time frames at large scales. The star denotes the intersection of all three spheres, and, while it is not always necessary to aim for the star (i.e., manipulate soil, flora and fauna) in restoration, we argue that it is important to consider each sphere and their interactions at the outset and plan restoration accordingly. Example ecological concepts that pertain to the star are outlined at the base of the figure and explored further in the main text.
Table 1. Ecological concepts with direct application to restoration practice. (a) Concepts with an established history of application in restoration (see also Young et al. 2005); (b) concepts being incorporated into restoration practice; and (c) concepts with potential that have yet to be fully realized. Recent advances in concepts are listed in the third column and examples of technological advances that have facilitated the practical application of concepts appear in the far column. Technological advances that have facilitated global networks of experiments and widespread exchange of information and ideas have in turn contributed to advances of many of the concepts listed. A major challenge is working out context dependency—i.e., under what circumstances can the different ecological insights be best utilized to achieve restoration goals. Another challenge is identifying emerging ecological concepts that may influence restoration success (e.g., the importance of chemical ecological cues Dixson et al. 2014).

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reinstating locally important ecosystems or species and/or involving local communities in conservation and reconnecting people with nature. This range of projects can be implemented from small-scales by individuals or community groups (e.g., Thomas 2009), to large-scales by government agencies and programs (e.g., Yin and Yin 2010). Ultimately, project directors may wish to engage people with nature, to restore nature for its own sake and/or to benefit human wellbeing. Restoration offers the potential to incorporate different motivations and this is reflected in the plurality of restoration goals. The switch from single to multiple goals parallels changing concepts of the relationship(s) among conservation, nature and people over the last century (Mace 2014).

Developing clear goals for restoration facilitates shared understanding and allows progress to be monitored (Hobbs and Norton 1996). Arguably, this articulation has increased in importance since Bradshaw’s address (December 1982). At that time, the predominant ecological worldview was of deterministic systems approaching some kind of equilibrium in essentially unchanging environmental conditions. The goal for many restorationists was hastening a return to the pre-disturbance equilibrium state. In essence, there was a clear goal for restoration, not open to debate except perhaps with regards to methodology. Success was generally measured against static compositional targets that were assumed to relate to a properly functioning ecosystem, usually a managed or unmanaged reference state (Ruiz-Jaen and Aide 2005). Rehabilitation of some systems incorporated explicit functional targets, for example soil stabilization at former mine sites.

In the ensuing decades, awareness grew of simultaneous and rapid environmental changes, including climate change and global biodiversity decline. These abiotic and biotic environmental changes, which sometimes led to rapid ecosystem change with apparent hysteresis (e.g., Suding et al. 2004, Groffman et al. 2006, Suding and Hobbs 2009, Samhouri et al. 2010), necessitated a radical rethink of classical restoration goals (e.g., Harris et al. 2006). Changes called into question aims of restoring to some historic species composition or to within the historic range of variability (Swetnam et al. 1999). There was a growing appreciation of non-equilibrium dynamics, alternative ecosystem states, and thresholds and barriers with concomitant acknowledgement of the major interventions sometimes required to reverse these state changes (Whisenant 1999, Hobbs and Harris 2001). Thus, environmental changes prompted a conversation about the degree of intervention required to meet traditional restoration goals, and also a debate about the restoration goals themselves, that continues to this day. Most recently, this took the form of a call for ecological restoration to be based on four principles which inform appropriate goals for restoration: increasing ecological integrity, sustainability, taking account of the past and future, and benefitting and engaging society (Suding et al. 2015).

It has been recently argued that systems are likely to change to such an extent that alterations are no longer reversible or even desirable given that historical compositional references could lead to ossification of systems (Harris et al. 2006). This may either be due to the extent or severity of changes, or because they render restorative action impractical or beyond available resources. Such “novel ecosystems” can then be considered as candidates for some other type of management that focuses on the benefits these systems can provide (e.g., particular ecosystem services or faunal conservation) (Hobbs et al. 2006, Hobbs et al. 2009, Hobbs et al. 2013). The idea of novel ecosystems is considered by some authors as an accurate depiction and necessary consideration of the current and future reality facing many ecosystem managers (Kowarik 2011, Belnap et al. 2012, Dooley and Audet 2013, Perring et al. 2013). However, it has also been criticized as a dangerous and baseless idea that runs the risk of lowering restoration standards and diminishing the restoration enterprise (Woodworth 2013, Murcia et al. 2014). These commentators suggest recognizing the existence of novel ecosystems threatens the progress made in restoration to date, whereas others suggest that incorporating alternative approaches to deal with radically altered ecosystems enlarges the range of goals available for restoration and could make for more efficient use of scarce management resources (Hobbs et al. 2014). This debate remains ongoing, and the ideas are being expanded and refined (Morse et al. 2014; Larson,
The greater awareness of complexity and contingency in ecology led to suggestions that references and endpoints should be viewed as dynamic (Norgaard et al. 2009, Hiers et al. 2012) or even that ecosystems could be allowed to develop without being directed at a particular endpoint (Hughes et al. 2012). Hence, there has been a growing call for future-focused goals that are dynamic, process-based and functional but that still account for historical knowledge, a so-called “Restoration v2.0” (Higgs et al. 2014), goals that align with anticipative management (e.g., Rogers et al. 2015). Ultimately, desired attributes of restored ecosystems will likely need to take far greater account of environmental change (e.g., Shackelford et al. 2013, Poff 2014).

