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RESEARCH ARTICLE

A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems

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Demand for restoration of resilient, self-sustaining, and biodiverse natural ecosystems as a conservation measure is increasing globally; however, restoration efforts frequently fail to meet standards appropriate for this objective. Achieving these standards requires management underpinned by input from diverse scientific disciplines including ecology, biotechnology, engineering, soil science, ecophysiology, and genetics. Despite increasing restoration research activity, a gap between the immediate needs of restoration practitioners and the outputs of restoration science often limits the effectiveness of restoration programs. Regrettably, studies often fail to identify the practical issues most critical for restoration success. We propose that part of this oversight may result from the absence of a considered statement of the necessary practical restoration science questions. Here we develop a comprehensive framework of the research required to bridge this gap and guide effective restoration. We structure questions in five themes: (1) setting targets and planning for success, (2) sourcing biological material, (3) optimizing establishment, (4) facilitating growth and survival, and (5) restoring resilience, sustainability, and landscape integration. This framework will assist restoration practitioners and scientists to identify knowledge gaps and develop strategic research focused on applied outcomes. The breadth of questions highlights the importance of cross-discipline collaboration among restoration scientists, and while the program is broad, successful restoration projects have typically invested in many or most of these themes. Achieving restoration ecology's goal of averting biodiversity losses is a vast challenge: investment in appropriate science is urgently needed for ecological restoration to fulfill its potential and meet demand as a conservation tool.

Key words: ecophysiology, ecosystem function, genetics, science strategy, seed science, soil science

Implications for Practice

- The absence of a current, comprehensive framework of the diverse scientific inputs required by projects aiming to restore representative, sustainable, resilient, and biodiverse ecosystems can result in research that does not meet pressing practical needs.
- Restoration scientists can contextualize their research within the framework developed here, target new reviews, and support funding strategies and multidisciplinary collaborations to optimize practical restoration outcomes.
- Restoration practitioners should consult the framework when seeking data and prioritizing research inputs, rather than solely relying on available opinion.
- With the framework, governments, planners, industry, and society generally can accurately consider the scale of the knowledge impediment when contemplating ecological restoration in planning development offsets or as a general solution to environmental and biodiversity challenges.

Introduction

The restoration of degraded or destroyed ecosystems is increasingly recognized as an important solution to the contemporary global biodiversity crisis (Jordan et al. 1988; Hobbs & Suding 2009; Menz et al. 2013). Programs such as the New York

Declaration on Forests, arising from the 2014 UN Climate Summit and calling for the restoration of 150 million hectares of forests by 2020 and a further 200 million hectares by 2030, attest to the immense and urgent global demand for

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ecosystem restoration (United Nations Climate Summit 2014). At the regional scale, offset tools created by planning authorities in many countries that aim to compensate for developments in areas with significant biodiversity values, demonstrate demand for technically precise ecosystem restoration (Quétier et al. 2014). Ecosystem restoration must succeed to very high standards if it is to be truly effective as a biodiversity offset or meet its promise to assist the conservation of biodiverse communities and the species they support. These standards can only be achieved with considerable scientific input (Burbidge et al. 2011; Menz et al. 2013). However, clear-headed assessments of the effectiveness of efforts in the restoration of biodiverse, functioning and self-sustaining ecosystems to date have found that success is often limited (Rey Benayas et al. 2009; Palmer et al. 2010; Quétier et al. 2014).

As the scientific discipline of restoration ecology exists to support ecosystem restoration, it bears some responsibility for the frequency of failure of restoration practice. Critically, restoration science can only lead to improved restoration outcomes if it addresses questions relevant to practice. The argument that some, indeed most, restoration science programs have no bearing on the most important practical issues for improving restoration success is not a new one (Cabin 2007). Preceding much of the development of the field of restoration ecology, Clewell and Rieger (1997) addressed the important question “What do practitioners need from restoration ecologists?” However, the claim that “few ecologists have performed the kind of practically valuable research programs they call for” is still made (Cabin et al. 2010). While much useful research takes place, it occurs in the absence of an up-to-date framework describing the scope of the practically valuable research that is required.

The science of restoration ecology is well structured (Perring et al. 2015), with guidelines for setting restoration goals and measuring success (e.g. SER 2004; Hallett et al. 2013; Shackelford et al. 2013); models of restoration processes and limitations (e.g. Cortina et al. 2006); frameworks for the field as a whole (e.g. Suding 2011); and a framework for its published output (Brudvig 2011). Some of restoration ecology’s overarching practical constraints, such as scalability (Menz et al. 2013), are well described, but perhaps not all. Comprehensive, practical restoration guidelines, often based on empirical studies, do exist for many ecosystems, but these catalog the practical solutions, rather than research problems. Finally, key textbooks (e.g. Galatowitsch 2012) emphasize the importance of science in restoration but again do not comprehensively review the necessary practical science. A framework of the science questions needed to improve practical restoration outcomes is not to be found among this structure.

Restoration science cannot lead to improved restoration outcomes if it fails to identify relevant research questions for critical steps in the restoration process. Here we develop a framework of biophysical research themes and questions that need to be answered for the recovery of an ecosystem that has been degraded, damaged, or destroyed (*sensu* SER 2004). We present the framework within five themes (Fig. 1), along with a list

of practical research questions (Tables 1–5) and examples of studies that address these questions (Table S1, Supporting Information). The themes are not goals to be selected among or traded-off: they are all a necessary part of the restoration process. Each restoration project is a unique challenge, but we argue that most of the questions that we identify here will require at least some attention during the planning process of any project. Our themes are structured to reflect the process and timelines of restoration; however, there is still some overlap: for instance, restoration substrates and hydrology need to be managed for establishment (theme 3) and growth and survival (theme 4).

