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TAKING THE LONG VIEW: INTEGRATING RECORDED, ARCHEOLOGICAL, PALEOECOLOGICAL, AND EVOLUTIONARY DATA INTO ECOLOGICAL RESTORATION

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Historical information spanning different temporal scales (from tens to millions of years) can influence restoration practice by providing ecological context for better understanding of contemporary ecosystems. Ecological history provides clues about the assembly, structure, and dynamic nature of ecosystems, and this information can improve forecasting of how restored systems will respond to changes in climate, disturbance regimes, and other factors. History recorded by humans can be used to generate baselines for assessing changes in ecosystems, communities, and populations over time. Paleoecology pushes these baselines back hundreds, thousands, or even millions of years, offering insights into how past species assemblages have responded to changing disturbance regimes and climate. Furthermore, archeology can be used to reconstruct interactions between humans and their environment for which no documentary records exist. Going back further, phylogenies reveal patterns that emerged from coupled evolutionary-ecological processes over very long timescales. Increasingly, this information can be used to predict the stability, resilience, and functioning of assemblages into the future. We review examples in which recorded, archeological, paleoecological, and evolutionary information has been or could be used to inform goal setting, management, and monitoring for restoration. While we argue that long-view historical ecology has much to offer restoration, there are few examples of restoration projects explicitly incorporating such information or of research that has evaluated the utility of such perspectives in applied management contexts. For these ideas to move from theory into practice, tests performed through research-management partnerships are needed to determine to what degree taking the long view can support achievement of restoration objectives.

Keywords: climate change, ecosystem function, phylogeny, resilience.

Introduction

Ecological restoration is a discipline that is both past and future oriented. Restoration practitioners aim to mitigate past environmental degradation while creating ecosystems that will be stable, resilient, and self-sustaining in the future (Clewell et al. 2004). Even projects that focus on restoring ecosystem function—rather than closely replicating historical communities—can benefit from ecological history that improves understanding of systems' functioning (Millar and Brubaker 2006; Higgs et al. 2014). Furthermore, the utility of history for informing contemporary restoration ecology does not end only centuries ago (e.g., pre-European settlement ecosystems as a New World restoration target) or even with the last glaciation before the Holocene (Egan and Howell 2005). Perspectives that take an even longer view, delving thousands or even millions of years into the past, can be useful in guiding contemporary restoration.

Studying how ecosystems, communities, and populations have responded to past disturbances provides the largest source of information on how they will respond to future changes. In this way, understanding the makeup of past ecosystems and their responses to disturbance can reveal potential future trajectories (history as revealing the future, sensu Higgs et al. 2014; see also Dietl and Flessa 2011; Dietl et al. 2015). Some disturbances impacting modern ecosystems have analogs in the historical ecological record that provide useful direction to contemporary restoration (Swetnam et al. 1999; Millar and Brubaker 2006). Moreover, disturbances that have the potential to incite the largest-magnitude changes—such as phenotypic or distributional changes in response to climate change—unfolded at

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deeper timescales than the tens to hundreds of years commonly considered in identifying restoration targets (Egan and Howell 2005). Working backward from data on community turnover at long timescales and from large disturbances, scientists can identify the factors that conferred resilience to past communities. The composition of these communities and the processes that shaped them can potentially help to design more resilient restored communities today.

We propose that long-view temporal perspectives have a role in restoration planning and design. Reference sites are invaluable for defining restoration goals, but there is additional information to be gleaned from recorded history, archeology, the paleoecological record, and evolutionary history. In some cases, historical ecological data can be a useful complement to contemporary data. In other cases, historical ecological data offer previously unconsidered opportunities for restoration or might even guide restoration in directions that would not be considered on the basis of contemporary data alone. Longer-term historical ecological data can also provide options for restoration objectives when restoration of habitats to a more recent predegradation state is impossible (Cavender-Bares and Cavender 2011; Balaguer et al. 2014). Use of historical data in restoration is not without constraints, such as limits to data availability, the fading historical record, challenges of matching contemporary management activities with targets influenced by ecological history, and previously unseen changes to ecosystems in the Anthropocene. Nonetheless, perspectives from the past may help advance the restoration of functional, resilient systems in the near future.

Historical Timescales and Their Relevance to Restoration

Historical information from different timescales can influence all steps of ecological restoration, from developing restoration goals and garnering public support for restoration to informing ongoing site management and prioritizing restoration efforts. In the following sections, we consider five streams of information: the contemporary landscape, recorded history, archeology, paleoecology, and evolutionary ecology. We describe the types of ecological information that can be garnered from each perspective and how they can inform ecological restoration (table 1; fig. 1). We focus on critical steps in the restoration process, particularly developing restoration objectives, implementing management, performing monitoring, and planning for resilience. In all cases, we stress the role of history as a guide rather than as a stable end point (Higgs et al. 2014). We follow Rick and Lockwood (2013) in using the term "historical ecology" to encompass recorded history, archeology, and paleoecology and also include under that term evolutionary history determined through phylogenies. This view of historical ecology comprises both natural environmental fluctuations and the effects of humans on ecosystems (Rick and Lockwood 2013).

Both historical ecologists and restoration ecologists note the value of integrating historical ecological data in restoration. Many of the 50 priority research questions in paleoecology are directly or indirectly related to restoration ecology, including issues such as invasive species, novel ecosystems, resilience, and climate change (Seddon et al. 2014). Similarly, restoration ecologists discuss the multiple ways history influences restoration ecology (Higgs et al. 2014). Management stakeholders value long-term ecological data, but barriers—such as lack of awareness of historical ecological information and insufficient testing of its applied usefulness—have prevented its adoption in restoration (Davies et al. 2014).

