

# Advancing terrestrial ecology by improving cross-temporal research and collaboration

Lauren Azevedo-Schmidt , Madeleine Landrum, Meghan M. Spoth, Nikhil R. Brocchini, Kit M. Hamley, Alessandro Mereghetti, Andrea J. Tirrell and Jacquelyn L. Gill

Lauren Azevedo-Schmidt ([lazschmidt@ucdavis.edu](mailto:lazschmidt@ucdavis.edu)) is affiliated with the Department of Entomology and Nematology at the University of California Davis, in Davis, California, in the United States. Lauren Azevedo-Schmidt, Madeleine Landrum, Meghan M. Spoth, Nikhil R. Brocchini, Kit M. Hamley, Alessandro Mereghetti, Andrea J. Tirrell, and Jacquelyn L. Gill are affiliated with the Climate Change Institute at the University of Maine, in Orono, Maine, in the United States; Madeleine Landrum, Nikhil R. Brocchini, Kit M. Hamley, Alessandro Mereghetti, Andrea J. Tirrell, and Jacquelyn L. Gill are affiliated with the School of Biology and Ecology at the University of Maine, in Orono, Maine, in the United States; and Meghan M. Spoth is affiliated with the School of Earth and Climate Science at the University of Maine, in Orono, Maine, in the United States.

## Abstract

Ecology spans spatial and temporal scales and is inclusive of the history of life on Earth. However, research that occurs at millennial timescales or longer has historically been defined as paleoecology and has not always been well integrated with modern (neo-) ecology. This bifurcation has been previously highlighted, with calls for improved engagement among the subdisciplines, but their priority research areas have not been directly compared. To characterize the research agendas for terrestrial ecological research across different temporal scales, we compared two previous studies, Sutherland and colleagues (2013; neoecology) and Seddon and colleagues (2014; paleoecology), that outlined priority research questions. We identified several themes with potential for temporal integration and explored case studies that highlight cross-temporal collaboration. Finally, a path forward is outlined, focusing on education and training, research infrastructure, and collaboration. Our aim is to improve our understanding of biodiversity patterns and processes by promoting an inclusive and integrative approach that treats time as a foundational concept in ecology.

Terrestrial ecological research spans scales, approaches, and temporal extents (figure 1), each of which have their own strengths, limitations, and biases. The temporal grain (table 1) and extent of ecological analyses span days to eons, and most ecological processes are time dependent, including demography, dispersal, community assembly, and disturbance—processes that, themselves, influence ecological communities and processes over a range of timescales (Delcourt and Delcourt 1988). Despite this, ecological research is often separated by research communities researching the ecological processes of today (or modern ecology, referred to in the present article as *neoecology*) and those who study the past (or *paleoecology*; Jackson 2001). Paleoecologists further divide themselves as *deep*, which is typically ecological research involving organisms or deposits that are from the Pliocene or older (e.g., more than 2.5 million years; Jackson 2001), as opposed to *near-time* ecological research from the Quaternary, which typically involves subfossils in Pleistocene or Holocene deposits. Although ecologists working in the fossil record typically call themselves paleoecologists, *neoecologist* is typically a term used by paleoecologists to differentiate themselves from colleagues working on the scale of days to decades; most neoecologists simply refer to themselves as *ecologists*. Furthermore, this bifurcation fails to acknowledge the growing number of researchers who work across scales, integrating actualistic studies or modern experiments with reconstructions of past organisms or ecosystems. In any case, the temporal boundaries of our subfields do not necessarily themselves capture the timescales relevant to the lifespans of organisms or the patterns and processes we seek to understand (DiMichele et al. 2004), nor do they capture the breadth of time that a given individual researcher, because many paleoecologists span numerous time bins