This dynamic focus in an era of environmental change has led to many policy documents and management agencies aiming to achieve a goal of ‘resilient’ ecosystems through restoration. The concept has its roots in ecology, where the original definition is the capacity of an ecosystem to absorb change and disturbance and still maintain the same relationships between populations or state variables (Holling 1973). Thus, one can see its conceptual appeal for managing dynamic ecosystems in the face of global changes. However, it is fair to say that the concept of resilience remains difficult to quantify especially in a restoration context (Brand and Jax 2007, Standish et al. 2014). Emerging research on the contribution of functional diversity to resilience offers a promising way forward to operationalizing the concept (e.g., Laliberté et al. 2010). From a restoration perspective, it is important to note that highly degraded states may be very resilient to change, hence requiring large management inputs to return to a more desirable condition (Standish et al. 2014).

Clearly stated goals, as developmental trajectories or as compositional or functional endpoints, increase ecological understanding through assessment of the appropriateness, achievability and the relative progress of the system towards stated goals (Zedler 2007, Hobbs et al. 2009). The idea of measuring ecological progress against well-defined restoration success is one aspect that has changed little since Bradshaw’s address in 1982, and also refers to the idea that applied and fundamental sciences are arrayed on the same continuum and should influence each other (Lawton 1996, Hobbs and Harris 2001). It allows us to ask: how are ecological concepts faring against the ‘acid test’? In other words, are advances in ecological concepts aiding the setting and achievement of ecological restoration goals? In the ensuing sections, we will explore these questions by discussing how established and emerging ecological concepts, together with technological advances, have been influencing the science of restoration ecology and practice of ecological restoration since Bradshaw’s address over 30 years ago. Firstly we discuss concepts that aid achievement of compositional goals, then functional goals, at the patch scale. We then outline concepts and approaches that are useful at the landscape scale, and finally explore the human dimension to ecological restoration. We illustrate our review with site-specific examples and technological advances. However, explicit tests of many ecological (and socio-economic) ideas remain absent in a restoration framework, and knowing the relative importance of different processes in different locations is an ongoing challenge that restoration ecologists need to address.

**Restoring Species Composition Requires More than Just Plants**

Restoration is often seen as a largely plant-focused enterprise (Young 2000). Indeed, at the time of Bradshaw’s presidential address, although acknowledging the importance of fauna in organic matter decomposition and pollination, he stated: “From the point of view of the reconstruction of a properly functioning ecosystem they [animals] play little part since it is the first trophic level which is so crucial to any ecosystem”. In this section, we first present conceptual ecological advances and some technological advances that have aided the establishment of plants in ecosystems, usually to achieve compositional targets. We then highlight, in turn, recent evidence detailing the vital part that soil resource supply, soil biota (especially fungi), plant-soil feedbacks and fauna play from the outset in
achieving these compositional goals. We particularly focus on the interactions amongst these facets (Fig. 2) that can determine achievement of goals.

Plant establishment requires the identification, and, if necessary the removal, of barriers to effective plant germination and survival. It may be possible for this to occur through facilitation of dispersal/creation of gaps to promote spontaneous establishment of plants (Baeten et al. 2009). However, in other areas and particularly for restoration at scale, the removal of barriers necessitates the efficient collection, handling and use of large volumes of viable seed. The development of the restoration seed bank concept, in conjunction with a systems approach, has highlighted the connected nature of processes ranging from seed procurement at scale, breaking of dormancy and emergence, to early establishment and subsequent maturation of the young plant at restoration sites (James et al. 2011, Merritt and Dixon 2011, James et al. 2013). Without considering all components of this chain of seed use, there remain impediments to increasing the likelihood of plant establishment in a cost-effective and predictable manner (James et al. 2013).

Recent technological advances to aid successful revegetation (Table 1) include improved seed handling, processing and quality assessments of wild collected seeds (e.g., X-ray seed viability analysis/ex situ storage) (Crawford et al. 2007, Probert et al. 2007, Martyn et al. 2009), and the use of treatments and germination stimulants to overcome dormancy and promote germination (Merritt et al. 2007, Turner et al. 2013). Furthermore, proven agricultural seeding technologies are being modified to suit restoration programs using native species (Jonson 2010). Seed enhancement technologies such as polymer seed coating and embedding seeds in a soil matrix with compounds that are known to assist in promoting germination and plant establishment, while reducing pathogen attack, are also rapidly being developed (Turner et al. 2006, Madsen et al. 2012, Madsen et al. 2014). In combination these technological advances have been shown to be critical in establishing sufficient plants for successful restoration in some systems (e.g., Turner et al. 2006). The vagaries of climate often influence recruitment and better predictions of climatic oscillations (e.g., El Nino phases) may aid restoration planning to improve plant establishment success in combination with these technological advancements (Holmgren et al. 2006).