Many reviews stress the importance of ecological history in guiding conservation and restoration. Nonetheless, it appears that few restoration studies and projects use historical ecological data in this way. To illustrate this, we used Web of Science (Thomson Reuters 2015) to query titles, abstracts, and keywords for articles in the applied restoration journal *Restoration Ecology* (from 1998 to 2014) for terms relating to the temporal scales reviewed here. A search for "histor*" returned 216 articles, but "anthropol*" and "phylo*" returned none, "paleo*" four, and "evol*" 29. We thus extend our review to include examples from the historical ecological literature that do not address restoration specifically but have applied implications that could be used to guide restoration projects. The examples mostly, though not exclusively, deal with plant communities and are disproportionately from North America.

We argue that historical ecology is underutilized as a guide for restoration. Few published studies use historical ecological data to inform restoration, and those that do tend to be relatively recent in scope, for example, tracking tens or hundreds of years into the past (Egan and Howell 2005). However, it may be possible to use knowledge of events that occurred much deeper in time—even millions of years ago—to influence contemporary restoration practice.

Sources of Historical Information

Information from a variety of contemporary, recorded historical, archaeological, and paleoecological sources can be useful in determining goals for restoration, managing restored ecosystems, and predicting ecosystem resilience (fig. 1). Sources of information about past ecosystems include analysis of contemporary sites, historical and archaeological artifacts left by humans, plant and animal remains, and physical and chemical data (table 1).

Contemporary sites contain clues to their own histories in terms of soil properties, species composition, and other factors. Comparisons among multiple sites show the range of variability over space and can be used to infer factors driving community structure and change. Historical sources add another dimension of information, allowing for comparisons of conditions over multiple time points. Using paleoecological and evolutionary information can reveal the imprint of historical processes on modern ecosystems. Delving into the history of how contemporary sites developed can enhance the utility of these sites for guiding restoration.

Contemporary Sites

Contemporary ecosystems contain evidence of the short- and long-term historical processes that influenced them, but signs of these processes are not always clear or easy to disentangle. Information of use to restoration managers can be gathered from the specific site(s) to be restored as well as contemporary reference sites (i.e., relatively undisturbed extant sites; White and Walker 1997; Schaefer and Tillmanns 2015). Data

Table 1

Restoration Questions That Could Be Addressed by Data from Different Temporal Scales

Restoration stage	Contemporary sites	Recorded history	Archeological/ paleoecological	Evolutionary
Goal setting:				
Habitat type	What is the habitat like in a reference site? What is the successional stage relative to restoration goals?	What was the habitat like in the recent past?	What was the range of past habitat types in the area? What factors drove habitat shifts? Was human activity influential?	
Species selection	What species are found in reference sites? Is it feasible to replicate these assemblages in restored sites?	What was the species composition in the recent past? Is it feasible to replicate these assemblages in restored sites?	What taxa and/or communities were most common and/or most stable in the past?	What is the desired level of phylogenetic diversity for restored communities?
Identifying constraints to restoration	What factors limit restoration effectiveness? Are they present in reference sites?	Does past human use and/or disturbance limit options for restoration?	Where do current conditions fit within the historic range of variability?	Can evolutionary theory guide restoration in the absence of complete ecological information?
Management:				
Invasive species	Are invasive species present in reference sites? How should they be managed?	When did invasive species arrive? Was their arrival associated with changes in community composition?	When did invasive species arrive in the area? Did they alter ecological dynamics?	How closely related is the invader to the resident community?
Disturbance	What disturbance regime is required to maintain reference sites? Is the reference disturbance regime feasible to implement in restored sites?	What was the level of disturbance in the recent past? How did humans influence the disturbance regime?	What were historic levels of disturbance? How variable was the disturbance regime over time? Did humans influence the frequency or intensity of disturbance?	How does disturbance alter community phylogenetic structure? Is there a relationship between phylogenetic and trait diversity? Is disturbance limiting the types of species that can persist in restored sites?
Monitoring	Are conditions at the restored site similar to those at the reference site in terms of diversity, composition, and functioning?	Are conditions in the restored site similar to those of the recent past?	Does the restored site have analogs in past communities and habitats?	Is community phylogenetic structure changing over time and with management? Is contemporary evolution influencing ecological outcomes?

from the site to be restored can be used to identify disturbances or constraints that might interfere with meeting restoration objectives. Clues in the site to be restored can also reveal past history. For example, decayed stumps have been used to recreate logging history (Marks and Gardescu 2005), which can influence restoration decisions, for example, focusing on reintroducing species sensitive to logging.

Contemporary reference sites provide information on environmental conditions, community composition, and ecosystem functions at sites similar to those being restored that have not been subjected to the same degradation (White and Walker 1997). Restoration practitioners can also evaluate what management actions may be necessary to maintain sites in the target (reference) state and expect similar management to be necessary at the restored site, even at later stages of the restoration. Further, reference sites can continue to influence restoration decisions by serving as baselines of comparison for monitoring the development of restored sites. Despite the importance of reference sites and large literature advocating their use, less than half of contemporary restoration projects use reference sites as a guide (Wortley et al. 2013).

A limitation of using contemporary reference sites is that they may be only a small or unrepresentative remnant of the original system because of the effects of habitat loss, fragmentation, and other disturbances (White and Walker 1997). High-quality reference sites may no longer exist; those that do are subject to shifting baselines, that is, reference systems themselves may have undergone significant changes relative to the past (Pauly 1995; Rick and Lockwood 2013). Furthermore, dynamics of long-lived species may not be detectable when using only contemporary information (Davies and Bunting 2010). When available, other sources of historical ecological information can be used to place extant reference sites in a broader context.

