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TOWARD PREDICTION IN THE RESTORATION OF BIODIVERSITY

# Interpreting variation to advance predictive restoration science

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## Summary

**1.** Ecological restoration is a global priority that holds great potential for benefiting natural ecosystems, but restoration outcomes are notoriously unpredictable. Resolving this unpredictability represents a major, but critical challenge to the science of restoration ecology.

**2.** In an effort to move restoration ecology toward a more predictive science, we consider the key issue of variability. Typically, restoration outcomes vary relative to goals (i.e. reference or desired future conditions) and with respect to the outcomes of other restoration efforts. The field of restoration ecology has largely considered only this first type of variation, often focusing on an oversimplified success vs. failure dichotomy. The causes of variation, particularly among restoration efforts, remain poorly understood for most systems.

**3.** Variation associated with restoration outcomes is a consequence of how, where and when restoration is conducted; variation is also influenced by how the outcome of restoration is measured. We propose that variation should decrease with the number of factors constraining restoration and increase with the specificity of the goal. When factors (e.g. harsh environmental conditions, limited species reintroductions) preclude most species, little variation will exist among restorations, particularly when goals are associated with metrics such as physical structure, where species may be broadly interchangeable. Conversely, when few constraints to species membership exist, substantial variation may result and this will be most pronounced when restoration is assessed by metrics such as taxonomic composition.

**4.** *Synthesis and applications*. The variability we observe during restoration results from both restoration context (how, where and when restoration is conducted) and how we evaluate restoration outcomes. To advance the predictive capacity of restoration, we outline a research agenda that considers metrics of restoration outcomes, the drivers of variation among existing restoration efforts, experiments to quantify and understand variation in restoration outcomes, and the development of models to organise, interpret and forecast restoration outcomes.

**Key-words:** adaptive management, biodiversity, contingency, human land use, managed landscapes, reference conditions, restoration ecology, restoration targets

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## Introduction

The alteration of natural ecosystems for human land uses is the leading threat to biodiversity and predominant modifier of ecosystem functioning (Vitousek *et al.* 1997; Foley *et al.* 2005; Cardinale *et al.* 2012; Newbold *et al.* 2015). In response, ecological restoration has been widely used to increase biodiversity and improve ecosystem functioning in human-modified landscapes (Rey Benayas *et al.* 2009; Suding 2011; Montoya, Rogers & Memmott 2012; Crouzeilles *et al.* 2016). Restoration of degraded ecosystems is a recognised global priority (Aronson & Alexander 2013; Menz, Dixon & Hobbs 2013; Suding *et al.* 2015) and numerous ambitious large-scale and international restoration projects are underway (e.g. the Bonn Challenge to restore 150 million ha of forest by 2020; Chazdon *et al.* 2017; and the expansive and expensive restoration of the Florida's Everglades; Sklar *et al.* 2005). Success in these and all restoration efforts is predicated on the ability to reliably restore ecosystems.

Yet, in practice, restoration outcomes may be highly unpredictable (Suding 2011; Perring *et al.* 2015). Levels of biodiversity and ecosystem functioning in restored systems typically fall short of those in intact ecosystems (Rey Benayas *et al.* 2009; Crouzeilles *et al.* 2016). Moreover, seemingly similar restoration practices may result in substantial variation in the biodiversity or functioning of the restored system and, while the science is advancing, we typically lack an understanding of the processes that lead to this variation (Suding, Gross & Houseman 2004; Suding & Hobbs 2009; Brudvig 2011; Suding 2011; Norden *et al.* 2015). This, in turn, hampers restoration practice and has resulted in repeated calls for restoration ecology to develop into a more strongly predictive science (e.g. Hobbs & Norton 1996; Palmer, Ambrose & Poff 1997; Hobbs & Harris 2001; Young, Petersen & Clary 2005; Brudvig 2011; Suding 2011; Perring *et al.* 2015). Here, we argue that to advance toward this goal, the issue of variability in restoration outcomes must be explicitly confronted.

We confront two important forms of variation: (i) how conditions within restored ecosystems differ from goals (i.e. reference or desired future conditions) and (ii) how conditions differ among restored ecosystems. Understanding the causes of variability during restoration will enable the development of restoration practices that more predictably meet objectives. We consider how variability results from interacting ecological processes and from the restoration efforts themselves, in light of the metrics used to evaluate restoration outcomes. We conclude by considering directions for future research to understand the drivers of variability during restoration and transfer this understanding to advance predictable restoration practice.

