
ANNUAL MEETING

Review of ESA SYMP 7: A Dynamic Perspective on Ecosystem Restoration—Establishing Temporal Connectivity at the Intersection Between Paleoecology and Restoration Ecology

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Landscape connectivity is vital not only spatially, but also temporally; as ecosystems change, it is important to be aware of past, present, and future variables that may impact ecosystem function and biodiversity. As climate and environments continue to change, choosing appropriate restoration targets is becoming more challenging. By considering the paleoecological and paleoenvironmental record

for a given region, restoration practitioners are not only able to bear witness to that region's dynamic history, but also potentially identify multiple, alternative natural ecosystem states. Indeed, one of the deliverables of conservation paleobiology, a field that applies paleontological data and methods to present-day conservation, is to inform restoration targets. Consideration of future change is equally important, and paleoecological and paleoclimatological data are essential for informing models that can help us understand how climate change is affecting species and ecosystems at different temporal scales. The symposium "A dynamic perspective on ecosystem restoration: Establishing temporal connectivity at the intersection between paleoecology and restoration ecology" gathered representatives from macroecology, paleoecology, and restoration ecology to share their perspectives on temporal connectivity and how consideration of an ecosystem's past, present, and future can positively impact restoration and conservation. Some speakers approached the topic theoretically, while others considered it from a more practical and applied standpoint. The goals of the symposium were to build a stronger relationship among the subdisciplines, stimulate new ideas, and identify data and/or products that would be useful to share across subdisciplines.

Jenny McGuire from the Georgia Institute of Technology opened the symposium by presenting results from her work that aims to inform the creation of dynamic landscapes that will allow for plants and animals to adapt to rapidly changing climate. She does this by integrating spatial ecology with Quaternary fossil occurrences. Using pollen records spanning the last 20,000 years, she first addressed the question of how long plant biomes tend to persist and how long it takes for them to recover following a state change. Plant biomes had a median residence time of 300 years, but notably, residence times were shorter when rates of temperature change were larger (Wang et al. 2020). Moreover, it took longer for biomes to recover when rates of temperature change were the highest, and biomes were unable to recover at all 35% of the time (Wang et al. 2020). These results suggest that plant biomes have shifted quickly in the past during periods of rapid climate change and will likely do so in the future. But, to what extent will plants and animals be able to track changing climates in a human-impacted landscape? To address this second question, McGuire considered the climate connectivity of natural land areas and found that, given projected climate change, organisms living in just 41% of natural patches will be able to track changing climate through adjacent natural land areas (McGuire et al. 2016). However, by allowing organisms to move along climate gradient corridors and traverse through human-impacted areas, 65% of natural areas achieve climate connectivity (McGuire et al. 2016). These results suggest that organisms that have difficulty moving across human-impacted areas will have a harder time tracking changing climates, leading to the final question considered, which species are most impeded by a human-impacted landscape? Drawing on fossil mammal data, McGuire and colleagues interrogated the degree to which mammalian climate niches have shifted over the last 12,000 years (Pineda-Munoz et al. 2021). Notably, mammalian niches have shifted by 65% from postglacial times to the present and their realized niches today do not approximate their earlier niches. Furthermore, mammals are differentially able to tolerate human impacts; many small-bodied mammals are expanding their climatic niches into regions of high human impact while many large-bodied taxa are contracting their niches. It will become important, therefore, to prioritize connectivity for those animals that have lower tolerance for humans. Together, these studies demonstrate that fossil data are not only informative but also necessary for contextualizing present-day conditions and planning for the future.