Recorded History

Recorded history is information directly documented by humans, such as species lists, written descriptions from journals or travelogues, oral histories, drawings, photographs, and maps. Historical records can provide information on species assemblages and ecosystem structure (e.g., canopy openness). These

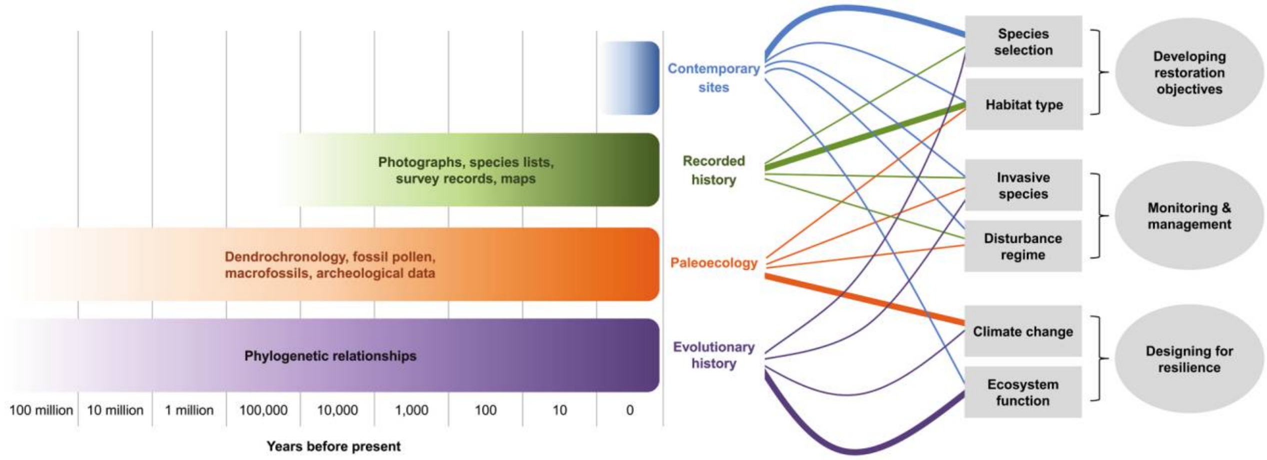

Fig. 1 Historical timescales and their potential contributions to ecological restoration. Thick lines indicate the main use of each type of data currently. Thin lines indicate additional uses (or potential uses) of historical information in informing restoration.

sources of information provide baselines for assessing community change over time and have frequently been used to establish restoration objectives (Radeloff et al. 1999; Swetnam et al. 1999; Bolliger et al. 2004).

Archaeology

Archaeology can clarify restoration objectives and inform management activities by shedding light on past human impacts to communities. Humans have managed ecosystems for thousands of years through actions such as prescribed burning, agriculture, and harvesting and transport of plant and animal species—even in areas earlier thought to be pristine and free of human impact (Hayashida 2005; Alagona et al. 2012; Rick and Lockwood 2013). Past human settlement can have legacy impacts on ecosystem properties that last for centuries (Hejcman et al. 2013). Past human activity can also constrain the possible trajectories of ecosystems, even with restoration interventions (Higgs et al. 2014). Therefore, knowledge of past human impacts is important for developing feasible restoration goals (Foster et al. 2003) and separating anthropogenic effects from longer-term natural cycles (Swetnam et al. 1999; Millar and Brubaker 2006).

Paleoecology

Paleoecological data can complement perspectives from recorded history and archeology and extend beyond those sources of information into the distant past, to a time before both human records and humans. Analysis of dendrochronology (tree rings), preserved biological remains, and isotopic/biochemical compounds (Hayashida 2005; Dietl et al. 2015) can reveal past community trajectories, species invasions, extinctions, and community responses to changes in climate and disturbance regimes.

Evolutionary History

A phylogenetically informed approach to restoration would use the evolutionary history of species to shape management of contemporary communities. Greater phylogenetic diversity of plant communities—species being drawn more broadly from across the tree of life—is associated with increased ecosystem function (Srivastava et al. 2012). The link between phylogenetic diversity and ecosystem function is based on niche conservatism, the idea that closely related species share similar functional traits and thus similar ecological niches (Wiens and Graham 2005). In this way, maximizing the evolutionary distance between co-occurring species can increase niche breadth. In some cases, phylogenetic diversity is even more strongly related to ecosystem function than functional diversity, because it accounts for ecologically important but unmeasured latent traits not captured by measured traits (Cadotte et al. 2009; Pearse and Hipp 2009; Díaz et al. 2013). Because of the close relationship between phylogenetic diversity and ecosystem function, phylogenetics can be a useful tool in restoration, influencing objectives, management, and monitoring (Hipp et al. 2015).

Limitations

All of these approaches are subject to data limitations, including a fading record through time, poor spatial and/or temporal resolution, limited taxonomic resolution, and inconsistent preservation. Recorded data can be subjective, ambiguous, or inconsistent because of social norms and values dictating what types of information on which species were recorded and preserved (Edmonds 2005; Lucia et al. 2008; Alagona et al. 2012). Records from the Public Land Survey (PLS) have become a standard, valuable resource for restoration ecologists in the United States, but even this rich data set represents only a snapshot of past communities (Shea et al. 2014) and is subject to surveyor bias and taxonomic uncertainty (Schulte and Mladenoff 2005). Similarly, pollen data are valuable for reconstructing past plant communities but are limited in taxonomic resolution and constrained by variability in pollen output and preservation (Peters 2010). For example, grasses, which are extremely important in many restorations, cannot be identified beyond family using pollen (Davis 2005). There are also several limitations to the use of phylogenetic data in restoration ecology. The relevance of phylogenetics for restoration has rarely been tested (but see Cavender-Bares and Cavender 2011; Verdú et al. 2012; Whitfield et al. 2014), and concepts and tools of phylogenetic ecology are relatively new and not widely known (Hipp et al. 2015).