## Paying attention to variability

The hallmark of a mature restoration science will be the ability to reliably restore ecosystems based on well-articulated goals (Bradshaw 1987; Hobbs & Norton 1996; Suding 2011). Restoration goals are defined based on a variety of metrics that target the structure, function and diversity of the restored system (Ruiz-Jaen & Aide 2005; Rey Benayas *et al.* 2009). Yet, for any given metric, restoration outcomes vary and understanding this variability is a critical step toward the goal of prediction.

We suggest two key ways to consider variation in restoration outcomes. The first—variability among restored, unrestored and goal (i.e. reference, or desired future) conditions—has been the focus of restoration ecology research (Rey Benayas *et al.* 2009; Crouzeilles *et al.* 2016). This consideration of 'mean responses' has illustrated that, on average, restoration causes biodiversity and ecosystem service metrics to approach (but not necessarily achieve) goal conditions (Rey Benayas *et al.* 2009). The second—how restoration outcomes compare to one another—has received much less attention from restoration ecologists. This second consideration is important because the outcomes of restoration may vary substantially, even when similar approaches are employed on relatively similar sites. For example, variation in plant communities among restored tallgrass prairies in the Midwestern United States can be explained through differences in management decisions related to the diversity and composition of seeds sown during restoration, soil attributes, and the successional age of the restoration site (Grman, Bassett & Brudvig 2013; Grman & Brudvig 2014). Likewise, variation in weather from year to year can affect restoration outcomes, even when similar restoration methods are employed (Bakker *et al.* 2003).

This distinction between mean responses to restoration and among-restoration variation has important implications for the predictability of restoration outcomes. In Fig. 1 we illustrate four restoration outcome scenarios. Scenarios A and B both show the same mean response (centroid of points), whereby restorations on average match a goal, but are distinguished by very different degrees of variation among restoration efforts. Scenario A contains little variation (a highly predictable outcome), whereas scenario B presents substantial variation and a less predictable outcome. As a consequence, scenario A's results would more consistently be characterised as fully successful, whereas scenario B's results are only sometimes successful. Similarly, scenarios C and D represent similar mean responses; however, in these cases the mean does not match the goal as well as in scenarios A and B. Again, predictability differs and, as a consequence, the more predictable scenario C results in fewer efforts that would be deemed successful—in other words, restoration can be characterised as predictably unsuccessful. Owing to the high amount of variation (unpredictability), scenario D actually results in some outcomes that meet the goal.

These examples in Fig. 1 illustrate additional important points for restoration practice. First, instances of