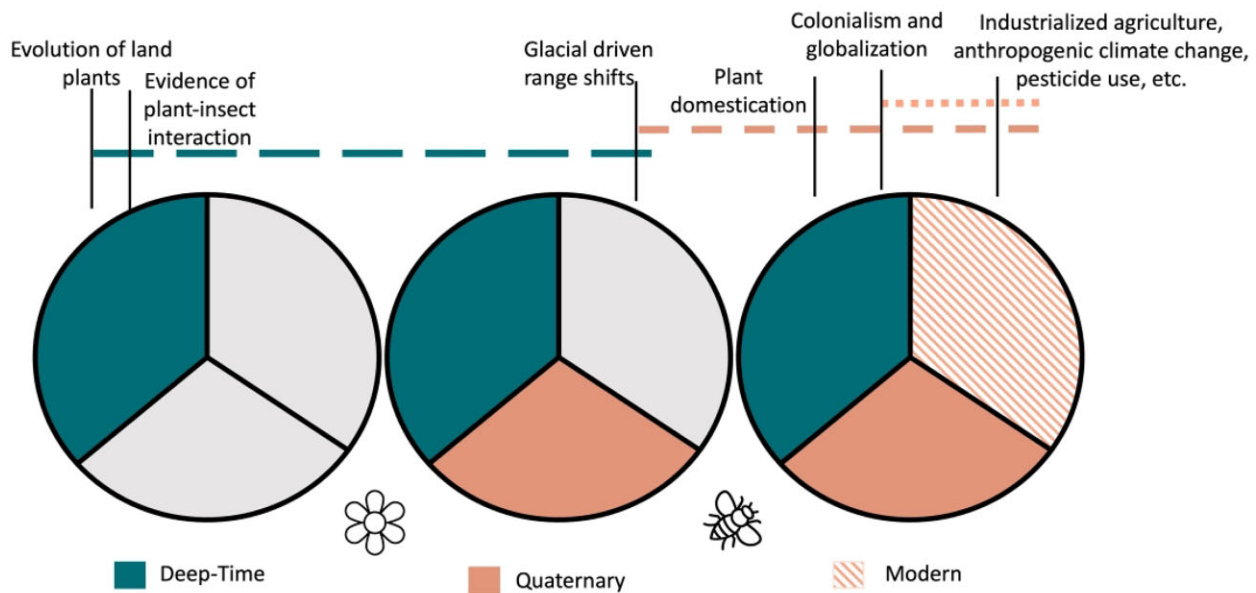
in order to address particular ecological questions. This has led to multiple calls through the years for a better integration of ecological research across timescales (e.g., Flessa and Jackson 2005, Rull 2010, Birks 2012, Smith and Boyer 2012, Gavin et al. 2014, Yasuhara et al. 2015, Bakker et al. 2016, Manzano et al. 2020, Nieto-Lugilde et al. 2021, Goodenough and Webb 2022).

Regardless of their tools and approaches, ecologists working across all timescales often ask similar questions (table 2; Willis et al. 2010, Bennington and Aronson 2012, Kiessling et al. 2019), although our studies may have different temporal grains and extents (figure 1; Turner et al. 1989). A species, community, or ecosystem is the integration of processes and events that span the 3.7-billion-year history of life, which means that ecological understanding depends on incorporating information from a range of temporal perspectives. Direct observations and experimental manipulations provide powerful insights about ecological processes across hours to decades (*neoecology*), whereas centennial to millennial scale observations provide valuable perspectives on natural populations and environmental variability, range shifts, community assembly, and long-term responses to global change (*paleoecology*). At the scale of millions of years, the ecoevolutionary and biogeographic processes driving macroscale biodiversity patterns begin to emerge; study at these scales is necessary to contextualize the magnitude and scale of modern biodiversity losses (e.g., Dietl 2016, Price and Schmitz 2016).