Understanding methodological limitations and integrating data from multiple sources can help researchers interpret past conditions (Lucia et al. 2008; Whipple et al. 2011). Of course, historical data are relevant to restoration practitioners only when they are available and accessible (Davies and Bunting 2010; Brewer et al. 2012; Davies et al. 2014; Gillson and Marchant 2014). Collaborations between restoration scientists/practitioners and researchers in historical ecology can help address these limitations. For example, paleoecological data are becoming more widely available to nonexperts through the development of databases (Brewer et al. 2012).

Uses of Historical Information in Restoration

Where it is available, historical ecological information is commonly used to establish reference points for restoration; this is particularly true for determining pre-European settlement conditions in North America. For projects where explicit reference sites are lacking, historical information can still be used to select native species and habitat types. More recently, paleoecological and archaeological studies have been used to elucidate a longer-term context for pre-European conditions. These studies have allowed restoration ecologists to consider historic ranges of variation rather than static time points when developing restoration goals and management strategies (Asbjornsen et al. 2005; Keane et al. 2009). Finally, as restoration ecologists increasingly plan for novel climatic conditions and human influences, they can look to the past to understand factors that impart resilience to communities and ecosystems.

Setting Restoration Objectives

Historical ecological information can be used to develop support for restoration activities by documenting habitat destruction. In prairies, recorded history tracks the rapid decline in habitat area. Studying maps, Iverson (1988) documented loss of prairie area from 59% of Illinois in 1820 to approximately 0.01% in 1980, primarily as a result of agriculture. Such clear documentation of drastic declines in habitat area can help the public understand the need for restoration and be used to prioritize locations for restoration. Hessburg et al. (1999) used historic maps from the Cascade Mountains in Washington from 1938 to 1956, along with remote sensing, to identify forest patches in need of restoration and create a tool for restoration mangers to prioritize their efforts.

In contrast, historical ecological data can also be used to identify issues that are not of immediate concern for restoration. For example, Watson et al. (2011) used a combination of cultural and paleoecological sources to document habitat changes in the Elkhorn Slough estuary in California. Aerial photographs and historical maps indicated major declines in marsh area leading to concerns about marsh degradation. However, when the authors analyzed paleoecological data to reconstruct changes in salinity, sedimentation rates, and plant communities over the past 5000 yr, they found that some of the recently degraded marshes were products of anthropogenic sedimentation and that there is actually now more marsh area than there had been for most of the past. Given this and the fact that newer marshes could be difficult to sustain, they concluded that it may be wise to direct restoration efforts to other concerns rather than continue to protect marshes in this location.

In addition to prioritizing restoration effort, historical ecological information can also be used to identify constraints to restoration and modify project objectives accordingly. If it is impossible to restore habitats to a recent predisturbance state, there may be earlier conditions that can be identified as suitable alternatives. For example, it would have been impossible to restore Spanish sand quarries to the hills they were before mining, and such landscapes would have been unstable. However, Balaguer et al. (2014) identified a geomorphological reference of a cultural habitat from 1000 yr ago as a feasible target for restoration activity.

Species Selection

Restoration managers may be interested in restoring a particular past community, understanding the range of variability of past communities, or identifying stable communities to inform species selection for restoration. General Land Office/PLS records, which date to the late 1700s in the eastern United States, provide spatially broad community data for much of the country (Whipple et al. 2011; Shea et al. 2014). Shea et al. (2014) used PLS records from the mid-1800s to reconstruct tree communities for the Driftless Area of the Midwestern United States. Using data representing more than 100,000 trees, the authors found that oaks were dominant and savanna was the most common habitat type. The authors created a map of past tree communities paired with environmental data, such as topography and soil characteristics, to inform restoration.

Data from multiple time points can be used to show the range of conditions over long time periods and provide a historical context for more recent conditions. For example, pollen analysis of sediments from 13 lakes on a 450-km^2 sand plain in northwestern Wisconsin was used to place the vegetation patterns recorded by the PLS during the 1850s and 1860s (Radeloff et al. 1999) into a historical context (Hotchkiss et al. 2007; Tweiten et al. 2015). Maps showing current and reconstructed vegetation communities at 100-yr intervals over the past 1200 yr (fig. 2) revealed that the mixed pine and oak communities recorded by the PLS developed relatively recently. White pine pollen became more common and the influx of charcoal from forest fires decreased with the onset of Little Ice Age climatic conditions (Hotchikss et al. 2007; Tweiten et al. 2015). These results demonstrate the transient nature of plant communities and suggest that conditions indicated in the PLS may not be an ideal restoration target (Hotchkiss et al. 2007), particularly given that Little Ice Age climatic conditions are not representative of current or future climatic conditions in this region. The longer paleoecological record provides an important perspective on the natural range of variability in this landscape that can be used to define more sustainable restoration goals.