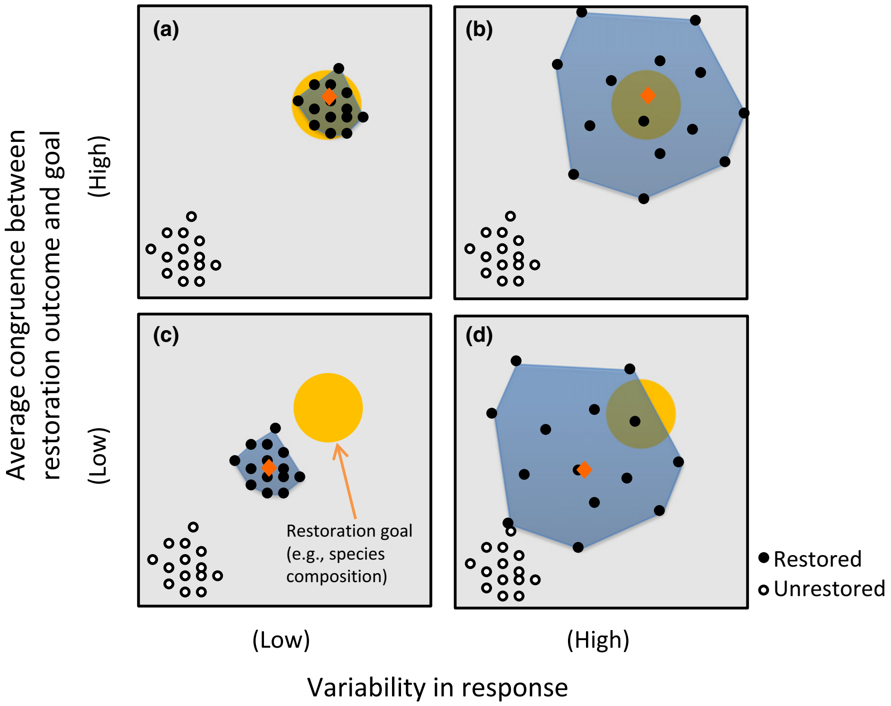

**Fig. 1.** The outcomes of restoration may differ in mean responses (orange diamond) as well as the degree of variability around a mean response (blue shaded region). To date, the field of restoration ecology has focused on mean responses—how restoration outcomes compare to unrestored and goal conditions, indicated by gold circles (i.e. the comparison of panels a and b to c and d). Very little attention has been given to variability in responses among restoration projects (indicated by the dispersion of points in blue polygons), or situations leading to more vs. less variation in outcomes (i.e. the comparisons of panels a and b or c and d).

highly variable outcomes suggest either a need to refine restoration approaches or, perhaps, the need for prioritisation. For example, the difference between scenarios A and B might be due to the approaches employed or other drivers, such as land-use legacies or landscape composition. The latter case may lead to avoiding restoration at locations supporting conditions that lead to unpredictable outcomes. Second, although we call for increased consideration of variability in restoration [among conditions (unrestored, restored, goal) and among restoration efforts], we do not suggest that restoration practitioners should necessarily seek to minimise variation among efforts. Indeed, variability among restoration outcomes may play a critical role in reversing widespread biotic homogenisation (Olden 2006) by promoting landscape-scale (gamma) diversity through beta diversity and heterogeneity in functioning among restoration efforts (Matthews & Spyreas 2010; Martin & Wilsey 2012; Grman & Brudvig 2014). Although this argues for avoiding homogeneous restoration outcomes, there is also little sense in generating variability through a diversity of failures (although, in practice, failures may be quite homogeneous, dominated by one or a few undesirable species, like in scenario C; for example, Matthews & Spyreas 2010). The key is to develop approaches that result in the widest possible variety of outcomes within the range of desired conditions.

## Interpreting variability—digging to the root causes of variation in restoration outcomes

The ability to predict the outcomes of future restoration activities hinges on the capacity to explain the outcomes of existing restoration efforts. By understanding the root causes of variation in restoration outcomes, we might generate predictions for the results of future restoration efforts, given the particular details of these new efforts (planned restoration actions, site conditions, etc.). Given the complexity of ecological systems, the challenge to such efforts is that many factors and processes must be considered to generate robust explanations such as the site's natural history, level of degradation, restoration actions and environmental conditions at the time of restoration efforts (Fig. 2; see also Hobbs & Norton 1996; Palmer, Ambrose & Poff 1997; Brudvig 2011).

The pre-restoration environmental conditions at a site typically delimit the ultimate goals of a restoration and the acceptable range of variation for a restoration outcome. Site conditions are dictated by the site's natural history (i.e. pre-degradation system attributes) and history of human land use (Fig. 2), which may impact soil fertility, seed bank composition/density, pre-restoration vegetation composition and other aspects of site conditions (Bakker *et al.* 1996; Suding, Gross & Houseman 2004; Matthews *et al.* 2009; Brudvig *et al.* 2013; Grman, Bassett & Brudvig 2013; Mesquitade *et al.* 2015; Dickens *et al.* 2016). Together,