Soil resource supply also affects the attainment of restoration goals by influencing community assembly and plant-plant dynamics. Traditionally, plant strategy theory (Grime 1979) and plant competition theory (Tilman 1982) formed the basis of restoration interventions; for example, the use of species with traits that allowed establishment and growth on toxic waste from mine spoil (such as hyperaccumulators and other stress tolerators (Kramer 2010)) or attempting to reduce high nutrient supply levels to aid the development of the desired community composition by altering competitive interactions (e.g., Marrs 1993, Perring et al. 2009). This focus has been broadened to include facilitative (Brooker et al. 2008) and parasitic (Pywell et al. 2004, Demey et al. 2015) relationships. Facilitation has proven to be especially important for restoration in semiarid environments, for instance through planting nurse plants to provide appropriate conditions for survival and growth of target species (Padilla and Pugnaire 2006, Siles et al. 2008).

Soil biota are also required to improve soil structure and conditions and hence restoration success (Harris 2009). Insights from agriculture have long suggested the use of facilitative legumes to ameliorate soil conditions (Bradshaw 1983, Wong 2003). More recent studies have shown mycorrhizal inoculation improves plant survival and growth (e.g., Requena et al. 2001, Pineiro et al. 2013) although in some systems it may be the presence of a mycorrhizal network (Simard and Durrall 2004, Teste et al. 2009, Booth and Hoeksema 2010), as opposed to the presence of certain mycorrhizas alone, that facilitates successful restoration.

Knowledge of above- and belowground linkages (Wardle et al. 2004, Bardgett and van der Putten 2014) and especially plant-soil feedbacks (Kardol and Wardle 2010) have been utilized in restoration ecology. Plant-soil feedbacks are generally used to describe the negative or positive conditioning effects that a particular plant species has on the soil community which influences subsequent growth and recruitment of the same or different species (van der Putten et
The few plant-soil feedback experiments in a restoration context suggest that restoration of a soil community may be crucial for establishing late successional plant communities (e.g., De Deyn et al. 2003, Kardol et al. 2006, Middleton and Bever 2012) although success is not always observed (Kardol et al. 2009). Much remains to be learnt about where feedbacks are likely to affect restoration success, including how closely related plants may be affected by soil biota (Anacker et al. 2014).

There is increasing recognition of the importance of considering fauna from the outset in restoration, both for their role in ecosystem degradation and recovery, and for aiding the reinstatement of plant communities (e.g., Newsome et al. 2015). In the past, reinstating a plant community was assumed to provide ‘habitat’ for fauna: the “field of dreams” concept, or “build it and they will come” (Palmer et al. 1997, Sudduth et al. 2011, Frick et al. 2014), but it is now recognized that fauna can be critical for ecosystem recovery through their role in, for example, seed dispersal, pollination and/or nutrient cycling (e.g., Tucker and Murphy 1997, Majer et al. 2007, Lomov et al. 2010). The lack of attention to fauna from the outset can also lead to a lack of provision of key resources for them (e.g., tree hollows or logs Vesk et al. 2008), spatial mismatches between restoration and faunal requirements, and imbalances (from the perspective of defined restoration goals) in the faunal communities that develop (Miller and Hobbs 2007). Establishing tree islands in degraded areas can attract faunal components (e.g., birds) which in turn may instigate further system changes (e.g., through seed dispersal of desired species) (i.e., applied nucleation Zahawi et al. [2013]). Technological advances in satellite technology and GPS collars (Matthews et al. 2013) will also improve our understanding of habitat use by fauna, and this will improve our ability to provide suitable habitat.

The addition or removal of key faunal species can have complex and far-reaching effects on ecosystem composition and structure, particularly if these species are ecosystem engineers or top order predators (Dirzo et al. 2014, Ripple et al. 2014, Seddon et al. 2014, McCauley et al. 2015) (see also functional effects in next section). The importance of key species has been highlighted by studies showing the influence of top predators, such as wolves or bears, in structuring plant communities through their effects on herbivore populations and behavior via antagonistic and mutualistic relationships (as described eloquently in Leopold’s “Thinking Like a Mountain”; Leopold 1949, Ripple and Beschta 2007, Grinath et al. 2015). Overabundance of herbivores, such as deer, has important effects on plant community dynamics, often, for instance, preventing tree regeneration (Côté et al. 2004, Hobbs 2009). Removal of grazing either by fencing, culling or reintroduction of predators is often a prerequisite for effective restoration of desired plant communities (Prober et al. 2011). Given that restored areas are often subject to heavy grazing pressure (e.g., Koch et al. 2004), it seems likely that the absence of top predators may result in restored areas developing different plant communities than if these predators were present.

In summary, a variety of ecological concepts have been applied for the achievement of compositional restoration goals. However, providing guidance to practitioners as to when and where particular approaches may be most appropriate to apply remains difficult. Identifying what concepts are likely to be most valuable now and in the future is clearly an avenue for future research (see Challenges and Opportunities... section).