In ecosystems that were rapidly transformed by humans before natural communities could be described, evidence from the paleoecological record can be particularly valuable. For ex-

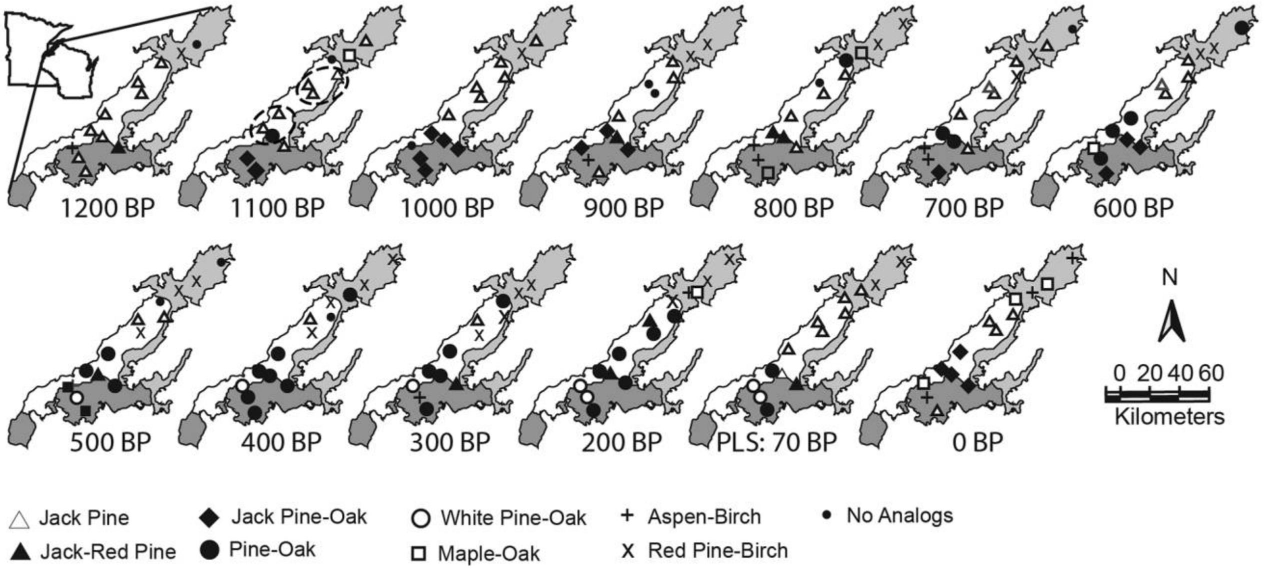

Fig. 2 Inset map (top left) shows the location of the northwestern Wisconsin sand plain. Maps show vegetation changes at 100-yr intervals over the past 1200 yr (BP = years before present, where present is 1950 AD). Symbols indicate the vegetation community represented by pollen at each site over time. Dashed lines in 1100 BP map indicate sites surrounded by coarse sandy soil and few fire breaks (northern) and abundant fire breaks (south). Shading indicates three vegetation regions described from Public Land Survey data (Radeloff et al. 1999); white indicates jack pine forests and barrens, light gray indicates closed-canopy mixed pine forests, and dark gray indicates oak and pine savannas. Updated from Hotchkiss et al. (2007) using sites from Tweiten et al. (2015).

ample, on San Cristóbal Island in the Galápagos, cattle destroyed the vegetation in the 1930s, while the first formal descriptions of the vegetation were not completed until the 1960s. Several native plant taxa were not included in restoration efforts because they had largely been extirpated before being documented (Bush et al. 2014). Managers have been removing exotic plant species and planting *Miconia robinsiniana*, an endemic shrub species. But pollen and sediment records document several other taxa that were abundant during the past 10,000 yr. Bush et al. (2014) suggest that these species should be included in restoration efforts to better reflect historic composition and possibly increase the resilience of restored vegetation.

Phylogenetic ecology can also be used to guide species selection for restoration. In ongoing work, we have found initial evidence that restored prairies in northeastern Illinois are less phylogenetically diverse than remnant prairies (W. Sluis, M. L. Bowles, M. D. Jones, and R. S. Barak, unpublished data). This appears to be driven by higher relative abundance of species from certain families in restored sites and the absence of species representing families that are rare but present in reference sites. Restoration seed mixes could be adjusted accordingly to approximate the phylogenetic diversity of prairie remnants, perhaps helping to increase their functional equivalency with reference sites (sensu Zedler and Callaway 2000).

Niche evolution may also influence the design of communities for restoration. Species with contrasting alpha niches (local niches at the scale at which species interact with one another) would be appropriate to plant together in a restoration. These species may have reduced competition due to differences in traits (Silvertown et al. 2006; Chesson 2014). For example, shallow- and deep-rooting species may be better able to coexist. On the other hand, it is likely to be beneficial for species used in restoration to have similar beta and gamma niches (habitat and geographical-range niches, respectively), since they would overlap in edaphic and/or climatic requirements. For example, wetland species share suites of traits that enable them to survive in waterlogged soils. Cavender-Bares and Cavender (2011) describe oak communities in Florida where closely related oak species did not co-occur at the site (alpha) level, though there were many closely related oak species present within habitats (beta) over the region (gamma). Replicating such patterns when they occur in reference communities may be important in selecting species for restoration.

Monitoring and Management

Invasive Species

While it is not difficult to observe and document the introduction and spread of recent invasive species, it is not always clear when a species invaded a site or what its impact has been (Hotchkiss and Juvik 1999; Lynch and Saltonstall 2002; Coffey et al. 2010). Fossil pollen data were used to support the exotic status of *Phalaris arundinacea* on Vancouver Island, British Columbia, Canada. Grass pollen was found in high concentrations only in upper (recent) layers of sediment in wetlands, not in the high-diversity native wetlands captured earlier in the record. It was thus inferred that nonnative *P. arundinacea* colonized only recently and should be controlled to manage for high plant diversity (Townsend and Hebda 2013). In contrast, paleoecological and genetic analyses from sediments of a Lake Superior wetland provide evidence that native genotypes of *Phragmites australis* have undergone recent, rapid expansion (Lynch and Saltonstall 2002).