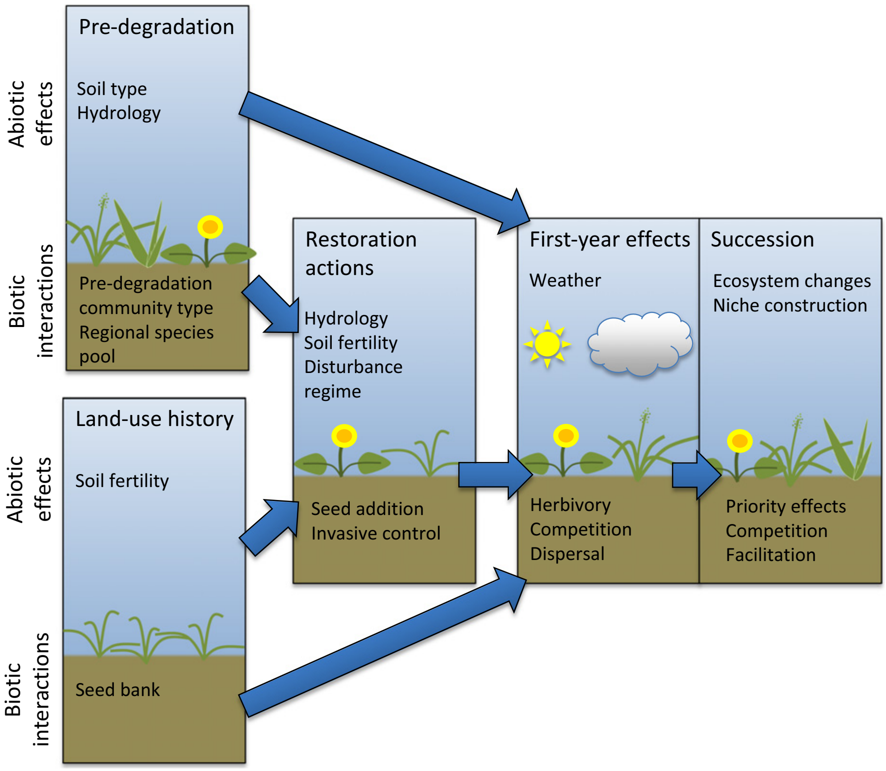

**Fig. 2.** Variation during restoration (among restoration efforts, or relative to goal conditions; Fig. 1) results from differences in pre-degradation conditions, land-use histories, restoration actions and system assembly starting the year restoration is initiated. Each of these sources of variation may be mediated through abiotic and biotic effects on the restored system.

these aspects of pre-restoration site conditions determine overarching aspects of the restoration goal (e.g. whether to attempt restoration of a historical ecosystem state vs. structure or function; Hobbs 2007; Hobbs, Higgs & Harris 2009), which may dictate the similarities between unrestored and goal conditions (Fig. 1). In turn, pre-restoration site conditions represent important sources of variation, making knowledge of conditions, such as land-use history, important to explaining restoration outcomes (e.g. Brudvig & Damschen 2011; Grman, Bassett & Brudvig 2013).

Restoration actions, themselves, may also explain variation during restoration (Fig. 2). Certainly, restoration efforts taking place through different methods will likely yield different outcomes (i.e. the comparison between panels a/b and c/d in Fig. 1). However, the details of how restoration is conducted can also impact the variation among similar restoration efforts (i.e. the comparison between panels a and b or c and d in Fig. 1). Important to this is how restoration activities interface with conditions at a particular place and time. For example, the presence of seed consumers, harsh soil conditions, or the sowing of more depauperate seed mixes during restoration can reduce the number of species that might establish at a restoration site, thus favouring less variation in restoration outcomes (i.e. spread in Fig. 1a,c; Germain *et al.* 2013; Grman & Brudvig 2014; Long, Foster & Kindscher 2014). These ideas merit more attention during work to interpret variation among restoration efforts.

Following initial restoration actions, variation among restoration efforts is shaped by how successional dynamics play out over time (Fig. 2). Conditions during the first year of restoration, such as precipitation, consumer abundances, or natural influx of individuals from the surrounding landscape, may be particularly important for the subsequent restoration trajectory by favouring the establishment and initial growth of some species over others (Bakker *et al.* 2003; Vaughn & Young 2010; Stuble, Fick & Young 2017). In spite of having received little attention, pre-restoration site conditions and first year effects are likely to interact in important ways (Fig. 2). For example, sown plant establishment may be particularly low in drought years at sites with sandy soils, or due to strong competition with weeds at sites possessing substantial seed banks. Subsequent successional dynamics are influenced by the interplay of biotic interactions, abiotic system development, and continued extinction and colonisation dynamics, resulting from restoration actions, land-use legacies, abiotic site conditions, and landscape context (e.g. Opperman & Merenlender 2000; Eviner & Hawkes 2008; Matthews & Endress 2010; Germain *et al.* 2013; Helsen, Hermy & Honnay 2013; Dickens *et al.* 2016). Together, these processes fall within the purview of numerous ecological theories including community assembly, plant-soil feedbacks, succession and trophic dynamics (e.g. Paine 1966; Connell & Slayter 1977; Chase 2003; Fattorini & Halle 2004; Van der Putten *et al.* 2013), which hold promise for explaining variation in restoration outcomes.