As with other subdisciplines, such as community ecology, ecosystem ecology, and behavioral ecology, ecologists working across different timescales generally use different field and laboratory methods to collect data that may be similar (e.g., community composition) but that may have different sources, taxonomic

Received: August 28, 2023. Revised: September 17, 2024. Accepted: September 30, 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com)



**Figure 1.** The conceptual framework shows the importance of incorporating deep-time (dark green), quaternary (tan), and modern (textured melon) perspectives into ecological research, using plant–insect interactions as an example. The temporal resolution of the source data (deep time, quaternary, or modern) is represented by the length of the dashed lines, whereas the resolution or extent is represented by the width of the dashes (i.e., less space between the dash marks indicates greater resolution). Although the extent of the deep-time record is greater, the grain is often coarser than other time bins. The vertical black lines mark ecological events rooted in time that influenced plant–insect interactions. Finally, the pie charts are meant to visualize the value of the temporal source data and what is lost when it is not considered within the overall framework. Although the example we provide is plant and insect centered, these concepts are widely applicable across organisms and environments.

resolutions, or even scales (Perry et al. 2021); paleoecologists often work with proxy data reconstructed from natural archives, whereas neoecologists are able to directly observe and even manipulate their study systems. This mismatch of temporal scales between neo- and paleoecologists leads to varying conceptions of time. A survey of marine conservation biologists showed that 67% of its respondents reported using long-term data, but 49% of those respondents indicated that “long-term” data referred to decadal scales, whereas only 5% considered timescales of thousands of years “long term” (Smith et al. 2017). Importantly, however, the organisms and ecological processes we study often represent the amalgamation of processes that transcend the differences exhibited in our approaches and perspectives. Although some studies have addressed questions across multiple timescales, questions remain as to whether the patterns or processes observed at one time scale matter at others (Jackson 2001, Willis et al. 2010a, Ash et al. 2017). For example, because neoecology grapples with systems affected by multiple global changes (which has long been a central interest of paleoecology), neoecologists are investigating which timescales may best allow for the detection of critical transitions or regime shifts (Price and Schmitz 2016, Estes et al. 2018, McGuire et al. 2023). Although a growing number of studies are integrating across timescales (table 2, figure 2; e.g., Boulton and Belcher 2019, Kiessling et al. 2019), there are still opportunities to enhance cross-temporal collaboration, which has become particularly relevant to the interconnected biodiversity and climate crises.

Here, we explore the past, present, and future of cross-temporal ecological research: We first present a brief overview of the history of ecology as a temporally integrative discipline and then highlight shared agendas (see the “The past: ecology’s roots as a temporally integrative field” section; table 2) from an analysis of two major horizon-scanning efforts in neoecology (Sutherland et al. 2013) and paleoecology (Seddon et al. 2014), as well as several

case studies that have fostered new insights through temporal integration of research agendas and themes. Finally, we provide recommendations for how ecologists working across timescales can approach this work going forward. This is not meant to be an exhaustive review of all ecological subdisciplines or systems but, rather, a demonstration of the power of cross-temporal integration and of where opportunities lie. Notably, we focus on terrestrial examples, because this was the main focus of Sutherland and colleagues (2013) and Seddon and colleagues (2014), and it represents where the collective ecological expertise of the present authors lies (ironically, the siloing of paleo- and neoecology mirrors that of terrestrial and aquatic or marine ecology; *sensu* Munguia and Ojanguren 2015). As ecologists whose work spans the temporal gamut described in the present article, our goal is to foster an improved understanding of our systems across timescales (Bennington et al. 2009, Smith et al. 2023) and to create a more impactful, inclusive, and collegial approach to cross-temporal interdisciplinary research.