Looking further back into the paleoecological record in Hawaii, it was found that native palms in the genus *Pritchardia* disappeared from the record around the time of rat introductions. This led to the recommendation that contemporary practitioners control rats as part of palm restoration efforts (Burney and Burney 2007). In contrast, fossil pollen data were used to demonstrate that several species thought to be invasive—on the basis of modern observations of their adaptation to disturbance (the fern *Dicranopteris linearis*) or widespread distribution and aggressive behavior (the moss *Sphagnum palustre*)—were in fact native to Hawaii (Hotchkiss and Juvik 1999; Karlin et al. 2012).

Disturbance Regime

In many ecosystems, the structure and composition of vegetation as well as nutrient cycling are influenced by the frequency, intensity, and magnitude of fires, wind storms, extreme droughts, floods, or insect outbreaks. To be effective, restoration projects may need to replicate or mimic natural disturbance regimes (McLauchlan et al. 2014). Where there are long-lived trees, fire-scar records have provided valuable information about the nature of fire regimes and their variation over time (Heinselman 1973; Swetnam et al. 1999; Guyette et al. 2006). Such information is relevant to restoration managers, since reinstating a historical fire regime could aid recovery of biological diversity and ecosystem function (Bergeron et al 2004).

Where dendroecological records are lacking, charcoal preserved in lake sediments can provide information about past fire regimes (Gavin et al. 2007; Higuera et al. 2009; Lynch et al. 2010). While these records typically lack the fine temporal and spatial resolution of tree-ring records, they offer the potential to examine how disturbance regimes were affected by major changes in climate and/or vegetation that occurred beyond the range of tree ring records. This long-term perspective is useful in predicting how resilient communities will be to future climatic changes (Lynch et al. 2014).

In the Garry Oak savanna of Vancouver Island, British Columbia, Canada, anthropological and paleoecological evidence (dendrochronological, fossil pollen, and charcoal data) was used to determine that the savanna's open structure was maintained by burning by indigenous peoples (McCune et al. 2013). The savanna persisted even in climatic periods that would favor closed woodlands (McCune et al. 2013). This finding provides an interesting decision point for modern restoration: should savanna structure be maintained as a cultural landscape, or should forest closure be allowed? The decision on whether to maintain past anthropogenic levels of disturbance may depend on the resources needed to maintain them and the values placed on these cultural landscapes by stakeholders (Motzkin and Foster 2002; Dunwiddie 2005).

Grazing is another source of past and contemporary disturbance that may be relevant to restoration managers. Campbell et al. (2010) found that arid rangeland grazed earlier in the season (i.e., winter-spring grazing) was phylogenetically and functionally more similar to ungrazed sites than those grazed later in the season. Grazing was also found to affect plant biodiversity over a 400-yr time span in Scottish upland sites. Hanley et al. (2008) used fossil pollen data to uncover past plant communities and livestock prices to determine past grazing pressures. Findings such as these can guide the intensity and timing of grazing and other disturbances, when they are compatible with management objectives at restored sites.

Monitoring Ecosystem Changes

Phylogenetic ecology could be used to monitor ecological change in restored sites and help predict future trajectories. In vulnerable communities, it may be important to assess whether phylogenetic diversity is declining and whether species' vulnerability to extirpation is phylogenetically autocorrelated. For example, in fragmented tropical forests of Mexico, while species richness declined, phylogenetic diversity did not, indicating low phylogenetic conservatism of traits associated with vulnerability to forest fragmentation (Arroyo-Rodríguez et al. 2012). In this case, ecosystem function and stability may thus be maintained, despite the loss of tree species. In contrast, if vulnerability is a phylogenetically conserved emergent property of species, then certain disturbances could cleave entire branches from communities' evolutionary trees, likely reducing ecosystem function (Díaz et al. 2013). If continued monitoring reveals a decrease in phylogenetic diversity over time, additional management may be needed to restore phylogenetic diversity.

Further, restoration ecologists may be able to monitor restored sites using the relationship between a community's evolutionary structure and its trait similarity, linking species' ecology today with their evolutionary history (Pearse et al. 2015). Figure 3 shows hypothetical relationships between similarity of traits among co-occurring species (horizontal axis, ecologically similar vs. dissimilar) and the mode of evolution of those traits (vertical axis). In this case, traits that are similar in co-occurring species show evidence of convergent evolution (bottom left), while traits that are dissimilar show evidence of constrained (conserved) evolution (top left). These relationships (termed fingerprint regressions; Pearse et al. 2015) could be used in restoration planning, for instance, in seed mix design and setting compositional targets. Such relationships could also be used to monitor changes in restored communities over time. Managers could assess whether the relationship between evolutionary and ecological processes found in functional reference systems is preserved in restored systems. Perhaps by matching these patterns, managers could increase the likelihood of the restored system being functionally equivalent to reference sites and resilient to future changes.

Using the Past to Restore for Future Resilience: Climate Change and Ecosystem Function

Restorations can be explicitly planned for the future while also being informed by ecological history. Alagona et al. (2012, p. 65) suggested that "the past may be imperfect as a model for

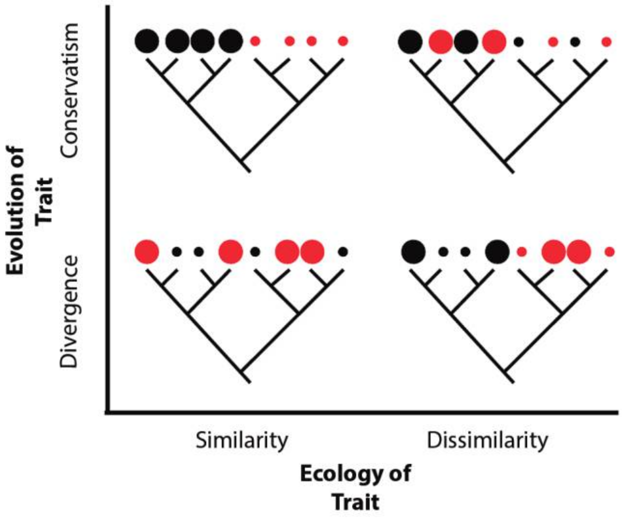

Fig. 3 Conceptual framework for the placement of traits according to their ecological and evolutionary structure. Based on figure 3*B* of Cavender-Bares et al. (2006) and termed a fingerprint regression by Pearse et al. 2015. In each quadrant of the space, a phylogeny is plotted with a trait (represented by the size of the circles) and likelihood of species coexisting represented by the color of the circles (one community shown in red and another in black). Fingerprint regressions could be used to develop restoration goals based on reference communities from the present or the past as well as to monitor changes in the biodiversity of restored communities over time.