Although sociopolitical factors often have critical bearing on restoration outcomes, our framework focuses on biophysical determinants. Engineering to correctly design sites may also involve research that we have not considered. The majority of published restoration research has focused on plant communities (Brudvig 2011), a bias perhaps even stronger in practice. Nonplant organisms provide essential ecosystem services and function, and we address their restoration in this context. We recognize that the restoration of fauna, fungal, and bacterial communities in themselves present different challenges requiring different research. Following SER (2004), we assume that the objective of restoration is to support the establishment of a normally functioning, locally representative, resilient, sustainable, and biodiverse ecosystem integrated within a broader landscape ecological context. Although this definition reflects a focus on biodiversity conservation solutions, our framework is robust to the relaxation of some definition elements. Our objective is to collate and structure a list of questions that researchers and practitioners should keep in mind when planning research: we provide context to justify the inclusion of questions, not comprehensive review. Our approach is to describe the issues within each theme, identify where research has proven, or should be expected, to improve restoration outcomes, and then identify the questions to address these issues.

Setting Targets and Planning for Success

When planning restoration projects, it is critical that clear targets are set (Shackelford et al. 2013). These should follow from the project’s purpose but ultimately all involve understanding how ecosystems depend on site environmental attributes, assessing the attributes of sites and attempting to optimize the match between target ecosystem and site conditions (Hobbs & Suding 2009). Adapting for climate change may add to this complexity, with the appropriate community for a site moving away from historic analogs (e.g. under a drying climate, if assisted migration is acceptable, a target community from a historically drier region may be an acceptable target, if not, interventions to improve soil water availability may be required). In all cases, a reference site or state needs to be identified and characterized (Table 1).

Identification of reference sites enables the setting of quantitative restoration targets through measurement of their species richness, community composition, density, habitat structure, and function. As most of these factors

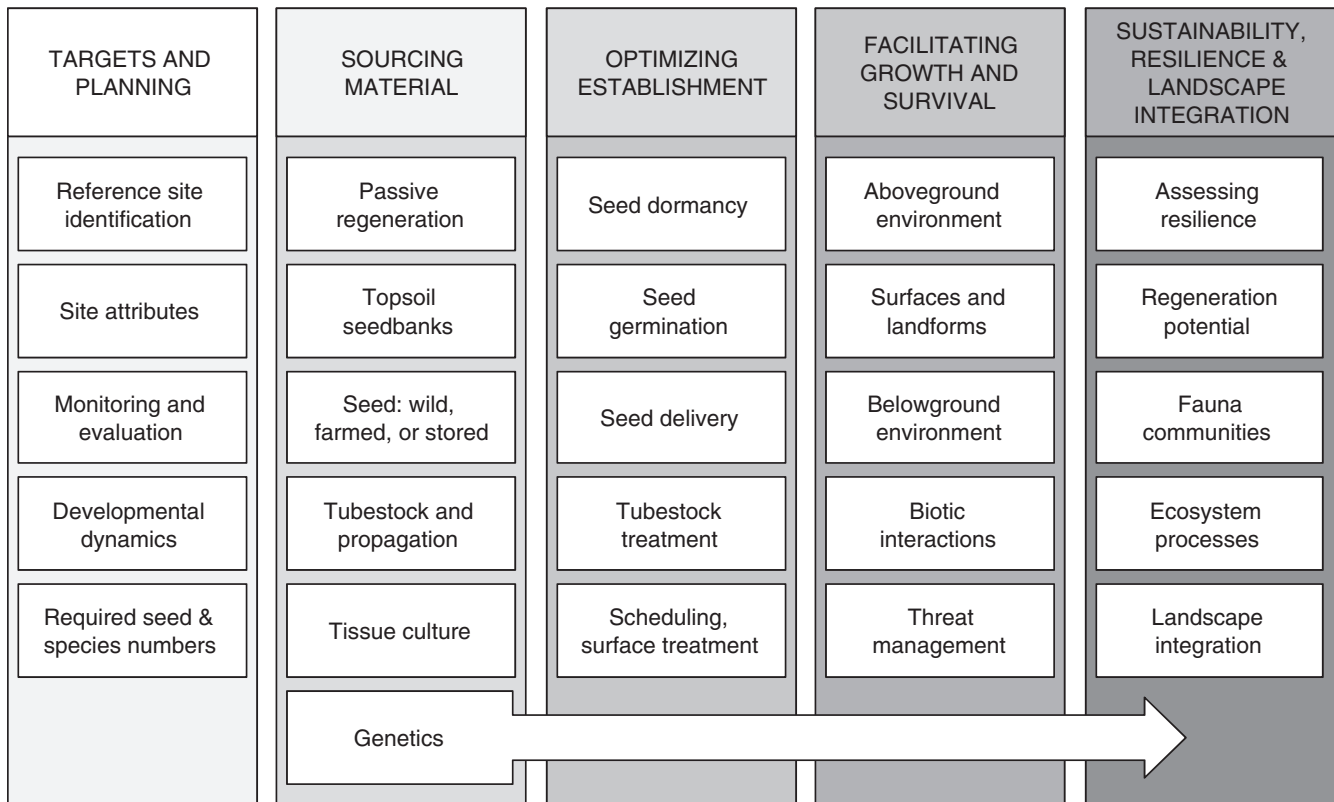


Figure 1. Framework for the practical science questions required for effective biodiverse and sustainable ecosystem restoration.

Table 1. Research required to optimize target setting and planning for restoration success.