## The past: Ecology’s roots as a temporally integrative field

Much of the foundational work in ecology was done by widely read naturalists with interdisciplinary backgrounds, often including training in geology, as well as biology (Jackson 2001). Such long-term perspectives arguably contributed to some of the most important advancements in the field; Charles Darwin drew heavily on work by Lyell and other geologists to inform his theory of evolution (Rudwick 1998). Henry Chandler Cowles, who studied botany and geology as an undergraduate, drew from both disciplines to develop foundational theories about succession and space-for-time substitution (Cowles 1899). E. Lucy Braun, who also studied geology as well as botany, drew on her knowledge about glacial histories in her work on the biogeography of Eastern North

**Table 1.** Glossary of terms used within the manuscript in alphabetical order.

Term	Definition
Actualistic studies	Modern study that tests assumptions around past processes and patterns
Bipartite networks	A network built on graph theory that focuses on the properties, structural dynamics, and relationships between the structure and function of networks. Bipartite networks therefore consist of nodes of two different natures that are linked between dissimilar nodes.
Cenozoic	The current and most recent era covers the last 66 million years. This era is notable as the age of the mammals, following the extinction of nonavian dinosaurs.
Climate refugia	Regions that serve as a refuge for flora or fauna during periods of extreme climate or climate transitions. Traditionally refugia is used in reference to the migration of flora downslope and poleward following glacial periods.
Fossil record	The mineralized remains or imprint of organic life preserved within sedimentary processes. The fossil record can be used to study long extinct organisms, but the record is limited to materials that can withstand geologic processes.
Holocene	The last 11,700 years of Earth's history, defined by the end of the last major glacial epoch.
Hyperthermal event	A sudden warming of the planet that occurs at a geologic time scale (e.g., PETM). Altitheal, hypsithermal, and climatic optimum have all been used to describe warming events.
Mega-annums	A period of 1 million years.
Megaherbivore	Terrestrial herbivores weighing 1000 kilograms (2200 pounds) or more.
Pleistocene	The oldest epoch of the Quaternary (11,700 years ago- 2.58 million years ago).
Pliocene	The epoch preceding the Quaternary Period (2.58–5.33 million years ago).
Proxy	A variable that indirectly represents a variable of interest (e.g., fossil pollen as a representation for past vegetative composition).
Quaternary	The current and most recent epoch of the Cenozoic Era, occurring from 2.58 million years ago. The Quaternary is defined by the growth and decay of continental ice sheets as related to the Milankovitch cycles and their associated environmental changes.
Refugia	An area in which a population can survive a set of unfavorable conditions.
Subfossil	Remains of an organisms that are not completely (i.e., permineralization or the replacement of organic material with inorganic) fossilized
Taphonomic	The processes of fossilization that includes transport, burial, compaction, and preservation.
Temporal extent	The total length of a time period such as 1000 years or 500,000 years
Temporal grain	The resolution of the event or the frequency at which the event occurred.

American forests (Braun 1947). However, despite these early works, subsequent decades saw an increasing trend toward disciplinary specialization that has resulted in neocologists and near- (Quaternary) and deep-time ecologists often being separated in different departments, attending different conferences, and publishing in different journals. Although specialization can lead to important insights and methodological advances, a trend toward temporal siloing has arguably created barriers to ecological understanding; neocologists rarely cite long-term data (Silvertown et al. 2010, Willis et al. 2010, Cusser et al. 2020, 2021), whereas paleoecologists initially emphasized the study of patterns, because direct mechanisms can be harder to detect in the fossil record (Fenton 1935), although this is changing (Kelley et al. 2013); however, following the quantitative revolution of the 1970s, paleobiologists are increasingly adopting the statistical approaches used by neocologists (Sepkoski 2005).

As the subfields developed, a growing divide began to reflect how paleoecologists discussed their relationship to ecology. In 1935, Carroll Lane Fenton defined paleoecology as a third branch of ecology (along with autecology and synecology) and emphasized that “despite its geologic affiliation, paleoecology rests on