Moving from Compositional to Functional Goals in a Changing Environment

Attention in restoration is increasingly turning to achievement of functional goals, beyond those classically considered in rehabilitation projects (Montoya et al. 2012, Shackelford et al. 2013). Functional goals, such as the delivery of ecosystem services or reinstatement of trophic networks, often aim for resilience to anticipated change. Trait-based ecology has great potential to help achieve functional goals in the restoration of degraded systems and we elucidate this potential, across trophic levels, in this section. Restoring functioning ecosystems will necessarily involve including, and understanding, the interactions between the environment and flora, fauna and soil biota more broadly, and all the ideas require testing in a restoration framework
The response-and-effect trait framework (Suding et al. 2008) conceptually demonstrates how functional trait targets can be used in restoration goals, and this framework has been operationalized by the development of a quantitative approach for translating trait targets into plant species assemblages that can be directly used in restoration (Laughlin 2014). In the quantitative framework, systems can be restored by selecting plant species to suit current, or changing, environmental filters (using response traits), or to optimize specific ecosystem processes or functions (using effect traits) (Suding et al. 2008, Laughlin 2014). The response-and-effect trait framework can also be used to understand multi-trophic linkages in ecosystem service provision (Lavorel et al. 2013).

Response traits can be used in restoration goal setting by selecting plant species with functional characteristics that should enable persistence under specific abiotic conditions (Suding et al. 2008). For example, if a restoration practitioner is interested in restoring a native community that will be resilient to predicted future occurrences of drought, drought-adapted species can be selected—however, where drought tolerance of species is not known, a trait target can be set that includes suitable plant species with higher leaf mass per area and higher wood density as these traits confer greater tolerance to moisture deficits (Laughlin 2014). There are limits to setting specific trait targets as knowledge of which traits drive fitness and performance along environmental gradients is still developing (Webb et al. 2010). Recent work has highlighted the need to move beyond considering adult leaf and root traits to also assessing seed and seedling traits when considering the role of functional traits in restoration performance (Larson et al. 2015). Assessment of multiple traits is likely to improve the ability of restoration practitioners to develop restoration that is more resilient to future environmental changes.

In addition to choosing plant species based on their traits for specific edaphic/climatic conditions, response traits are also affected by biotic processes. Funk et al. (2008) suggested that strategically increasing the abundance of native plant species with functional traits similar to non-native plant species can increase biotic resistance to invasion, through limiting similarity. However, a meta-analysis of experimental studies testing the effect of functional similarity on invasion success, only found evidence for this in synthetic experimental assemblages, and not in more ‘natural’ removal experiments (Price and Pärtel 2013). Hence “restoration through reassembly” (Funk et al. 2008) may only be useful as a guiding principle when communities are built de novo. Importantly, trait-based predictive models can be used in an experimental context to test hypotheses about which traits and species combinations will be most effective at achieving the functional targets. The effectiveness of these targeted trait values for achieving restoration success can then be monitored over time for different experimental conditions and targets can be adjusted as we learn which traits help achieve restoration goals (Laughlin 2014).

Effect traits may be used in restoration to set functional targets to provide specific ecosystem services (Montoya et al. 2012, Perring et al. 2012). Biodiversity and ecosystem function studies have established clear links between functional composition and varied ecosystem services (Lavorel and Grigulis 2012) but there are few examples in a restoration context (e.g., Doherty et al. 2011). Large-scale experiments are needed, especially in woodland systems, given the grassland and microbial focus of this research (Cardinale et al. 2012). Furthermore, there is still room to improve our fundamental understanding of the links between biodiversity and ecosystem services (Mace et al. 2012, Balvanera et al. 2014) in addition to its application to restoration. Research is required on the importance of functional diversity and identity in regulating restoration outcomes, rather than just focusing on species numbers per se (see also TreeDivNet www.treedivnet.ugent.be; and Verheyen et al., in press). Restoring some functions for instance could involve a few species with particular traits that are critical to ecosystem processes e.g., pollination and seed dispersal can be conducted by ‘hub’ species (Forup et al. 2008, Menz et al. 2011).

Many ecosystem services rely on interactions between plants and other trophic levels (e.g., Kremen et al. 2007), but few studies have examined functional trait links between these components of biodiversity. Recently, Lavorel et al. (2013) developed a conceptual framework for...
linking plant functional diversity with other trophic levels for the quantification of ecosystem services. In an application of this framework, Moretti et al. (2013) demonstrated that, under land management change, a plant trait (leaf dry matter content) related to the grasshopper trait of dry body mass which then acted as an effect trait on primary production via a negative link to plant biomass. Thus, the functional goal of restoring ecosystem services likely needs to consider trophic levels other than plants. This consideration extends to vertebrates, but we are not aware of research that has specifically utilized the response-effect framework to include these organisms.

Fauna affect the flow of energy through ecosystems via trophic cascades and networks (Terborgh and Estes 2010, Sandom et al. 2013b, Fleming et al. 2014). In addition to the importance of trophic cascades in determining ecosystem composition (see previous section), trophic network theory highlights the importance of key species in ensuring a functioning ecosystem. Conceptual developments include acknowledging that trophic networks contain strong and weak links and trophic modules (Kondoh 2008). Varying link strengths likely determine the extent to which loss or addition of a particular species affects the success of restoration efforts. In addition, many recent studies have highlighted how a changing environment (warming in particular) has created a ‘trophic mismatch’ between the emergence of prey species and the breeding of their predators, typically leading to reduced breeding success in the predators (Both et al. 2009, Donnelly et al. 2011). While this phenomenon, to the best of our knowledge, has not been studied in restored areas, it highlights that the complexity of trophic networks provide many challenges to increasing the success of restoration efforts.