## Hierarchies of predictability

Restoration takes place at a variety of scales, from localities to landscapes, with success evaluated by numerous metrics, spanning physical structure, biodiversity, and aspects of functioning (Ruiz-Jaen & Aide 2005; Brudvig 2011). These diverse considerations are important, yet from the perspective of achieving restoration success, present the possibility that predictability may vary among metrics and scales (Lockwood & Pimm 2004).

In general, the ability to predictably achieve a goal will depend on the number of factors constraining the outcome and on the response that is being evaluated (Fig. 3). For example, restoring the physical structure of a tropical forest—a coarse goal—may be reliably achieved, whereas restoring a particular tree community composition—a fine goal—will be more difficult and unpredictable (Shoo *et al.* 2016). A simple reason for this is the nested nature of these goals: there are many possible community compositions that might develop during forest restoration, yet the vast majority of these will produce a structure we would call forest. Thus, as the number of conditions that achieve a goal declines, the particular context and history of a restoration —that is, physical conditions, chance events that lead to arrival of individuals, interactions among individuals—become more important (Fukami *et al.* 2005; Matthews *et al.* 2009). Conversely, as the influences of these particularities become less important, different contexts and histories can lead to functionally-similar outcomes.

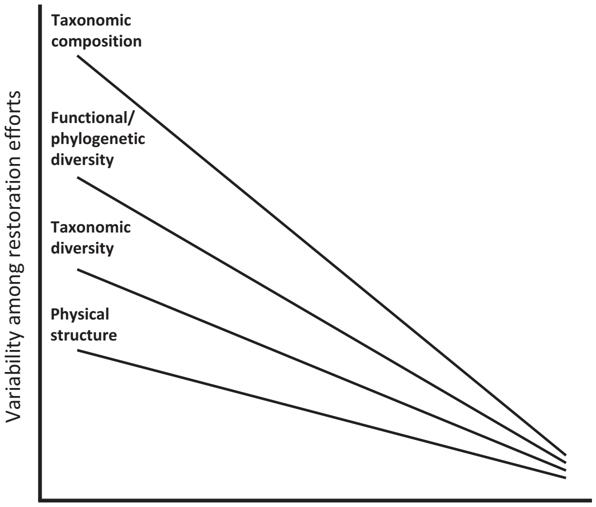

**Fig. 3.** The variation we perceive among restoration efforts is an interactive consequence of the context of restoration and how restoration is assessed. When factors (e.g. harsh environmental conditions, limited species reintroductions) preclude most species, little variation will exist among restorations, particularly when goals are associated with coarse metrics such as physical structure, where species may be broadly interchangeable. Conversely, when few constraints to species membership exist, substantial variation may result and this will be most pronounced when restoration is assessed by fine metrics, such as taxonomic composition. For the sake of simplicity, relationships are depicted as linear, but may take nonlinear forms.

Together, these concepts suggest a hierarchy of predictability among various measures of restoration outcomes. We propose a general ordering from: (i) measures of physical structure for which species can be functionally redundant (Lockwood & Pimm 2004; Suganuma & Durigan 2015), to (ii) measures of diversity, such as richness and evenness, that do not consider species identities (Matthews, Spyreas & Endress 2009; Turley & Brudvig 2016), to (iii) measures of diversity that account for species identities, but for which species may still be functionally redundant of one another, such as functional or phylogenetic diversity (Fukami *et al.* 2005; Helsen, Hermy & Honnay 2012; Barber *et al.* 2017; Tucker *et al.* 2017), to (iv) highly-specific measures of communities, such as taxonomic composition (Matthews, Spyreas & Endress 2009; Turley & Brudvig 2016; Barak *et al.* 2017). Much of this ordering represents hypotheses in need of testing and, at present, we know of only one study that has performed such a test (Laughlin *et al.* 2017), which broadly supports this ordering. Additional tests are needed and these should consider various diversity metrics (Tucker *et al.* 2017), aspects of structure, and focal ecosystem types (e.g. terrestrial vs. aquatic). Moreover, additional work will be necessary to investigate whether an analogous hierarchy of predictability might be developed for aspects of ecosystem functioning, such as primary productivity and nutrient cycling. With this, important questions remain to be answered about if and how functioning follows from the restoration of ecosystem structure and diversity (e.g. Zedler & Callaway 1999; Bullock *et al.* 2001, 2011; Montoya, Rogers & Memmott 2012).