biologic viewpoints, because it considers fossils as organisms, not as constituents of sediments” (Fenton 1935). Only two decades later, Paul E. Cloud (1959) described paleoecology as being situated squarely within geology (although he noted its parent disciplines were paleontology and ecology). By the late twentieth century, a number of Quaternary paleoecologists were noting a growing disconnection between ecology and paleoecology, calling for the need to apply geohistorical data to understand modern ecological phenomena (Delcourt and Delcourt 1988, Hunter et al. 1988, Jackson 2001), although Jackson (2001) also pointed out a lack of dialog among Quaternary paleoecologists and those working in deeper-time records. A recent resurgence of calls for cross-temporal integration (Flessa and Jackson 2005, Louys 2012, Jackson and Blois 2015, Yates et al. 2018, Buma et al. 2019, Manzano et al. 2020, Nieto-Lugilde et al. 2021) has arguably been driven by a growing recognition of the fossil record's relevance to global change research, particularly as we face future climate analogs that resemble the Pliocene or the Eocene (Burke et al. 2018); abrupt climate change, novel ecosystems, range shifts, and extinction dynamics are all areas where paleoecological data have helped shape modern theory (Foster et al. 1990, Jablonski and Sepkoski

**Table 2.** Comparison between Sutherland and colleagues (2013) review of neoecology to Seddon and colleagues (2014) paleoecology research goals provides an opportunity to compare the future of these subdisciplines.

Unified theme	Process	Neoecology		Paleoecology		Case Studies
		Sections	Percentage of questions	Sections	Percentage of questions	
Community and ecosystem processes	Ecosystem function and process	3	42	1	16	3.2.1. How did life recover in the aftermath of the K-Pg extinction?
	Evolution on various timescales	1	10	1	16	
	Biodiversity with a spatial focus	1	20	1	20	
Understanding the Anthropocene	Human impacts and climate change	1	17	1	14	3.2.2. What role do megaherbivores play in structuring plant communities and their resilience to climate change?
Methodology	Furthering the field	1	11	2	34	3.2.3. How will fire regimes change in a warming world?

Note: The sections and questions of the respective reviews were sorted into our three unified themes: Community and Ecosystem Processes, Understanding the Anthropocene, and Methodology and then further divided into subthemes. The percentages were calculated by taking the number of questions within a section and dividing it by the overall number of questions (Sutherland et al. 2013,  $n = 100$ ; Seddon et al. 2014,  $n = 50$ ) before multiplying it by 100. The focus (i.e., more important within neo- or paleoecology) was determined by evaluating (less than a 10% difference in the two groups) the differences in percentage of questions within a topic. Case studies that emphasize these findings are listed with the section they correspond to in the manuscript.