the future, but it is an indispensable guide for understanding a world in flux." Perspectives from historical ecology can inform the restoration of communities and ecosystems that will be resilient and functional in the face of future change.

Climate Change

Looking at the past is the best way to predict the effects of climate change on communities and ecosystems (Jackson 2007). Many North American plant species originated 20–40 million years ago and have thus been exposed to numerous periods of warming and cooling over that time period (Millar and Brubaker 2006). Understanding the trajectories of species and communities over past climate changes can help inform design and implementation of modern restorations. Paleoecological and evolutionary data—combined with modeling—allow for the reconstruction of past responses to climate change and can help contemporary restorationists plan for the future.

Paleoclimate reconstructions paired with paleoecological data expand the range of conditions that supply perspective to restoration efforts. The paleoecological record contains examples of community stability over thousands of years, despite climate change (Brubaker 1975; Minckley et al. 2011), as well as sometimes dramatic and rapid community changes in response to climate change (Grimm 1983; Umbanhowar 2004). There are also no-analog pollen records from the past during the late glacial periods of the Quaternary, from 17,000 to 12,000 yr ago (Williams and Jackson 2007). These communities contained species that still exist today but are no longer found together in ecological communities (Williams and Jackson 2007). Such communities also existed much more distantly in the past, for example, during the Paleocene-Eocene Thermal Maximum (PETM), a period of intense climatic change ca. 55.8 million years ago that is used as an analog for today's anthropogenic climate change, since warming during the PETM was also caused by elevated carbon dioxide emissions (Dietl and Flessa 2011; McInerney and Wing 2011). Studying plant macrofossils from before, during, and after the PETM, Wing and Currano (2013) determined that plant community composition during the PETM is distinct from that before or after. This reflects migration rather than extinction, since missing species reappeared in the fossil record following the PETM. That there was little evidence of mass extinctions during the warming of the PETM may provide some comfort to restoration ecologists today. However, it is unclear to what extent current warming will mirror that of the PETM, especially as contemporary rises in carbon dioxide emissions are occurring at much faster rates than during the PETM (McInereny and Wing 2011).

Most pollen-based vegetation reconstructions do not provide the spatial resolution necessary to reconstruct the heterogeneity of vegetation at the scale of landscapes. However, as more data from closely spaced sites with similar climate but differences in soils and topography are collected, it is becoming possible to reconstruct landscape-scale vegetation patterns. In North America, there are several regions with a dense grid of sites, including the upper Midwest (Umbanhowar 2004; Nelson and Hu 2008; Lynch et al. 2014) and New England (Foster et al. 2006; Oswald et al. 2007, 2011). Data from networks of sites are particularly useful for understanding which parts of a landscape are most resilient and which are more likely to undergo state shifts in response to climatic changes (Ireland et al. 2012; Lynch et al. 2014; Tweiten et al. 2015).

Paleoecological and phylogeographic data, along with species distribution modeling, are being used to determine the locations of past climate refugia—areas where species survived periods of intense climate change—and to predict the locations of future refugia (Gavin et al. 2014). Management can be prioritized to conserve and/or restore these areas in preparation for further change (Millar et al. 2007; Shoo et al. 2013). Similarly, phylogenetic data can be used to determine species that are likely to be vulnerable to climate change. Willis et al. (2008) studied the phylogenetic signal of changes in species' abundance and flowering time after 150 yr, using data initially collected by Henry David Thoreau in Concord, Massachusetts. They found that lineages with flowering times that did not track with climate change were declining and in danger of local extirpation. Thus, phylogeny, along with historical data, could be used to identify vulnerable species that would be unlikely to adapt (through evolution or plasticity) to changing climates and prioritize those species for interventions, such as assisted migration (Vitt et al. 2010).

Historical and modeling data can also be used to identify locations for establishing neonative communities, defined as restoring species to an area where they were found in the past but do not currently occur (Millar et al. 2007). On a shorter timescale, dendrochronology in combination with climate projections can be used to identify the tree species and communities most vulnerable to changing climates (Williams et al. 2010).

Fulé (2008) recommends focusing management on forest habitats that are likely to persist through climate change—such as higher-latitude, higher-elevation sites—and using both historical and predicted climate data to engineer forests in areas where they are likely to persist in future climates.

Restoration practitioners may be able to use evolutionary theory to develop restored communities with greater potential to adapt in the face of future change (Sgrò et al. 2011). Both inter- and intraspecific genetic variation are thought to maximize evolutionary potential in restoration seed mixes (Broadhurst et al. 2008; Kettenring et al. 2014). Furthermore, increasing evolutionary potential may be accomplished by maximizing phylogenetic diversity of restored sites (Forest et al. 2007; Rosauer and Mooers 2013). Building corridors between fragmented sites is also thought to increase evolutionary potential by allowing for increased gene flow between populations (Sgrò et al. 2011; Haddad et al. 2014). In addition, conserving centers of endemism—areas of high historical evolutionary diversification—may be important for preserving evolutionary potential in the face of an uncertain future (Jetz et al. 2004).