Fauna can also be important ecosystem engineers in many ecosystems (e.g., Sandom et al. 2013a) and, by definition, their presence will fundamentally influence the type of restored community that develops. Beavers provide a classic example of an ecosystem engineer that act as potential restoration agents through slowing water flows and altering stream morphology with subsequent cascading impacts (Albert and Trimble 2000, Pollock et al. 2014). Indeed, it is possible that accepted restoration goals and practices for rivers may need to be reassessed because they are based on a reference situation that lacks the influence of beavers (Burchsted et al. 2010). Restoration may aim to reintroduce such engineers; indeed beavers have a long history of translocation accompanied by interesting methodologies including via parachute (Heter 1950).

Recent debates discuss the extent to which species might be substitutable, and hence functions performed by recently extinct species could be reinstated by the translocations of closely related extant species (e.g., Griffiths et al. 2013, Hunter et al. 2013). An extreme form of this approach is what has been dubbed “rewilding” (e.g., Donlan et al. 2005), in which functional equivalents of long-extinct but presumably key-stone species are introduced to ecosystems. Debate over this approach has mirrored larger discussions in restoration about the appropriateness of different reference systems on which to model restored ecosystems, and, if past ecosystems are to be used as a template, how far into the past is it appropriate to consider? It is likely that some time spans are too large a gap to restore across, because in the intervening time ecosystems have almost certainly developed into a new condition. This time gap likely varies widely between ecosystems and continents and whether restoration goals are compositional or functional.

The restoration of function may also rely on interactions among plants and soil, for example nutrient cycling involves complex interactions between plants, soil biota and their associated traits (Kardol et al. 2015). Simulation modeling using trait frameworks provides a means to advance fundamental understanding in this area, and may have application to ecological restoration (Ke et al. 2015). Additionally, recent technological advances in high throughput DNA sequencing and functional gene analysis may allow rapid assessment of what functional genes are present in systems and how they relate to soil microbial composition and ecosystem function (Zimmerman et al. 2014). The functional (and compositional) gap between reference and restored ecosystems (Rey-Benayas et al. 2009, Banning et al. 2011) may likely be due to the decoupling of above- and belowground linkages.
that occurs following land clearance and the time taken for ecosystems to approach the chosen reference. This idea remains an untested hypothesis but the decreasing cost of these genetic technologies should allow its investigation, including testing the reintroduction of specific functional genes and phylogenetic diversity to improve restoration outcomes.

Magnitude of Environmental Changes Requires Restoration at Scale

Restoration science and practice has traditionally considered mainly the restoration of particular ecosystems or patches in particular places. However, the scale of environmental changes requires the adoption of a landscape perspective in restoration, for instance where there has been regional hydrological change or large scale deforestation or tree mortality (Allen et al. 2015). In this section we explore the ecological concepts underpinning restoration at scale drawing on the field of landscape ecology in particular. Further, we explore the challenges and opportunities that a multi-functional landscape perspective provides for ecological restoration in a changing environment.

The need to scale-up restoration activities demands that the patch-based approach consider processes at the broader landscape- and regional-scales, for example movement of water or dispersal of biota (Menz et al. 2013). This need has perhaps been most evident in efforts to restore aquatic ecosystems with consideration of processes from the scale of individual river reaches through to entire regional river or wetland systems (e.g., Culotta 1995, Gunderson et al. 1995). Advances in the application of Geographic Information Systems (GIS) technology have brought new understanding to questions around aquatic dispersal. For instance, in the Great Lakes Basin, common assumptions about restoring connectivity for fish populations through tackling problems with dams misses opportunities to aid dispersal by addressing barriers created by the far more numerous road crossings; opportunities that were only made apparent through GIS analysis (Januchowski-Hartley et al. 2013). Ecological restoration is harnessing the power of such technologies for more effective landscape-scale restoration.

There is ongoing effort to find cost-effective, practical and successful methods for achieving broad-scale restoration (Jonson 2010, St Jack et al. 2013). Technological improvements can be complemented with the use of simulation models to identify restoration priorities based on habitat characteristics and land-parcel prices (e.g., Torrubia et al. 2014). However, upsampling may not always be straightforward, with the adopted management approach depending on the type of landscape under consideration. Where individual management units are significantly smaller than the landscape in which they sit (for instance, in agricultural landscapes with fragmented native ecosystems or urban and peri-urban areas) effective landscape management requires coordination of, and co-operation among, multiple landholders and managers, each with potentially conflicting goals and approaches (Gobster 2001). This is presumably less of an issue in larger management units such as large pastoral properties or national parks.

Landscapes are likely to comprise an array of patch or ecosystem types in different conditions, each providing an array of benefits or disbenefits, and each likely to require differing management approaches, both individually and as part of a broader landscape or regional strategy (Zedler et al. 2012, Hobbs et al. 2014). This patchwork provides an opportunity for restoration: an overall goal of landscape multifunctionality may allow the provision of multiple ecosystem services that would not be possible by considering the individual patch scale alone (Jarchow and Liebman 2011, Potschin and Haines-Young 2011, Schindler et al. 2014). Recent initiatives point to effective ways to map and assess ecosystem services at landscape scales (Nelson et al. 2009, Kareiva et al. 2011) while policy instruments such as payments for ecosystem services provide mechanisms for achieving multifunctionality through funding restoration (van Noordwijk et al. 2012).