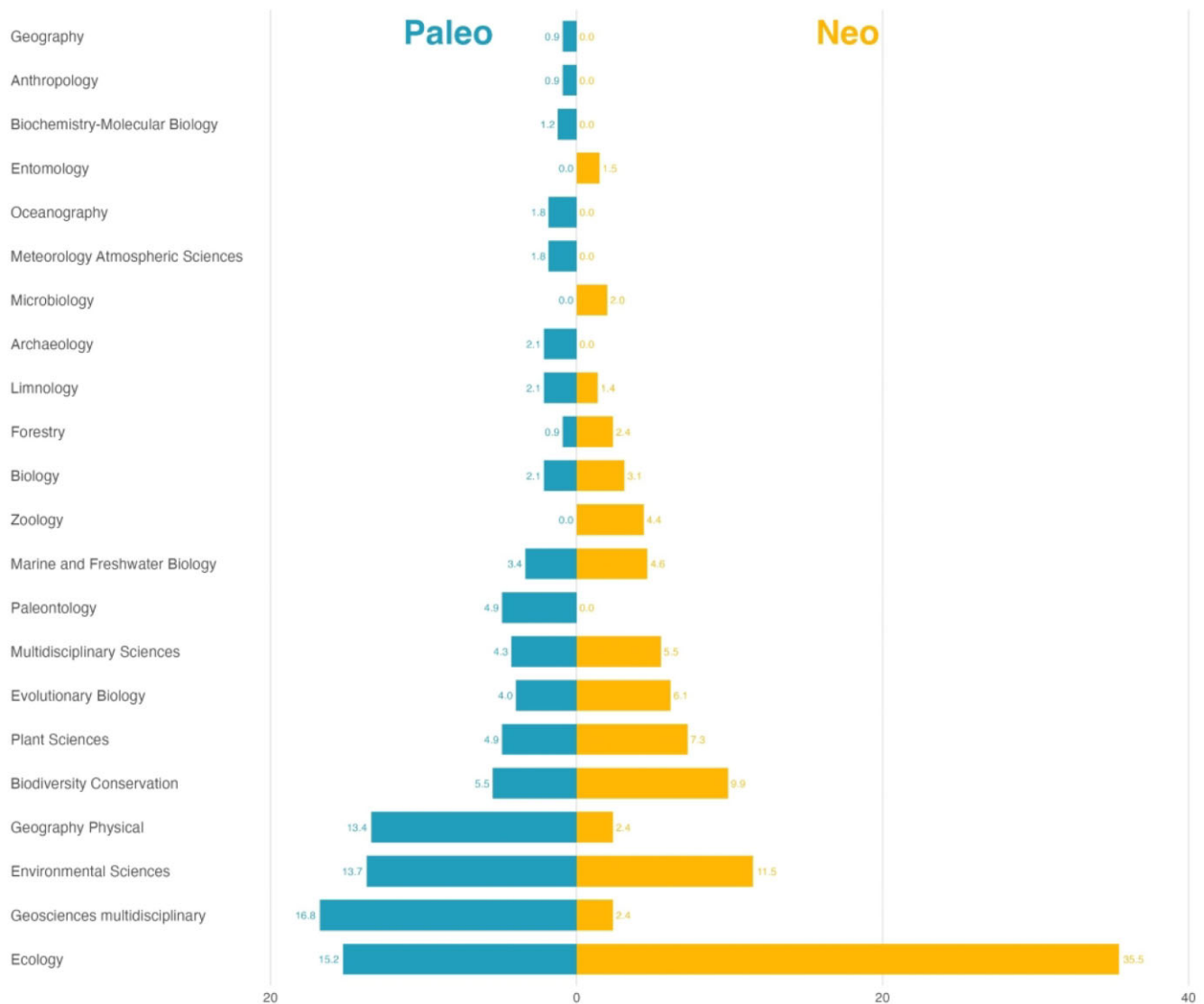
1996, Gavin et al. 2014, Jackson and Blois 2015, Birks 2019). This lack of temporal integration notably applies to both neo- and paleoecologists, because paleoecologists rely on observations and measurements from modern-day ecosystems to interpret fossil records, including the actualistic studies that validate proxy work (Jackson 2012). Modern ecology typically deals with short-term records generated over subannual to decadal scales, whereas the fossil record captures broader temporal extent (Wolkovich et al. 2014). Understanding the drivers of patterns and short-term responses in contemporary ecosystems is vital for interpreting past records, particularly in an era of interacting global changes. However, recent efforts do indicate some progress toward improved temporal integration, particularly in the field of conservation paleobiology (Dietl and Flessa 2011), which seeks to apply paleontological perspectives to conservation practice (Dillon et al. 2023). Notably, however, extending this work into conservation practice has lagged (Groff et al. 2023), indicating that there are still opportunities to recenter time as a focus of ecological inquiry (Wolkovich et al. 2014).

## The present: Identifying shared research priorities across timescales

Two community-curated horizon-scanning efforts by Sutherland and colleagues (2013) and Seddon and colleagues (2014) provide a powerful opportunity to assess areas of cross-temporal interest and identify shared research priorities working across timescales. Although these papers were published a decade ago, the research agendas they outline are still widely relevant (both papers are actively cited; figure 2) and represent two data sets with similar methodologies that provide a state-of-the-field snapshot of research interests and priorities. To our knowledge, the research priorities outlined by the two communities have not previously been compared.