The context of a particular restoration may also have strong bearing on the predictability of outcomes, particularly outcomes based on fine metrics such as community composition (Fig. 3). The predictability of a restoration outcome should increase as environmental conditions (harsh soils) or restoration approaches (species-poor seed addition, competitor removal) limit the number of potential species inhabiting a site (e.g. Germain *et al.* 2013; Grman & Brudvig 2014; Long, Foster & Kindscher 2014). Importantly, the resulting variation that we perceive will depend on the metric by which restoration is evaluated. At one extreme, exceptionally harsh conditions or other actions limiting membership to one or a few species will result in a highly predictable outcome, particularly when restoration is being assessed by a coarse metric such as physical structure. At the other extreme, where many species arrive and most can survive, the outcome of restoration may be strongly influenced by the vagaries of chance dispersal events, priority effects, and other factors and, thus, can be highly unpredictable, particularly when assessed by fine metrics, such as taxonomic composition (Fig. 3).

## Toward a future of predictive restoration

Understanding the causes of variability is necessary, but ultimately not sufficient for predicting the outcomes of restoration efforts. How can restoration advance from retrospective to prospective, allowing land managers to broadly and confidently forecast the outcomes of their restoration activities? We suggest a research agenda that involves: (i) Expanding the template of restoration responses being considered, (ii) Increasing our understanding of variation among existing restoration efforts, (iii) Experimenting to understand mechanisms driving variation in restoration outcomes and (iv) Developing models to organise, interpret and forecast restoration outcomes.

### EXPANDING THE TEMPLATE OF RESTORATION RESPONSE

Restoration ecology research has focused on understanding the mean responses of biodiversity to restoration actions (e.g. do restored sites have more or less diversity than unrestored sites vs. reference sites?), where biodiversity has been narrowly measured at the taxonomic level (Rey Benayas *et al.* 2009; Brudvig 2011). We call for an expansion of this template, to explicitly consider variability among restorations and additional aspects of biodiversity.

Work to quantify and explain variability among restoration efforts will help to determine how often variability is incorporated into restoration planning and goal setting, and the causes of variability among restoration projects. Several knowledge gaps remain. For example, are restored sites more or less variable in measurable outcomes, relative to degraded or reference sites? Are there restoration approaches that lead to more vs. less variability? What are the relative influences of restoration practices, underlying site conditions (e.g. soils, landscape context) and stochastic events (e.g. fire, drought) for variability during restoration? How does variability scale with space and, with this, how do insights generated through experiments and monitoring in smaller plots (e.g. Martin & Wilsey 2012) translate to the landscape scales at which conservation planning may take place (Schmitz 2005)? Answering these questions will assist with confronting practical problems, such as identifying restoration approaches that are most likely to result in consistent levels of success, and that maximise desirable landscape-level heterogeneity.

Biodiversity can be considered at a variety of scales—from genes to landscapes—yet restoration research has focused narrowly on taxonomic biodiversity when evaluating outcomes (Brudvig 2011; Hipp *et al.* 2015). Expanding to consider other measures of biodiversity, such as those related to functional traits and phylogenetic relationships, would provide added insights into restoration outcomes and, as we explain above, likely have bearing on how we interpret variability and judge success during restoration. Numerous questions remain unanswered regarding what we will learn by expanding how we consider biodiversity during restoration: Beyond being alternative measures of biodiversity, do functional and phylogenetic measures of biodiversity provide information about community composition and diversity of restored communities that is unique from other diversity metrics (Larkin *et al.* 2015; Turley & Brudvig 2016; Barber *et al.* 2017; Barak *et al.* 2017)? And if so, will this new information help to shape restoration goals or quantify restoration success (Hipp *et al.* 2015)? Functional and phylogenetic measures of biodiversity may inform how systems function in terms of nutrient cycling, hydrology, trophic dynamics and other aspects, or how species coexist with each other (or not) over the course of restoration (Bullock *et al.* 2011; Montoya, Rogers & Memmott 2012; Srivastava *et al.* 2012; Li *et al.* 2015; Menge & Chazdon 2016). In what ways do specific functional trait values relate to particular restoration objectives, such as the establishment and persistence of target species or the provisioning of desired ecosystem services (Laughlin 2014)? Trait response-effect frameworks are useful (Lavorel & Garnier 2002; Suding *et al.* 2008) because they consider the ways that communities respond to environmental conditions through species' traits and, in turn, how aspects of ecosystem functioning are affected by the set of traits possessed by a community (Eviner & Hawkes 2008; Perring *et al.* 2015); however, empirical tests within restoration are essentially absent (though see Zirbel *et al.* 2017). Addressing these and other questions will require advancement on a number of fundamental fronts to which restoration studies are primed to contribute, such as elucidating the relationships between biodiversity (variously defined) and ecosystem functioning under realistic field conditions (Cardinale *et al.* 2012; Wardle 2016) and the long-term re-assembly of ecological communities based on measured functional traits (McGill *et al.* 2006; Funk *et al.* 2008).