Conceptually, discussion of landscape restoration has progressed from ideas about habitat size and number (e.g., several small reserves versus one large reserve) to habitat corridors and then to assessing the role of the whole landscape matrix in promoting or inhibiting biotic movement (Lindemayer et al. 2008). The management of the matrix could determine restoration outcomes.
for biodiversity, with three core matrix effects (movement and dispersal, resource availability and abiotic environment) being modified by five dimensions: spatial and temporal variation in matrix quality, its spatial scale, the longevity and demographic rates of species relative to the temporal scale of matrix variation, and adaptation (Driscoll et al. 2013). Landscape connectivity is increasingly seen as a key conservation and restoration goal, particularly as a strategy to allow biotic movement in response to changing environments (Roever et al. 2013, Tambosi et al. 2014, Okin et al. 2015). Deciding what and where to restore is a key challenge for future landscape-scale restoration efforts (McRae et al. 2012, Torrubia et al. 2014). Decisions may be aided by technological advances around, for instance, the application of climate velocity models in conjunction with more traditional ecological models to ascertain areas of potential future habitat suitability as targets for restoration efforts (Hamann et al. 2015).

Landscape and regional approaches require effective ways of directing and prioritizing restoration efforts. Numerous decision support approaches to this problem are evolving (e.g., Thomson et al. 2009, Wilson et al. 2011, Egoh et al. 2014), although deciding what characteristics should be included in the prioritization process is not a straightforward process (Knight et al. 2011, Tambosi et al. 2014). Decisions will in any case continue to include both local and landscape dimensions—for instance, priorities for restoration involving weed management will depend on the likelihood of weeds spreading from one patch to another (e.g., Trueman et al. 2014).

**Restoration in Complex, Socio-Ecological Systems**

The importance of the human dimension in ecological restoration was recognized early (e.g., see remarks in Bradshaw 1983, Geist and Galatowitsch 1999), and restoration is widely acknowledged to be value laden, context driven, prone to disagreement and compromise, and experiential (Egan et al. 2011). There is increasing recognition of the importance of social and economic factors in determining restoration success (e.g., Jacobs et al. 2013) and the need to understand the human dimension in meeting restoration goals (Gold et al. 2006, Egan et al. 2011, Naiman 2013, Shackelford et al. 2013). There is growing emphasis on the requirement to consider ecological, socio-economic and governance aspects of ecosystem management (Carpenter et al. 2009, Hobbs et al. 2011). This idea is not new: As the Ecological Society of America was just emerging from its teenage years in 1935, Aldo Leopold noted that: “One of the anomalies of modern ecology is the creation of two groups, each of which seems barely aware of the existence of the other. The one studies the human community, almost as if it were a separate entity, and calls its findings sociology, economics and history. The other studies the plant and animal community and comfortably relegates the hodge-podge of politics to the liberal arts. The inevitable fusion of these two lines of thought will, perhaps, constitute the outstanding advance of this [20th] century” (quoted in Knight and Riedel 2002).

Although restoration may focus on ecosystems and non-human species, it is primarily a human endeavor, with a range of motivations and goals. Some types of restoration will be driven mostly by economic considerations, while others will be more focused on participatory or eco-cultural perspectives. Whichever perspective predominates in any given situation, there is increasing recognition that cost-effectiveness is an essential ingredient for good design of restoration projects (McConnachie et al. 2012). Cost effectiveness will be enhanced by solution scanning (Sutherland et al. 2014) and is a pre-requisite for broad scale restoration. Additionally, restoration of ecosystems and their services can be seen as having important socio-economic benefits (e.g., job creation, farm income) that have only recently begun to be factored into assessments of restoration success (Aronson et al. 2010, Nielsen-Pincus and Moseley 2013, Wortley et al. 2013) and thus cost effectiveness. Ecological restoration is now a big business, with many non-governmental organizations and government agencies investing large amounts of money in the enterprise and many businesses making money from undertaking restoration at all scales. Cunningham (2002) has suggested that we are entering the era of the “restoration economy” where more and more economic activity is derived from restoring existing infrastructure and repairing ecosystems rather than investing in new infra-
structure.

Egan et al. (2011) identified three themes characterizing human involvement in restoration: participation (e.g., volunteering; collaboration); power (e.g., restoration economics; politics, planning and governance); and, perspective (ecocultural restoration; restoration-based education). They suggest that to improve restoration success, participation has to be embraced as an integral part of the process. There are two main arguments for embracing participation: on the one hand democratic rights and public skepticism about science, and on the other involvement of stakeholders leading to greater quality, durability and ownership of decisions (Reed 2008). There is surprisingly little empirical research to test these arguments (e.g., van Marwijk et al. 2012, Petursdottir et al. 2013), but decision making quality appears to be strongly dependent on the processes involved, especially highly skilled facilitation (Reed 2008). Community restoration/conservation projects that perceive local people as the solution to habitat degradation, and involve them at all stages of project development, appear to perform better than large scale ‘integrated conservation and development projects’ (Horwich and Lyon 2007). For instance, Reyes (2011) argued that a controlling and hierarchical approach to restoration led to a poor restoration outcome following a chemical spill in Spain, while an inclusive and heterarchical approach led to successful restoration in Costa Rica. Restoration outcomes will likely be improved when power relations are overtly recognized and discussed and multiple perspectives of restoration, nature and people’s role in both are dealt with respectfully (Egan et al. 2011).