Next, Jens-Christian Svenning of Aarhus University combined macroecological and paleoecological perspectives to examine the effects of large herbivores on ecosystems and make

recommendations for conservation and restoration. Large herbivores have significant effects on vegetation; more intact, diverse herbivore assemblages promote vegetation heterogeneity, which is a key driver of biodiversity at local scales (Bakker et al. 2016, Pausas and Bond 2019), which is a key driver of biodiversity across spatial scales (e.g., Stein et al. 2014). Furthermore, in intact ecosystems, the largest herbivores are typically not top-down controlled (Hopcraft et al. 2010). From a paleoecological perspective, we know that rich faunas of large herbivores were the standard for about the last 30 million years, but this changed abruptly with the expansion of early modern humans (e.g., Sandom et al. 2014, Smith et al. 2018). This faunal down-sizing has had consequences. For one, based on a recent analysis of empirical data, Svenning showed that regions that have experienced lower levels of past megafaunal extinction, such as Africa and Asia, have much greater large herbivore biomass today (Fløjgaard et al, 2021). Because of this ubiquitous loss of megafauna, current levels of vegetation consumption in most of the world's natural areas are much lower than they would have been in the absence of this late-Quaternary down-sizing (Pedersen et al. 2020). Large-bodied mammals are also important for the dispersal of many plants and for nutrient redistribution, and the late-Quaternary faunal losses have caused mammal assemblages to have lost a mean of 74% of their average movement capacity, with likely strong consequences for biotic community dynamics, for example, in response to future climate change (Berti and Svenning 2020). Given the significant loss of these animals and their importance to enhancing biodiversity, Svenning argued that there is a key role for megafauna-based rewilding in restoration efforts, but that shifting baselines make it easy to set targets too low (Svenning 2020, Monsarrat and Svenning 2021).

G. Lynn Wingard of the U. S. Geological Survey gave the third presentation in which she used a restoration case study in the Florida Everglades (USA) to make the argument that understanding the past is the key to planning for the future. In the Florida Everglades, it is thought that restoring the natural hydrology (i.e., the timing, delivery, quantity, and quality of water) will pave the way for the subsequent recovery of habitats and species. It is difficult, however, to know what the natural hydrology was like in the past when few observational records exist, and no instruments were in place prior to alteration of the regional hydrology. The solution in this system has been to use paleoecologic data on past salinities to adjust the regional hydrologic model to simulate conditions prior to the construction of canals and water management (Marshall et al. 2014). The mismatch between the present-day observed values and paleo-based estimates reveals that salinity was consistently lower in the past in the south Florida estuaries, and indicates that there was a greater volume of freshwater flowing through the wetlands to the coast. These results are being used to develop performance measures and targets for salinity in the estuaries to guide restoration. In looking to the future, Wingard proposes using “anticipatory target setting” in which paleontological data are used to detect long-term natural trends within ecosystems. The aim was to use this information to restore ecosystems to their natural trajectory of change at some time in the future rather than attempting to return to a pre-existing state (Wingard et al. 2017). The greater Everglades ecosystem has been evolving and changing over the last 5000 years in response to climate and sea level, so attempts to restore the ecosystem that does not account for these natural shifts revealed in the paleontologic record will not be sustainable and will result in additional costs.

The final presentation in the symposium was given by David Moreno-Mateos from Harvard University who focused on quantifying ecosystem recovery time and incorporating that information into restoration. Because it is challenging to directly measure recovery, Moreno-Mateos and co-authors compiled a set of over 100 chronosequences from all over the world to examine potential

patterns in forest ecosystem recovery. Of the parameters for which there was enough information (e.g., abundance, diversity, similarity, or the cycling of carbon and nitrogen), the data show that even after 150–300 years, these parameters have not returned to predisturbance levels, and full forest recovery could take ≥ 400 years (Rodríguez-Uña et al. 2021). Nonetheless, these types of metrics may be overly simple; greater complexity in the recovery process could be captured by measuring the structure and function of interaction networks and/or the genomic response to the release of an impact or disturbance. Moreno-Mateos first hypothesized that more complex metrics, which involve more ecological information, will take longer to recover (Moreno-Mateos et al. 2020). In support of this first hypothesis, a study of abandoned meadows in the Netherlands showed that it took decades for interaction networks among soil microorganisms to become more complex by increasing both the number and strength of links (Morriën et al. 2017). To test this hypothesis, he is examining above- and belowground interaction networks in forests; for example, 140 years after abandonment, the community of mycorrhizal fungi interacting with a beech tree community at former mine sites in northern Spain still differs from the community at sites not affected by mining (Rodríguez-Uña et al., *in review*). Similarly, agricultural fields abandoned 600–800 years ago in southwest Greenland contain the same number of species as undisturbed sites, but the functional composition differs as do the interaction networks, such that the disturbed networks are more vulnerable. Moreno-Mateos further hypothesized that genetic diversity should increase as populations are released from the selective pressures created by chronic anthropogenic impacts. To test this second hypothesis, he will focus on those species that are metacommunity hubs and examine how they recover genetic diversity using whole-genome sequencing to target specific functions of interest and increase the adaptive potential of the species. The Brazil nut tree is the focus of a pilot project that seeks to understand how the species has changed genetically since the release from domestication.