To assess the degree of overlap among the priority research agendas for neo- and paleoecology, we assigned the questions identified in the two papers into three themes: community and ecosystem processes (i.e., research about species, interactions, communities, and ecosystem processes), global change (i.e., applied science to understand conservation, management, and anthropogenic impacts), and methodology (table 2). We selected these broad themes because they are timescale neutral and represent the major groupings within both manuscripts. Assigning questions into these broad themes allowed us to identify not only areas of overlapping priority but also areas where either paleo- or neoecologists—but not both—had identified significant interest. Areas of shared overlap can be interpreted as areas of research where future cross-temporal collaboration would be especially fruitful. Areas that do not overlap could either reflect areas that had been the subject of past focus in one field (and that is therefore not considered in future priorities), in which case they could indicate topics where engaging with existing literature from different timescales could be useful in developing future research priorities.

Sutherland and colleagues (2013) sorted 100 questions into seven sections, whereas Seddon and colleagues (2014) had 50 questions divided into six sections. The two review papers had similar methodologies, where questions were solicited from the research communities of each subdiscipline, which were then refined, combined, or eliminated during workshops to identify research priorities. It is important to note that both papers resulted from exercises involving a subset of experts in each field; questions were solicited from the broader community, and workshop participants were selected from a pool of applicants. Although the neo- and paleoecological communities were not formally surveyed, efforts were made to reach as broad a representation of these research communities as possible (e.g., listservs, direct emails). A different community of scientists may have identified different research priorities,



**Figure 2.** Using the Web of Science, we created a visualization of the journal subdisciplines that cite Sutherland and colleagues (2013; yellow or neo) or Seddon and colleagues (2014; blue or paleo). Each subdiscipline is listed on the y-axis, with the x-axis showing the percentage of overall citations. To normalize the difference in overall citations, the bars represent the percentage of the total citations within the temporal range (Sutherland et al. 2013,  $n = 798$ ; Seddon et al. 2014,  $n = 328$ ). The precise percentage is provided at the top of each bar. This visualization emphasizes that paleo- and neocology are largely drawing from within their temporal ranges. Sutherland and colleagues (2013) is most highly cited with the ecology subdiscipline, whereas Seddon and colleagues (2014) is most highly cited within multidisciplinary geosciences. However, Seddon and colleagues (2014) was also highly cited in ecology, environmental science, and physical geography, likely reflecting the different departments and subdisciplines paleoecologists are in. The total citation counts for each subdiscipline can be found in supplemental [table S2](#).

particularly at the workshop stage, although the organizers strove for a broad representation of expertise. For our analysis, all of the questions were kept in the original sections of their respective paper, and we instead assigned sections to our themes on the basis of the original section description. A full list of which sections (and their respective questions) were compiled into each theme and more detailed methods can be found in supplemental [table S1](#).

To normalize discrepancies in the number of sections and questions within each previously published manuscript, we first tallied the number of sections assigned within each paper to the general themes outlined above. The percentages of questions within each section were then calculated by taking the number of questions within a section and dividing by the total (Sutherland et al. 2013,  $n = 100$ ; Seddon et al. 2014,  $n = 50$ ). These values were then used to compare across publications as a measure of focus.

## A quantitative comparison of neo- and paleoecological research agendas

Broadly, our analysis of the Sutherland and colleagues (2013) and Seddon and colleagues (2014) horizon-scanning papers indicates that neocology and paleoecology share considerable overlap in priority research agendas, although our subfields use different vocabulary and methodologies (table 2). Three of the five sub-themes showed similar importance for neo- and paleoecologists. We found that the influence of anthropogenic global change on ecosystem dynamics was a research priority for both Sutherland and colleagues (2013) and Seddon and colleagues (2014; table 2), indicating an area in which future collaboration would be beneficial. Sutherland and colleagues (2013) specifically called for continued research on the scale and types of ecological monitoring used within neocology, whereas Seddon and colleagues

(2014) focused on building new methods within paleoecology that could detect human impacts (see [supplemental table S1](#)). Evolution was similarly a unifying theme of shared importance across various timescales, which is unsurprising, given its core role in disentangling ecological processes (table 2). Evolution was slightly more of a priority within the paleo community (16%; table 2) than the neoecology (10%; table 2), which could reflect the fact that paleoecologists regularly work across broad time spans and temporal scales. Regardless, this shared overlap in interest shows promising avenues for future collaborations, especially as we grapple with the drivers and mechanisms of evolution from the micro to the macro scale.