### UNDERSTANDING VARIATION AMONG EXISTING RESTORATION EFFORTS

Restoration ecology is a field built on case studies, with much early work focused on comparing one or few restored sites to degraded or reference conditions. There is now an increasing focus on comparisons across groups of sites, permitting insights into the causes of variation in restoration outcomes. Such comparative, retrospective studies and related meta-analyses have illustrated the influences of (sometimes subtle) differences in management, landscape context, land-use history and other factors for the diversity or composition of restored communities (e.g. Fagan *et al.* 2008; Brudvig & Damschen 2011; Grman, Bassett & Brudvig 2013; Matthews 2015; Moreno-Mateos *et al.* 2015; Norden *et al.* 2015; Crouzeilles *et al.* 2016). Additional work is needed along these lines, to interpret variation among existing restoration efforts, including consideration of additional response metrics, such as functional ecosystem attributes.

Retrospective studies that probe the influences of temporal variability in environmental conditions, such as initial year weather conditions, will help to understand the degree to which restoration efforts may be inherently unpredictable (Vaughn & Young 2010; Grman, Bassett & Brudvig 2013; Stuble, Fick & Young 2017). Success in these efforts will hinge upon record keeping by restoration practitioners (of site preparation methods, seed lists, fire records, etc.) and the inclusion of 'failed restorations', alongside successes, in models to explain the full range of variation in restoration outcomes.

### STRONG INFERENCE THROUGH MECHANISM-ORIENTED EXPERIMENTS

The gold standard for understanding the causes of variability and, ultimately, predictably successful approaches in restoration will be experiments. Experiments in restoration ecology can be full-scale restoration practices that are explicitly experimental (e.g. Brudvig *et al.* 2007), restoration manipulations replicated across sites with various management approaches or contexts, such as surrounding landscape composition (e.g. Holl *et al.* 2017), or smaller scale manipulations (i.e. plot experiments) of specific putative mechanisms that might shape restoration outcomes, such as nutrient limitation or seed arrival (e.g. Turley *et al.* 2017). These types of experiments are complimentary and can elucidate processes limiting recovery of ecosystems following human disturbances (Pywell *et al.* 2002; Turley *et al.* 2017), afford strong inference into the effects of restoration and, when designed across many factors and levels, aid the development of optimal restoration approaches (Weiher 2007).

Yet, a critical recognition is that the factor(s) limiting recovery and the optimal approach to restoration is likely to vary among localities, over time, and across focal species groups (Eviner & Hawkes 2008; Reid, Holl & Zahawi 2015; Dickens *et al.* 2016; Reid *et al.* 2016). Resolving such context dependencies remains a formidable challenge to restoration ecology. We suggest that success will be afforded by the broader use of distributed experiments, whereby an identical experiment or restoration approach is conducted across many locations. By considering how outcomes differ among locations based on measured site attributes, such as soil conditions, landscape context, or invasion pressure, insights may be gleaned into context dependencies structuring recovery and optimal restoration approaches for particular site conditions (e.g. Pywell *et al.* 2002; Dickens *et al.* 2016; Reid *et al.* 2016), information that land managers can subsequently map to their locations and efforts. A particularly exciting and powerful prospect is the development of restoration research networks conducting distributed experiments (Borer *et al.* 2014) affording the sorts of broad-scale insights into generalities and context dependencies in restoration beyond the scope of an individual research group.

Adaptive management approaches may afford additional insights into variability during restoration. Adaptive management works by refining competing models of the relationships between restoration inputs (i.e. management activities) and outcomes, by continually inputting monitoring data (Moore *et al.* 2011). Results from one 'cycle' of adaptive management are used to adjust future management schemes, providing greater predictive power to restoration managers and organisations (Murray & Marmorek 2003). For example, the US Fish and Wildlife Service's Native Prairie Adaptive Management Initiative uses adaptive management to determine the effects of several management actions (including prescribed burning and grazing) on plant biodiversity and invasion (Hunt *et al.* 2015). Studies of adaptive management in ecological restoration may provide an important bridge between retrospective studies, in which sites may vary considerably in both management and monitoring, and highly controlled experiments, while also affording unique insights through their iterative approach.