Effectively combining ecological and social considerations likely requires a coupled socioecological systems (SES) framework approach, which recognizes complex interactions between people and ecological entities and processes (Peralta et al. 2014). Socio-ecological systems are the epitome of complex adaptive systems (sensu Levin 1998) and generally consist of a resource system, resource units, users and governance systems (Ostrom 2009). Qualitative investigations of SES have been conducted (e.g., case studies in Turner II et al. 2003) though less commonly in a restoration context. Restoration is arguably more likely to be successful if capacity in, and overlap among, the social, technological and ecological spheres is enhanced (Jacobs et al. 2013). Using American chestnut (Castanea dentata) as an example, Jacobs et al. (2013) demonstrated how technological advances in blight resistance potentially allow C. dentata’s successful reintroduction. However, this would only be possible with an adequate understanding of the contemporary ecology of eastern North American forests which are substantially changed from when the chestnut was extirpated (McEwan et al. 2011). Jacobs et al. (2013) note the critical need for a deeper understanding of societal influences (including governmental policy and regulation, collaborative networks and cultural or economic valuation) when setting and achieving realistic restoration goals, particularly around genetic modification. In their qualitative analysis, restoration of American chestnut to eastern North American forests will only be successful (i.e., C. dentata will once again be present) if social as well as technological and ecological aspects are taken into account (Jacobs et al. 2013).

Quantitative evaluations of coupled SES, especially in a restoration context, are even rarer (e.g., Jellinek et al. 2014). However, the ability to quantitatively describe these systems will likely lead to better evaluation of broader policy options and potential leverage points to improve restoration outcomes, especially as situations begin to lie outside the range of previous experience (Cooke et al. 2009, Hobbs et al. 2011, Rounsevell et al. 2012). For instance, Watkinson et al. (2000) showed that an interaction between an ecological variable (field weed population) and social variable (attitude to GM crops) was crucial to the ecological outcome (bird population dynamics) in agricultural landscapes. Simulation models and game theory (Buckley and Holl 2011) may be useful tools to understand complex SES and the effects of management interventions. Agent based modeling offers an especially useful way forward as it has the capacity to represent people, their behavior, and decision making processes in coupled models. Moreover, it is appealing for validation purposes due to a one-to-one mapping between virtual and real-world entities as opposed to the ‘average’ characterization of people in top-down equation based models (Rounsevell et al. 2012). It may be possible to use a trait-based approach to
support the expansion of such models beyond case studies, while there is also a need to represent institutional agents in SES models. A key challenge in this approach is the identification of actors who drive SES changes in the real world and the mapping of such actors onto agents in the models (Rounsevell et al. 2012).

Restoration is an inherently human enterprise, and as its scale of application broadens, more and more stakeholders will need to be included in planning and implementation. With increased participation, comes the challenge of reaching consensus over goals and prioritization of effort. Coupled socio-ecological systems analysis, both qualitative and quantitative, will likely aid in achieving restoration outcomes that are significant and meaningful for nature and for people, but it is not without its challenges, both technological and conceptual.

**Challenges and Opportunities for Restoration Ecology**

Clearly, there is a solid conceptual foundation from which restoration ecology can continue to build. Conceptual development, technological advances, and insights from other disciplines appear to be better equipping ecological restoration to tackle simultaneous environmental changes. However, a number of intersecting challenges and opportunities remain for the coming decades.

**Goals, priorities and human involvement for restoration**

An ongoing debate surrounds realistic and socially acceptable goals for restoration across scales and in a rapidly changing environment (Woodworth 2013, Hobbs et al. 2014, Murcia et al. 2014). Understanding people’s perceptions of nature and how they value it, both historical and modern versions, will help to inform this debate (Clayton and Myers 2009). The involvement of people provides a challenge of its own: how does one engage a globally ‘urban’ population which has become more decoupled from nature to become involved to do this? Allied questions focus on how to prioritize restoration activities, and determining what interventions should be carried out where in multifunctional landscapes (Hobbs et al. 2011). Successful resolution of these issues will likely require inclusive and participatory approaches, and the involvement of philosophers, economists, social scientists, landscape planners and the broader community. Frameworks such as anthromes may provide a means to aid decision making and prioritization at the global scale (Martin et al. 2014). Opportunities also exist for using simulation models to analyze cost-effective prioritization of restoration at the landscape scale (e.g., Torrubia et al. 2014).

**Addressing context dependency**

Understanding context dependency will strengthen the science of ecology (Belovsky et al. 2004) but it remains, according to some, the biggest challenge facing ecologists (Tylianakis et al. 2008). Developing a global evidence base to understand when different interventions work where, and why, would be a useful future avenue to pursue (Sutherland et al. 2004, Pullin and Knight 2009). Furthermore, it would be useful to consider how restoration ecologists can be involved in the design and implementation of large restoration projects, while at the same time encouraging more practitioners to explore the adoption of experimental approaches when conducting practical restoration activities. While this is largely classical adaptive management, there remain few examples of where this has been effectively implemented. Context dependency may even determine when the scientific method can directly aid ecological restoration, or when beneficial effects appear indirectly through, for example, increased prestige and visibility of projects (Cabin 2007).