1. What is the nature of regional environment-ecosystem associations that determine (1) appropriate targets for the project site or (2) appropriate sites for the project target?
2. What metrics, survey techniques, design, and tests are required to both adequately characterize the reference community and monitor restoration to allow unambiguous evaluation of progress and success at different time steps?
3. How should reference states and metrics consider successional dynamics and post-establishment development of restoration to enable evaluation of progress toward targets?
4. What species and how many seeds, tubestock, and so on of each are required to meet final targets given developmental transition likelihoods?

change through time, both with succession following natural disturbance and in restoration, targets should incorporate and allow for this change (Hiers et al. 2012). Post-disturbance succession can involve the initial presence of short-lived species that add to ecosystem diversity and may contribute to ecological function and resilience in both restoration and succession. However, reference communities are typically defined from mature phase vegetation and miss this diversity. This may not be a problem at one level, but successional species may provide fauna habitat elements and ecological functions that ensure ecosystem resilience, and it may be argued that the diversity represented by transient species should be counted when aiming for biodiverse restoration. Measured species richness is influenced by ecological and sampling factors; in addition, the density, richness, and composition of communities change as they develop in succession and in restoration (McGill 2011). Community composition is

infrequently quantified as a restoration target—it is absent from a review of measures of success in 301 restoration studies (Wortley et al. 2013)—yet measures based on ecological similarity are well developed in community ecology and should be more frequently applied in restoration (e.g. Koch & Hobbs 2007). Finally, characterization of reference sites allows monitoring and evaluation of restoration success, and requires consideration of survey extent, replication, techniques, and design, as well as statistical power, to ensure that monitoring is adequate to evaluate progress (Collins & Simberloff 2009; Matthews et al. 2009).

Converting restoration targets into a plan for restoration involves the creation of a prioritized species list with a target range of planting and/or seeding density for each species. Prioritization should reflect the importance of species in community definition (i.e. indicator species, dominance), structure, function, and similarity targets. Planting density should reflect

Table 2. Research required to optimize sourcing biological material for restoration.

5. To what extent might passive regeneration and dispersal achieve restoration targets?
6. What processes can be employed to enhance passive regeneration and dispersal?
7. From where should biological material (typically seed) be sourced to minimize negative impacts for ecological restoration?
8. For seed sourcing, is it better to mix genotypes (thereby increasing evolutionary potential) or match genotypes to local conditions (maximizing local adaptation)?
9. Might inbreeding or low genetic diversity within source population(s) impact on the success of ecological restoration?
10. When does outbreeding depression impact on the success of ecological restoration in populations established from composite or admixture provenancing?
11. What is the composition, richness, density, germinability, and longevity of available topsoil seed banks?
12. Can species returns from topsoils be maximized through changing harvesting, storage respreading, and treatment techniques?
13. How can spatio-temporal opportunities for efficient sourcing of large numbers of viable seeds from natural populations be predicted?
14. What techniques are appropriate to increase production of viable seeds in natural populations?
15. How can viable seed output be maximized in managed seed production facilities without compromising genetic diversity and integrity?
16. What are the optimal storage requirements to maintain long-term viability of seeds?
17. Can micropropagation techniques be adapted for efficient production of recalcitrant species required in restoration?

Table 3. Research required to optimize plant establishment in restoration.

18. What is the dormancy mode of seed of species required for restoration, and what approaches are required to overcome dormancy?
19. What conditions are necessary for optimal germination of species required for restoration?
20. What seed delivery techniques or seed enhancements could improve seed survival and germination and seedling establishment on site?
21. What tubestock pre-planting treatments are required to optimize establishment and survival on planting?
22. What scheduling or site manipulation is required to optimize seed germination and establishment of seedlings and tubestock?

mature phase targets, but consider probabilities of individuals transitioning between developmental stages (Hoelzle et al. 2012). Planting densities may be further adjusted to account for expected returns from dispersal of propagules from surrounding landscapes, in situ or returned topsoil seed banks (TSBs), and the need to risk-manage environmental extremes or threats. When seed or seedling availability is limited or costly, planting rates should be optimized to reduce seed waste and among-seedling competition (Merritt & Dixon 2011).

Sourcing Plant Material

In the simplest of cases, species may be able to naturally regenerate from sources already existing onsite, or through natural dispersal processes (Robinson & Handel 2000). Propagules dispersed by wind, water, or animals may have potential to naturally colonize and may not need to be targeted in restoration efforts (Öster et al. 2009). The potential of in situ and dispersal inputs for restoration may be enhanced by inducing germination from existing seed banks (Albornoz et al. 2013); manipulating the spatial distribution of plants to increase attractiveness to dispersers (Robinson & Handel 2000); prioritizing sites near remnant vegetation; excluding herbivores or competitors; providing protective cover (Maestre et al. 2003); and re-establishing natural hydrological regimes (Nilsson et al. 2010).

Where passive regeneration is inadequate, restoration material must be sourced externally. Genetic issues need to be considered when sourcing material for restoration, recognizing that species are spatially genetically structured; genetic diversity varies within populations; and the genetic makeup of mates can impact on fitness (Williams et al. 2014). These issues include

the source and composition of genetic diversity for restored populations in relation to current and/or future environmental variation, to address concerns largely associated with maladaptation, evolutionary potential, inbreeding depression, and outbreeding depression.

The sourcing of genetically diverse, local provenance material is recognized best practice (Vander Mijnsbrugge et al. 2010). Although “home-site advantage” suggests the use of locally adapted genotypes have a fitness advantage that will typically lead to better restoration outcomes when compared with nonlocal genotypes, this is not the case in all circumstances (Jones 2013). For example, local provenance genotypes may be a poor match to site conditions in highly modified landscapes, and cultivars, composite, or admixture provenancing may provide better outcomes (Breed et al. 2013). In addressing climate change, predictive sourcing may provide genotypes adapted to anticipated changes in climate at the restoration site (Breed et al. 2013; Prober et al. 2015). Ultimately, local-is-best may be thought of as a preferred, precautionary but context-dependent and testable assumption (Jones 2013). Defining “local” remains a challenging task, with researchers typically applying a spatial measure (e.g. 20 km; Krauss & Koch 2004). Broad geographic seed zones (Bower et al. 2014), genetic marker variation, and habitat matching have also been applied (Krauss et al. 2013). For future generations in a restored population, striking a balance between the extremes of inbreeding and outbreeding depression is a significant challenge for ecological restoration (Fig. 2A; Hufford et al. 2012). Inbreeding depression issues may be associated with collecting from small and/or isolated local source populations or a small total number of individuals (Broadhurst et al. 2008). Alternatively outbreeding depression

Table 4. Research required to optimize plant growth and survival in restoration.