Several of these ideas, including climate refugia and corridors, are tied into the concept of conserving nature's stage. This strategy focuses on conserving geological diversity (geodiversity) as a surrogate for biological diversity (Beier et al. 2015). Geodiversity is strongly tied to biological diversity, and conservation of geodiversity may help to mitigate species losses due to climate change (Gill et al. 2015; Lawler et al. 2015). Ensuring that restoration areas include geomorphic heterogeneity may be one way to prepare for a changing climate. Appropriate species (the actors on the stage) may be added as climates change (Comer et al. 2015). Conserving the stage will create diverse habitats for evolution in future climate regimes (Lawler et al. 2015).

Ecosystem Function

Sediment records are well suited for measuring changes in ecosystem processes in aquatic environments (Willard and Cronin 2007). Multiproxy approaches—including diatoms, magnetic susceptibility, biogenic silica, organic content, and nutrient fluxes to sediments—have been used to measure modern impacts of agriculture and the eutrophication of lakes and rivers (Edlund et al. 2009*a*; Engstrom et al. 2009) and then been applied to restoration goal setting (Edlund et al. 2009*b*).

Isotopic data are also widely used. For instance, Callaway et al. (2007, 2012) used radioisotopes to infer sedimentation rates in reference California coastal wetlands and determined that sediment accretion is currently keeping pace with sea level rise. This information can be used to set restoration targets for sediment accretion in restored sites so that restored wetlands can remain functional (tidal) in the face of predicted change. Also, these radioisotope data can be used to estimate the rate of carbon sequestration in wetlands, which is useful for restoration planning pertaining to climate change mitigation goals (Callaway et al. 2012).

Stable isotopes can be used to elucidate other ecosystem processes and potential restoration impacts as well. For example, stable isotopes from archeological middens have been used to identify changes in productivity and trophic status of various marine species in the Pacific Northwest over 4500 yr (Misarti et al. 2009), and ratios of nitrogen (N) stable isotopes in lake sediments have been used to estimate the abundance of migrating salmon in Alaska over the past 300 yr and changes imparted by commercial fishing and dam building (Finney et al. 2000). These data document the large-scale movement of N from the ocean to inland, oligotrophic lakes. In addition to providing baseline data to help establish restoration goals, it helps modern restoration workers to predict ecosystem effects of salmon restoration.

It is relatively more difficult to infer how terrestrial ecosystems functioned in the past. However, as collaborations between restoration practitioners and historical ecologists become more common, approaches for addressing past terrestrial ecosystem functioning are emerging (Dunnette et al. 2014; McLauchlan et al. 2014). Efforts are underway to integrate paleoecological data with ecosystem modeling to facilitate modeling of future ecosystems (PalEON 2015). These results will also be relevant to restoration ecologists.

The connections between key ecosystem functions and phylogenetic diversity may be the strongest argument for the use of phylogenetic information in restoration ecology. For example, more phylogenetically diverse plant communities are more productive and stable (Cadotte et al. 2008, 2012). In a plot experiment, Cadotte (2013) found an increase in primary productivity of 12 g/m^2 of biomass for every additional 5 million years of evolutionary history encompassed by an assemblage. Greater phylogenetic diversity of resident communities is also associated with reduced invasion by nonnative species (Davies et al. 2011; Li et al. 2015). In addition, greater facilitation was found between more distantly related co-occurring species used in arid lands restoration (Verdú et al. 2012). Plant phylogenetic diversity was also associated with greater productivity of soil microbes in gypsum ecosystems (Navarro-Cano et al. 2014). Productivity, stability, facilitation, invasion resistance—these are all factors that may enhance the achievement of restoration objectives (Rowe 2010; Wortley et al. 2013).

Phylogenetic diversity of plant communities is also associated with greater biodiversity support at higher trophic levels. In strip-mined lands restored to prairie in southern Ohio, butterfly species diversity increased with plant phylogenetic diversity (Cavender-Bares and Cavender 2011). Similar effects on higher trophic levels were seen in experimental manipulations of plant phylogenetic diversity, with phylogenetic diversity of plants predicting arthropod richness and abundance (Dinnage et al. 2012) and phylogenetic diversity (Lind et al. 2015). Conversely, phylogenetic diversity of insects may benefit plants. Increased phylogenetic diversity in pollinator communities reduced rates of self-pollination in the plant *Plectritis congesta* (Adderley and Vamosi 2015). This could help limit reductions in plant genetic diversity associated with habitat fragmentation.

Each of these approaches to planning resilient and functional restorations in the face of rapidly changing climates combines the ancient with the novel. A novel ecosystem is defined as one that cannot be returned to its historical trajectory and therefore can contribute better to landscape conservation and restoration if it is managed to provide ecosystem services (Hobbs et al. 2014). Using the approaches described above (e.g., designing species mixes with high phylogenetic diversity), restoration can be guided by ecological history, even in novel situations where objectives center on provision of ecosystem services (Willis et al. 2010; Cavender-Bares and Cavender 2011).

Just as it is worthwhile to use a range of spatial references in developing restoration targets and conceptual models for how restored ecosystems develop and respond to change, it is also worthwhile to use a range of historical conditions, especially given an uncertain future. Jackson and Hobbs (2009, p. 568) suggest that "restoration efforts might aim for mosaics of historic and engineered ecosystems, ensuring that if some ecosystems collapse, other functioning ecosystems will remain to build on." The historic ecosystems may also be a patchwork, with different restorations being informed by different slices of history and different approaches to historically informed restoration. This approach would support ongoing learning and adaptability of restoration as restoration approaches that are informed by ecological history are tested in a changing future (Millar et al. 2007).

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