A complementary area of research is to understand which ecological concepts are most useful to achieving restoration goals in different environmental and socio-economic contexts. Capability now exists for carrying out synthetic analyses of context dependencies in restoration outcomes using open access data and techniques such as meta-analysis. However, interchange of information between restoration practitioners and the academic field of restoration ecology, as well as comparability of measures of restoration outcomes, remains an important challenge (Young et al. 2005). Advances in digital technology, including speed and capacity of databases, allows for the sharing and analysis of information in ways not previously encountered, while
novel analytical methods to transfer results to data-poor systems are being developed (e.g., Lester et al. 2014). These endeavors may be further aided by developing globally distributed experiments (Borer et al. 2014), along gradients of management action and environmental factors, and through support of developing cyber-infrastructure (Michener et al. 2012). Ultimately, embracing complexity and context dependency in restoration activities may lead to more successful restoration as ecological principles are adopted, tested and adapted (Eviner and Hawkes 2008).

Maintaining evolutionary potential
Maintaining evolutionary potential in fragmented landscapes is a common ultimate goal of restoration (Mijangos et al. 2015) and this may be aided by offsite preservation of seeds in vaults (Holsinger 1995), and the application of controversial new techniques such as de-extinction (Sherkow and Greely 2013). However, the use of seed vaults, while maintaining the legacy of biodiversity, should not de-emphasize the importance of in situ adaptation that can occur in a changing environment (Schoen and Brown 2001, Leger 2008). The technique of de-extinction, and allied ideas around genetic modification, translocation and taxon substitution, raise serious ethical concerns (Minteer 2014) that will likely only be addressed through public debate.

Inter-disciplinary socio-ecological research with improved links to policy
It is increasingly important for restoration ecologists to become more aware of, and adept in applying, social science methods and conceptual frameworks; in essence, both ecologists and social scientists need to understand each other better (Cooke et al. 2009, St John et al. 2014, Buizer et al. 2015). This understanding may be best achieved through training young researchers in both social and ecological approaches rather than bringing teams of disciplinary focused researchers together that often speak very different languages (St John et al. 2014). It will also likely require a greater variety of techniques than are currently utilized to quantify human values and cultural ecosystem services, and greater emphasis on assessing the credibility of integrated models (Cooke et al. 2009). For example, a recent study used scenarios to understand the role of governance in achieving large-scale restoration in the agricultural landscape of the Tasmanian Midlands of Australia. The study helped to clarify the roles and responsibilities of landowners, government and other stakeholders, and to identify the types of restoration initiatives and political support likely to result in successful outcomes for biodiversity conservation (Mitchell et al. 2014).

Restoration ecologists also have the opportunity to become more involved in policy debates and development (Jorgensen et al. 2014). It is argued that integrating their research with policy, as well as tackling the challenges and opportunities of public outreach at the interface of ecology and society (Groffman et al. 2010), will improve restoration outcomes. For instance, Jorgensen et al. (2014) showed only three out of 58 articles in restoration-related journals that referred to climate change or global warming in the abstract identified specific policies relevant to their research results. In two of the three cases, the lead author was not a restoration ecologist. They argue that more explicit reference to policies and terminology recognizable to policy makers might enhance impact of restoration ecology on decision making processes (Jorgensen et al. 2014).

Concluding Remarks: Meeting the Environmental Challenges of the Coming Decades
In the 100 years since the founding of the Ecological Society of America (ESA), ecological concepts have been developed, refined, recycled and sometimes discarded. Restoration ecology, and its practice ecological restoration, provides an arena to further test established and emerging ecological theories. We reviewed how compositional and functional restoration goals, across scales, may be reached through the application of ecological understanding. An understanding of which concepts are most usefully applied where, and when, is a critical research priority. Importantly, we showed how the restoration enterprise will be unlikely to succeed without considering the human dimension. The need for interdisciplinary approaches and the integration of the social sphere and values-based perspectives with
‘objective’ science remains a challenge for meeting restoration targets. Now, as the ESA looks to its next century, this integration is of paramount importance, as the scale of the environmental challenges facing humanity becomes ever more apparent.

ACKNOWLEDGMENTS

All authors contributed to discussions and wrote sections of the paper. We acknowledge support from an Australian Research Council (ARC) Laureate Fellowship (R. J. Hobbs), the ARC Centre of Excellence for Environmental Decisions, the Natural Environmental Research Program Environmental Decisions Hub, the Western Australia Fellowship Programme (A. S. Whiteley) and support MFP received from the National Socio-Environmental Synthesis Center (SE-SYN). NSF Award DBI-1052875. Thanks to two anonymous reviewers, Erle Ellis, Stephen Murphy, Lyn Perring, Tim Seastedt, Kris Verheyen and Natasha Wiggins for valuable comments on earlier drafts of this article. Funding bodies had no bearing on the contents of the manuscript, nor the decision to submit.

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