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23. Are aboveground environmental conditions limiting growth and survival, and can artificial or natural structures or treatments be constructed or placed to ameliorate their effects?
 24. Can restoration landform design be optimized for growth and survival?
 25. Are restoration surface attributes impairing conditions for optimal growth and survival, and can treatments mitigate these effects?
 26. Are soil or substrate physical, hydrological, chemical, and biological attributes limiting and can they be manipulated to optimize plant growth and survival in restoration?
 27. Are the soil biota necessary for plant growth and survival present and what treatments can be employed to optimize their return in restoration?
 28. Can planting density, patterns, or sequences be varied to optimize survival and growth in restoration?
 29. What threats are likely to impact restoration outcomes and how can they be mitigated and managed?
-

Table 5. Research required to optimize sustainability, resilience, and landscape integration of restoration.

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30. How is resilience to disturbance and environmental stress developing in restoration?
 31. Is the potential for the persistence and regeneration of populations present or developing adequately in restoration?
 32. Is population size or genetic diversity limiting the production or fitness of seed in restoration?
 33. Can pollinator populations be supported to improve the production or fitness of seed in restoration?
 34. Can the habitat and resource requirements of fauna species be augmented to enhance biodiversity values and ecosystem function?
 35. Can key functional processes be introduced, managed, or enhanced to improve sustainability or population regeneration in restoration?
 36. Can restoration site location, orientation, and size be optimized to enhance connectivity, integration with the surrounding landscape, and landscape-scale restoration benefits?
-

is typically associated with species that have karyotypic variation, have variable habitat preferences or a long history of isolation between populations (Frankham et al. 2011). Among species that miss these criteria, transferring genotypes among populations has often proven to be highly beneficial (Frankham 2015).

Many plant species accumulate persistent seeds in the upper centimeters of soils. This TSB is often a preferred source of restoration material as it represents a source of many plant species with locally adapted genotypes (Koch & Hobbs 2007). TSBs may also contain beneficial soil biota that enhance plant establishment (e.g. mycorrhizal fungi and bacteria; Jasper 2007), can be harvested prior to planned disturbance, stored, imported, or directly transferred for use, and is often the most reliable and practical source for re-establishing a wide range of terrestrial ecosystems (Fig. 2B).

When TSBs and passive regeneration are unavailable or inadequate, farmed or wild-collected seed is often the next most effective source for restoration. If available and appropriately collected and stored, wild-sourced seed can be genetically diverse and locally representative. In the absence of sufficient wild-collected seed, seed production areas (seed orchards or farms) become increasingly important, especially for restoration at large scales (Merritt & Dixon 2011). However, in areas of high species diversity, seed orchards may only be practical for selected species, such as dominant or structurally important species. Irrespective of the steps in sourcing, seed sourced for restoration typically undertakes a period of storage, and ultimately derives from wild collection. Critical issues associated with the use of seed for restoration are viability, dormancy state, and germinability. Seed batches typically include seeds in a range of states: aborted or poorly developed due to genetic or maternal environment conditions (stress, resource limitation); damaged by invertebrates or pathogens

(prior to collection or during storage); nonviable due to low genetic fitness (e.g. due to inbreeding); damaged by collection or storage conditions; or viable but varying in water content, size, seed coat thickness, dormancy state, and so on. Much seed is collected and stored in fruits or with attached structures (bracts, wings), and the condition of these may also influence seed fate.

The efficiency and quality of ethical wild seed collections (i.e. that do not have unacceptable consequences for source populations) can be enhanced by optimizing collection time with respect to season, seed ripening and dispersal schedules, and quality of source populations (e.g. Kodym et al. 2010). In some cases, viable seed production of wild populations can be enhanced by human-mediated pollination, herbivore or predator exclusion, or resource supplementation (e.g. irrigation). Seed quality indicators, such as germinability and genetic diversity, can be influenced by source population size and connectivity, pollinator behavior, conditions during seed development, and collection and post-harvest handling (Hay & Probert 2013). Cultivation in seed production facilities can select for genotypes that germinate or grow quickly, or produce large quantities of seed in glasshouse conditions. This may lead to reduced genetic diversity and selection for genotypes maladapted to field conditions (Schröder & Prasse 2013). Seed storage conditions also influence viability, and appropriate procedures must be implemented to accommodate seed storage behavior and time (Offord & Meagher 2009). Given that seed viability deteriorates over time, testing is required to assess seed quality prior to use in restoration activities (Hay & Probert 2013).

Species rarity, intrinsically low seed production, recalcitrant storage behavior (i.e. desiccation sensitivity), and dormancy can make restoration from TSB or broadcast seed difficult or impractical for some species. These species may be grown as seedlings or propagated vegetatively by cuttings, division,