During the live discussion portion of the symposium, each of the four speakers spent about 10 minutes apiece summarizing their presentations and answering questions from the audience. This was followed by a general discussion among the panel and audience. Some interesting and important points were brought up throughout the hour. One topic that was visited repeatedly is the potential for misunderstanding present-day systems when paleontological data are lacking or ignored. For example, Jenny McGuire's work with North American mammalian records revealed that present-day niches do not approximate earlier niches, suggesting that assumptions made about climatic tolerances based on present-day distributions are missing a wealth of information about where those animals were in the past (Pineda-Munoz et al. 2021). It was similarly noted that it is important that we should not underestimate the climatic tolerances of species; it is easy to assume that present-day distributions of large herbivores, for example, are climatically driven, but we know from the paleontological record that these species have lived through much warmer conditions (Faurby and Araújo 2018). Ignoring this past legacy may lead us to underestimate recovery potential for these species.

Another fruitful discussion point centered around the idea of anticipatory target setting proposed by Lynn Wingard. This approach calls for long-term, natural trends to be identified in paleontological data such that ecosystems are restored to their own natural trajectory rather than to some pre-existing pristine state. Identifying a historical trajectory is not necessarily an easy task, however, because ecosystems are complex. In some ecosystems, as in the Everglades example, it may work to focus on restoring the biophysical components to their natural trajectory and thereby create appropriate conditions that will hopefully allow the remainder of the ecosystem components to follow.

This historical perspective on trends in ecological systems can also inform our ability to recognize succession resulting from natural disturbances versus directional changes or tipping points that result from human disturbances or more extreme natural events. David Moreno-Mateos argued that, although natural disturbances, like hurricanes or outbreaks, can be quite devastating, human impacts, like mining or intense agricultural transformations, could be comparable to a volcanic eruption stripping an entire ecosystem away. Indeed, evidence suggests that the probability of ecosystem recovery following disturbance began to decline about 3000 years ago (Wang et al. 2020). Human and natural impacts are also sometimes entangled; Florida mangroves, for example, have evolved to deal with hurricanes, but healthy mangrove systems need a balance of fresh and saltwater. This balance has been altered by water management practices and may impact the ability of the mangroves to recover from the increasing frequency and intensity of hurricanes that is projected under some climate change scenarios.

Finally, the panel considered the question of “over what time frame are paleontologic records relevant to present-day conservation and restoration?” The panel agreed that the answer to this question will vary somewhat depending on the scope of the study as well as the types of paleontologic records being used. While pollen and invertebrate records are quite robust, as are marine and estuarine records generally, the mammal fossil record is relatively sparse, which limits the types of conservation questions it can contribute to, especially prior to the last glacial maximum about 20,000 years ago (but for a deeper time example, see Archer et al. 2019). Nonetheless, many present-day species have adaptations that were acquired pre-Pleistocene, making older records relevant for gaining a broader perspective on what capabilities these species may have had in the past, and even deeper time studies can contribute to our understanding of how whole systems responded to climatic perturbations; while not necessarily addressing specific conservation questions, deep time paleontologic records can be relevant at a planetary systems scale.

This symposium emphasized the importance of considering time (past, present, and future) in conservation and restoration. Each of the four speakers demonstrated different ways in which knowledge of the past can provide information about ecosystems and/or species that would otherwise be unattainable. Continued communication and collaboration among restoration ecologists and paleoecologists will be important for developing future restoration targets.

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Data Availability

No data were collected for this review.

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