### MODELS TO ORGANISE, INTERPRET AND FORECAST RESTORATION OUTCOMES

Quantitative models are a cornerstone and, yet, may have unrealised potential to explain variability in restoration outcomes. Hierarchical models in particular provide the opportunity to predict restoration outcomes at different spatial and temporal scales and partition variation into multiple levels. Linear mixed effect models (Bolker *et al.* 2009) are commonly used to make inferences on 'fixed effects', such as restoration treatments, while 'random effects' are used to account for non-independence amongst individuals, plots, species or time periods. More thoughtful consideration of random effects could contribute to predicting restoration outcomes. For example, in a study of native plant restoration in sites dominated by an invasive cheatgrass, fixed effects, including herbicide application and direct seeding of native species, explained 58% of variation in invasive cheatgrass cover, while a random effect, transect membership, explained an additional 29% of variation (Munson *et al.* 2015). These types of analyses can directly measure the effect of restoration treatments relative to plot and landscape-scale heterogeneity (Laughlin *et al.* 2017). More complicated hierarchical models can include nonlinear effects, account for imperfect measurement, and predict outcomes across time and space (Clark 2007).

While the goal of statistical models is to explain observed data, theoretical models of ecological processes can play a role in scaling up restoration from local sites to landscapes. Conceptual models that describe ecological concepts are common in restoration ecology (Hobbs & Norton 1996; Young, Petersen & Clary 2005; Holl & Aide 2011), but theoretical models for restoration are rarer. For example, recent studies have translated the theories of community assembly and biodiversity effects on ecosystem function into testable models for restoration ecology (Laughlin 2014; Pichancourt *et al.* 2014). In contrast to conceptual models, theoretical models based on mathematical expressions, present assumptions and describe system dynamics in a more concrete and testable manner (Marquet *et al.* 2014). The scarcity of theoretical models to understand restoration is likely a consequence of mathematical barriers, such as the difficulty of analysing transient dynamics, and ecological barriers, such as variable outcomes across studies that obfuscate general patterns. Regardless, theoretical models could allow restoration ecologists to explore how ecological dynamics vary across a wide range of landscape heterogeneity. For example, they can be used to explain why seed limitation could limit tree canopy closure in some landscapes but not others (Caughlin, Elliott & Lichstein 2016). Moreover, theoretical models used to assess ecological resilience can provide land managers with insights to when a site may require future management actions and the mechanisms that may be disrupting the resilience of a system, which can improve the efficacy of management efforts (Angeler *et al.* 2015).

Perhaps the most powerful opportunity for modellers to extend ecological insights over heterogeneous landscapes will be to fit theoretical models representing ecological processes to real data. Size-structured population models are a key example from conservation biology that relate data on individual vital rates (growth, survival and reproduction) to population dynamics, and can be used for prospective analyses, including population viability analysis (Morris & Doak 2002). Developing and applying similar models to the increasingly large body of data on plants and animals of restoration interest would be a productive area for future research. Theoretical models also lend themselves to linking experimental data that can directly inform process but are limited in spatial extent, with observational datasets that are noisier but extend over larger areas (Wilson *et al.* 2015; Larios, Hallett & Suding 2017). Ultimately, fitting theoretical models to data could broaden explanations for variability in restoration outcomes across sites and study systems.

## Conclusions

Realising the full potential of ecological restoration for promoting biodiversity and ecosystem functioning will require advances to the predictability of restoration practice. This major challenge to the science of restoration ecology can be confronted through increased attention to variability among restoration efforts and between restored, unrestored and reference conditions. With this comes the critical realisation that the variability we observe during restoration results from both restoration context (how, where and when restoration is conducted) and how we evaluate restoration outcomes. Future work grappling with these issues through observation, experimental and modelling approaches will help advance toward predictive restoration science.

## Authors' contributions

All authors contributed to the ideas in this manuscript. L.A.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. Author order is alphabetical after the first author.

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## Data accessibility

Data have not been archived because this article does not contain data.

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