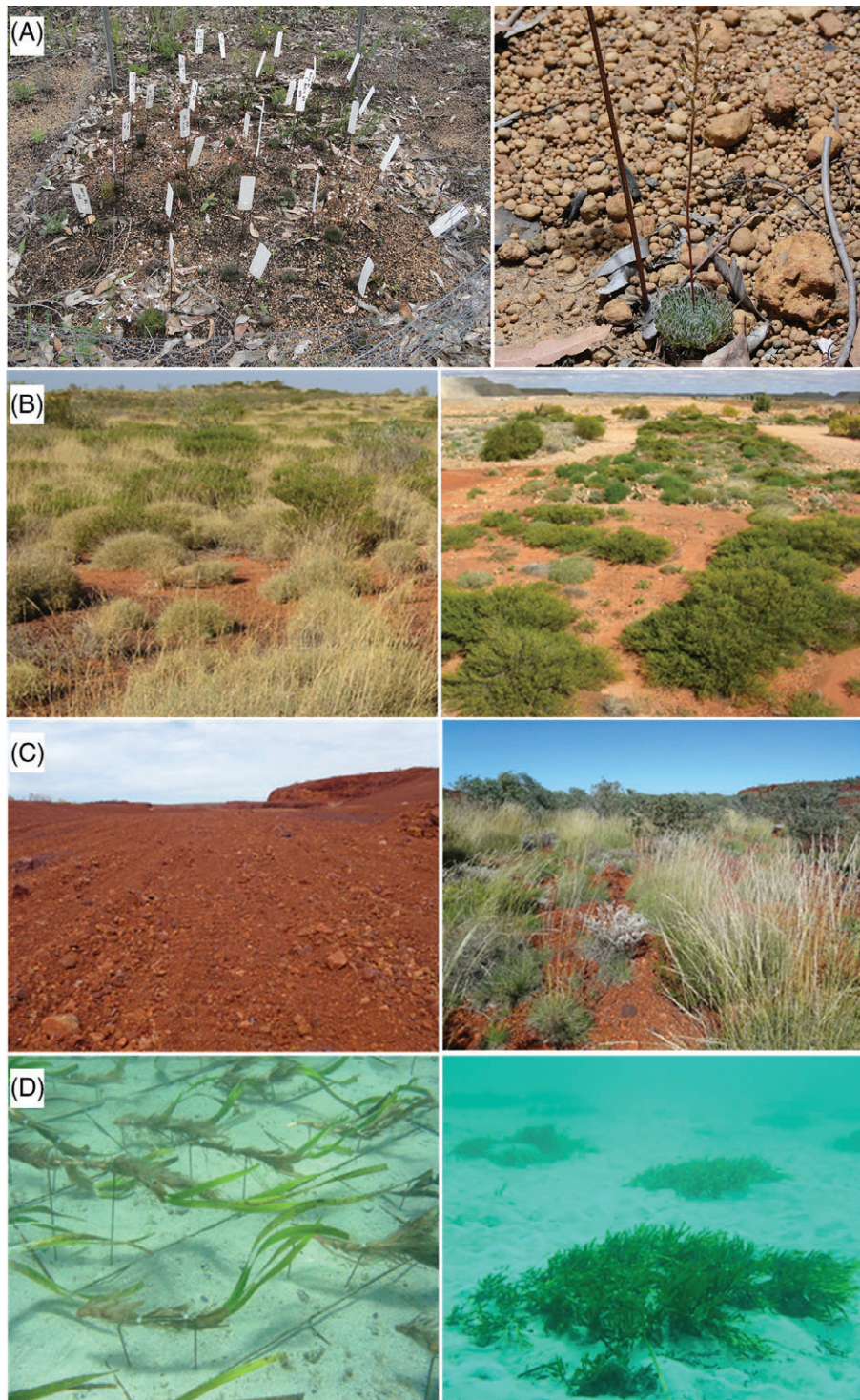


Figure 2. Examples of restoration site outcomes resulting from scientific research that improved long-term restoration outcomes. (A) Field trials assessing outbreeding depression in *Styliidium hispidum*: plants resulting from local, short-, and long-distance crosses planted in Jarrah forest, Western Australia (left). Life-time reproductive output (right) results indicate optimal intermediate outcrossing distance, due to inbreeding depression at small- and outbreeding depression at large scales (Hufford et al. 2012) (Photos by S. Krauss); (B) Restoration of *Triodia* hummock grasslands in the Great Sandy Desert after 5 years: vegetation cover and species richness were comparable with an undisturbed reference site (left) after addition of local topsoil in the restored site (right) (Photos by P. Golos); (C) Pilbara restoration: ripping the soil surface after landform reconstruction improved water flow within the site and plant growth (Photos by B. Stokes); (D) Restoration of a *Posidonia australis* seagrass meadow using transplants to stabilize sediment (left) (Photo by J. Verduin) and the addition of hessian bags on the seafloor, which provide anchorage points for naturally recruiting *Amphibolis antarctica* seedlings (right) (Photo by A. Irving).

or micropropagation (Reed et al. 2011), with propagation aspiring to produce hardy, restoration-ready tubestock suitable for restoration planting. Micropropagation (in vitro propagation using tissue culture techniques) can produce large numbers of disease-free plants and is routinely used for conservation/restoration of rare and threatened plants (Offord & Meagher 2009), with guidelines available for sourcing material suitable for tubestock production (Vander Mijnsbrugge et al. 2010). Somatic embryogenesis (asexual production of zygotic-like embryos from somatic tissues) is used for industrial-scale production in forestry (Germana & Lambardi 2016) and for species of conservation concern (Panaia et al. 2004), but has yet to be fully developed for restoration. In vitro propagation coupled with cryopreservation technology (Kaczmarczyk et al. 2012) provides an alternative to seed banking for propagation-recalcitrant species, as selected provenances can be efficiently stored long term, revived, and micropropagated as often as required, thus providing flexibility for restoring difficult species. Modern horticultural technology (heat beds, misting tents, cutting hormones and gels) and practices aid root development and prevent desiccation and fungal attack when establishing plants from cuttings or micropropagation.

Optimizing Plant Establishment

The largest bottleneck in the restoration of plants using broadcast seeds is the failure of viable seeds to germinate and establish as seedlings, with >90% of broadcast viable seeds commonly failing to establish in biodiverse restoration programs (James et al. 2013). Failure of seeds to germinate may be the result of low fitness, poor seed quality, inappropriate germination conditions, complex dormancy mechanisms, or environmental conditions that do not meet the requirements for germination (Merritt & Dixon 2011). Viable seeds that do not germinate may persist until suitable growing conditions arise, be lost through predation or pathogens, or displaced by wind or water (DeFalco et al. 2012). Seed dormancy remains poorly known for many species, significantly hampering their restoration (Merritt et al. 2007). Environmental cues breaking seed dormancy and germination are varied and complex, necessitating a systematic and often research-intensive approach to classify dormancy in order to maximize chances of recruitment. Baskin and Baskin (2014) review of species' dormancy type and requirements for germination may provide a critical starting point in order to tailor species-specific treatments for restoration needs.

Environmental conditions (temperature, water, light quality, and quantity), including the sequence and variation in these conditions, influences seed dormancy, germination, and seedling development rates (Baskin & Baskin 2014). Identifying seed germination requirements enables treatments that optimize establishment (Merritt et al. 2007). These may include optimizing burial depth through direct seeding, tilling or raking, and manipulating the chemical, physical (texture, roughness, hardness, and thermal properties), and hydrological (infiltration/repellence, water holding capacity, evaporation) properties of the soil surface and immediate subsurface. The

presence of seasonal and episodic variation in the environment also makes understanding these relationships critical in terms of the scheduling of restoration activities (James et al. 2013). Seed enhancements and technologies that overcome dormancy, improve germination, and increase seedling stress tolerance are receiving increasing attention in the scientific literature and may address the issue of recruitment failure in the field (Turner et al. 2013; Madsen et al. 2016). Seed coating and pelleting, which involves the application of polymers to seed surfaces, are employed in agricultural settings but are yet to be well adapted to restoration. These techniques provide the advantages of protecting against pathogens or seed predators, aiding in mechanized delivery, and enhancing establishment through the delivery of nutrients, germination-promoting agents, and agents that alter soil hydrological or physical properties (Madsen et al. 2016).

Planting tubestock provides an alternative method of establishing plants in a restoration site when they are inherently difficult to collect, store, or grow from seed (Palmerlee & Young 2010), or when species abundance is low. Production and planting of tubestock is time- and resource-intensive, which is usually prohibitive in large-scale applications. However, planted tubestock may have greater rates of survival as it has already passed through germination and emergence stages (Palmerlee & Young 2010). Failure of tubestock in restoration is associated with poor-quality stock not suited to sites (Griffiths & Stevens 2014); planting into substrates that preclude sufficient root growth (Benigno et al. 2012); planting that coincides with growth-limiting factors, such as drought or herbivory (Benigno et al. 2014); and poor planting methods (Dreesen & Fenchel 2010). Nursery practices (pot sizes, irrigation, temperature and lighting regimes, growing media) can all play a role in manipulating the size, growth phase, root architecture, root–shoot ratio, nutrient, and water status of tubestock to influence the likelihood of survival following out-planting.

Facilitating Plant Growth and Survival

Light, temperature, relative humidity, and wind are the primary elements of the aboveground abiotic environment influencing plant function and soil surface hydrology. In terrestrial systems, these factors drive evapotranspirational water loss and influence ecosystem processes such as carbon fixation and litter decomposition (Kucharik et al. 2006). Site-specific factors such as foliar dust, salt or chemical deposition, and frosts and particle abrasion can negatively influence plant growth and establishment (Wijayratne et al. 2009). Counteracting the impact and extent to which these factors affect restoration can be achieved by manipulating the abiotic environment; for example, baffles to reduce wind and airborne particle movement and the shading of plants to reduce evaporative stress (Torroba-Balmori et al. 2015). Studies manipulating some of these parameters in restoration (e.g. by providing protective structure such as tree guards) have resulted in beneficial outcomes, but not in all cases (e.g. Stevens et al. 2006).

The nature of restoration surfaces and landforms can contribute greatly to the success of restoration programs and a

number of treatments can be employed to optimize them. Restoration practitioners can influence water and air flow to enhance soil surface stability, and increase soil moisture infiltration and retention for the benefit of plant establishment and growth (Fig. 2D). These outcomes can be achieved by altering landforms, slope, and catchment geometries (Martín-Duque et al. 2010). Reclaimed soils frequently possess a combination of unstable hydrologic behaviors and low infiltration, leading to erosion (Merino-Martín et al. 2015). Slope angle, aspect, and landscape context determine the receipt of solar radiation, which influences soil temperature and evaporation potential, and affect the light and temperature experienced by growing plants. Common restoration treatments that influence these factors include manipulating soil surface features such as surface roughness, rock, litter, or mulch cover (Benigno et al. 2013); implementing treatments such as pitting, tilling, ripping, contour plowing, debris application, or planting of cover crops; and installation of benches or dams (Fig. 2C). Cover crops, tilling, or ripping can also counter the establishment of abiotic impediments to plant establishment and root growth such as surface crusting, hydrophobicity, and compaction (Szota et al. 2007).

As in natural systems, soil–plant interactions in restoration are complex: soils have many attributes relevant to plant survival and growth and these vary spatially, down profiles, and through time (Kardol & Wardle 2010). Soil or substrate attributes regularly interact with each other, climate, and the presence of plants and other organisms to effect plant growth and survival (Josa et al. 2012). Designing substrates to optimize restoration may require understanding the adaptations and tolerances of target species and communities in relation to soil physical, hydrological, chemical, and biological attributes (Azam et al. 2012). In some situations, such as restoration using mine tailings, nutrient toxicity may be a by-product of the mining process and can be detrimental to plant growth and survival (Wong 2003). Application of minerals through organic or inorganic fertilizers, altering soil texture or carbon content are common approaches to ameliorate toxicity, enhance soil development, or improve nutrition in restoration. However, in some cases, fertilization leads to undesirable outcomes (Daws et al. 2013). The use of hyper-accumulator plant species and the manipulation of soil biological communities to enhance soil development and to stabilize, extract, or leach toxic elements (i.e. phytoremediation) is a growing field or research, although with little impact thus far in the restoration of biodiverse ecosystems (Capuana 2011). If soils are substantially altered from those relative to a reference site, and manipulations are unsuccessful at returning them to their original state, target communities or restoration objectives may need to be revised to reflect new conditions—for example, a local halophytic community restored to salt-enriched sites, rather than the pre-existing community.

Above- and belowground interactions among organisms within and across trophic levels can critically enhance or inhibit growth and survival in restoration. Although ecosystem restoration generally relies on the establishment and management of aboveground plant diversity, belowground ecological processes are often overlooked in restoration (Kardol & Wardle 2010). This is despite widespread recognition of

ecological interactions such as nitrogen-fixing bacteria in the root nodules of Fabaceae and more than 80% of plants species exhibiting mycorrhizal associations (Bever et al. 2010). The absence of mycorrhizal partners for belowground interactions can potentially limit plant recruitment and survival, and alter important processes in nutrient cycling (Jasper 2007). The use of well-managed topsoils, alteration of carbon content, and deliberate inoculation of sites (e.g. from salvaged biocrusts) can be important approaches to restoring essential soil biota and the processes they support (Chiquoine et al. 2016).

The spatial pattern of neighboring plant individuals of different sizes and species can influence the distribution of resources and stresses in the environment, leading to variation in the establishment and survival of plants (Miller et al. 2010). Although resource competition can occur at any growth phase, positive interactions, in which the presence of an individual ameliorates stresses or enhances resources for others, are often stage-specific, potentially becoming neutral and then competitive as plants grow (Maestre et al. 2003). Understanding these interactions may allow the manipulation of planting densities, patterns, or sequences to enhance survival outcomes (Maestre et al. 2003).

Restoration sites are subject to a large number of potential threats from physical (e.g. erosion/sedimentation, altered hydrology), chemical (fertilization, pollutants), and biotic agents (pathogens, herbivores, weeds, pest animals), including humans (harvesting, mechanical disturbance, domestic grazing). If these processes have created or exacerbated the need for restoration, then they must be mitigated before restoration commences (Novacek & Cleland 2001). Early threat identification and mitigation is critical for restoration planning. Understanding processes that enable or enhance the activity of ongoing threats is the basis of developing effective management approaches. For instance, the addition of organic carbon to soil alters C:N ratios, microbial activity, and the relative availability of different nitrogen pools to potentially influence the competitive balance between short-lived weedy species and longer-lived native perennials (Prober et al. 2005).

Sustainability, Resilience, and Landscape Integration

Sustainability, resilience, and integration with the surrounding landscape are attributes of successful restoration programs (SER 2004), but are often not simple to plan or assess. Resilience, the ability to recover from stress or disturbance, is difficult to test without introducing stress or disturbances. Nonetheless, it may be important to assess resilience (e.g. to weed invasion, herbivory, fire; Herath et al. 2009) by experimentally imposing treatments, if mitigating the potential for stress or disturbance is a management action, and practitioners would like to know if, or when, this could be scaled back or discontinued. In terms of sustainability, the persistence of populations across generations is the ultimate sign of restoration success. Comparisons of population structure, resprouting capacity, seed production,

Table 6. Examples of well-documented projects incorporating scientific research into long-term ecosystem restoration. Themes are (1) setting targets and planning for success, (2) sourcing biological material, (3) optimizing establishment, (4) facilitating growth and survival, and (5) sustainability, resilience, and landscape integration. Years indicate the length of research and practice incorporated in the project. South Florida Natural Resources Center (SFNRC [<http://home.nps.gov/ever/naturescience/cecp.htm>])

System	Scale	Years	Source themes	1	2	3	4	5
Terrestrial								
Mediterranean grasslands, Europe	Landscape	3–21	Kiehl et al. 2010					
Ponderosa pine, U.S.A.	Regional	10	Allen et al. 2002					
Sagebrush steppe, U.S.A.	Regional	25	Hoelzle et al. 2012					
Atlantic forest, Brazil	Regional	30	Rodrigues et al. 2009					
Namaqualand (Karoo), South Africa	Regional	15	Carrick & Krüger 2007					
Jarrah forest, Australia	Regional	37	Koch & Hobbs 2007					
Banksia woodland, Australia	Local	15	Rokich 2016					
Tropical forests, South Asia	Regional	25	Ashton et al. 2014					
Aquatic								
Riverine wetland, U.S.A.	Local	15	Mitsch et al. 2012					
Coral reefs, Caribbean Islands	Regional	<10	Baum 2008; Johnson et al. 2011					
Seagrass meadow, U.S.A.	Regional	16	Orth & Mcglathery 2012					
Florida Everglades, U.S.A.	Regional	37	SFNRC					

seed dispersal, seed bank densities, and seedling recruitment between established restored and reference sites assess whether recruitment of desired species is possible or occurring at reference rates (Herath et al. 2009).

Developing the conditions needed to generate genetically fit seed may require an understanding of pollen and seed movement, plant breeding, and mating systems. Species that are self-incompatible or susceptible to inbreeding depression require pollination from unrelated individuals. Similarly, mating among clones or related individuals in self-compatible species may result in reduced seed fitness (Coates et al. 2007). Both of these issues are exacerbated by small population sizes and potentially low pollinator activity in isolated restoration sites (Ghazoul 2005). Ensuring adequate genetic diversity within the initial seed source can minimize relatedness among individuals (Broadhurst et al. 2008). Broadcast seeding typically randomizes spatial genetic structure within restored plant populations, helping to promote wide outcrossing among even near neighbors (Ritchie & Krauss 2012).

Restoration of pollinator services can be critical for plant reproduction, especially when small or isolated restoration sites may attract fewer pollinators (Menz et al. 2011). Ensuring that the life-cycle requirements of keystone pollinators are met, such as by augmenting or creating nest sites, may support increased pollinator populations (Steffan-Dewenter & Schiele 2008) and seed set. Given that restoration of diverse pollinator communities may be particularly challenging and that many plant species have specialized pollination systems (Fenster et al. 2004), it is important to restore at least some members of each pollinator functional group (*sensu* Ollerton et al. 2006).

The establishment of fauna communities in ecosystem restoration is critical for both their inherent value and their provision of important functions such as pollination, seed dispersal, soil aeration, nutrient cycling, and herbivory (Montoya et al. 2012). Plant communities and landscape features provide habitat and resources for fauna, but vegetation restoration may

not automatically lead to fauna recolonization (Craig et al. 2012). Often, specific habitat characteristics must be restored in order to support the target fauna community (Thomas et al. 2009). Given the diversity of fauna and their ecological requirements, fauna restoration may be best approached by targeting species that provide significant ecosystem functions or have conservation significance (Thomas et al. 2009). Meeting the requirements of species that need habitat elements associated with mature or late successional communities, such as tree hollows or rotting debris, may be particularly challenging, but can be achieved with the provision of artificial structures, rock piles, refugial trees, or woody litter (Craig et al. 2012). For rare species or those with limited dispersal potential, targeted translocation efforts may be necessary.

A large number of natural processes can influence the developmental trajectories, resilience, sustainability, and function of restored ecosystems, including flooding regimes, erosion and sedimentation, bioturbation, nutrient cycling, decomposition, plant-soil feedbacks, competition and facilitation, trophic interactions, pollination, and seed dispersal (Kardol & Wardle 2010; Montoya et al. 2012). Some of these may be reinstated with the initiation of restoration, some develop as vegetation and fauna establish, while others require deliberate intervention. Episodic or regular events, such as fire or flooding, play a critical role in geomorphologic and successional processes, maintaining nutrient budgets and cycles, and triggering recruitment episodes that enable population regeneration in some ecosystems (Raulings et al. 2011). As these processes can also be threats, managing their timing and impact may require careful planning (Reich & Lake 2015).

Many ecosystem processes involve large-scale connectivity, and integration of restoration sites with these landscape processes can aid restoration success. The scale, placement, and connectivity of restoration sites in the landscape affects the biotic and abiotic processes that determine the sustainability of restoration (Menz et al. 2013). Small fragments are less able to

support larger population sizes, potentially resulting in reduced genetic diversity and greater exposure to demographic stochasticity, resulting in reduced resilience, and fewer resources to support fauna and associated ecosystem processes (Coates et al. 2007). Connectivity with remnant ecosystems, through proximity or corridors, increases the likelihood of the colonization of new (desirable) species and genetic connectivity through movement of pollen, seed, and animals (Rudnick et al. 2012). As such, connectivity can enhance the species richness, resilience, and ecosystem function of restored areas (Robinson & Handel 2000). Finally, landscape context and connectivity can positively or negatively influence threats such as pest animals, weeds, or pathogens (Haddad et al. 2014). Small restoration sites, in particular, have relatively greater exposure to these outside inputs.

Landscape integration can also enhance ecosystem services and conservation outcomes at scales greater than the restoration site. Examples of these include altered hydrological, nutrient, and sediment flows, promotion of meta-population dynamics, colonization from restored nuclei, migration, dispersal, and wider landscape exploitation by fauna species able to use a mixture of landscape types (Shoo & Catterall 2013).

Restoration practitioners typically have limited opportunity to manipulate landscape connectivity or the shape or size of restoration areas. However, restoration of sites within or adjacent to less disturbed ecosystems may mean that they are more likely to receive positive rather than negative external inputs, and may reduce or eliminate small population size effects through connectivity. Similarly, optimizing the arrangement and location of restoration sites may promote restoration benefits at the landscape scale. If the values that are the focus of restoration operate at landscape scale, or rely on landscape connectivity, careful consideration of the location and arrangement of restoration is required.

Discussion

Restoration research that does not have a direct application in practical restoration can be of value (this paper?) but, where ecological restoration is required, the need for targeted research in restoration is clear. Restoration planners and practitioners need awareness of where they require science inputs, how to target, search, and interpret scientific literature, and the ability to mobilize research to fill knowledge gaps. The research framework presented here (Tables 1–5 and S1) identifies the scientific knowledge required, and is intended to assist planners to identify their research needs and focus on questions of practical priority. This framework should also allow researchers and practitioners to allocate often limited financial and biological resources to avoid wastage within projects. A further outcome of this framework is that it may allow qualitative comparison across biomes or ecosystems to identify systems in which capacity and knowledge are high or low, in which research investment is most required and may be most effective, and in which risks are highest if land use planning or development will lead to restoration requirements. Although this framework

of research questions is extensive, intensive, and potentially expensive, successful restoration projects have invested in many or most of these research themes (see selected examples in Table 6). An important attribute of the framework is the diversity of research fields that it encompasses. Although many individual questions may be addressed by research within a single field, effective restoration programs require multidisciplinary inputs. This needs to be recognized not only by restoration planners and managers but also by restoration scientists.

Echoing Ehrenfeld (2000), we believe that restoration practitioners, scientists, and, perhaps more importantly, planners and regulators must recognize that achieving restoration goals in all but the simplest systems is a significant challenge requiring substantial investment, including in science as demonstrated here. Without this investment, society must be realistic when contemplating restoration as a technological solution to global change and local planning problems. However, science-supported restoration may yet be able to achieve standards widely held to be too problematic or simply unattainable in many ecosystems—if it were supported by appropriate science and resourced sufficiently to try. If society is serious about meeting biodiversity conservation and environmental challenges in the face of global change, restoration science has a significant role, but must focus on relevant, practical needs.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. A practical framework for restoration science.

Appendix S1. List of references associated with Table S1.

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