The two subthemes that were focused toward one specific temporal bin were ecosystem function and process (neoecology focused 42%) and furthering the field (paleoecology focused, 34%; table 2). This lack of overlap between the temporal bins could represent an area of research that has already been a heavy focus. Topics such as range shifts and no-analog assemblages have been the focus of extensive research in paleoecology and so are unlikely to be highlighted as horizon scanning despite being identified as priorities to neoecologists. Similarly, paleoecology's stronger emphasis on methods is not surprising, given the challenges and limitations of working with proxy data. Although subthemes with a particular temporal focus show where the futures of neo- and paleoecological research are headed, similar to the subthemes with overlapping interest, they also represent areas in which ecologists across all temporal fields can collaborate. For example, the need to continue developing quantitative tools, ancient DNA, stable isotopes, and other approaches within paleoecology highlights a powerful opportunity to disentangle pattern and process by fostering collaborations with neoecologists doing experimental work.

The results reveal existing shared research priorities, as well as areas where a research theme is prioritized by one subdiscipline but not the other. Both categories represent areas for future collaboration and where such work can help break down temporal barriers. Research questions with shared overlap could manifest into novel approaches for tackling questions that bridge evolutionary history of organisms or patterns, whereas areas with specific temporal skews represent areas where one temporal domain can leverage the expertise of the other.

### Case studies highlighting cross-temporal advances in ecology

To highlight the utility of cross-temporal approaches, we provide several examples of case studies that demonstrate effective collaboration between neo- and paleoecology. When cross-temporal collaboration and dialog occur, we often see exciting advancements as a result, such as with the identification of climate refugia (Gavin et al. 2014), restoration ecology (Barak et al. 2016), the risks of specialists under climate change (Colles et al. 2009), and the ecological impacts of megaherbivores on woody vegetation (Bakker et al. 2016). This point can be illustrated by research on plant–insect interactions across all spatiotemporal scales (figure 1). Modern surveys of plant–insect interactions may fail to capture how range shifts, historical legacies, and coevolution influence contemporary patterns (figure 1), but by incorporating the full spatiotemporal breadth of research, a more complete story emerges. This type of integration is what we aim to facilitate in the future by showcasing examples of how this has been done successfully in the past. Here, we review recent research that highlights work being done within the unifying themes identified above (table 2). These case studies do not represent an exhaustive

list of all the past research that has been conducted that integrate paleo- and neoecological perspectives, but, rather, provide examples to inspire for future research.

The geologic past provides so-called natural experiments that allow for a deeper understanding of the ecological and evolutionary impacts of extinction on ecosystem biodiversity and recovery (Lockwood 2008). This is of particular interest for both paleo- and neoecologists as we face an ongoing extinction crisis, although whether this can be considered the sixth mass extinction is debated by paleontologists, who point to the challenges of comparing contemporary rates of extinction with that of the fossil record (Cowie et al. 2022). Although many extinction events took place over millions of years or longer, the Cretaceous–Paleogene (K–Pg, 66 million years ago) mass extinction represents a geologically rapid event that resulted in the highest temporal rates of extinction in Earth's history (Wilf et al. 2023). The K–Pg mass extinction was triggered by the Chicxulub asteroid impact 66 million years ago, which resulted in a loss of more than 60% of species (Schulte et al. 2010), including all nonavian dinosaurs (e.g., Brusatte et al. 2015), and local extinction rates of up to 90% for plants (Stiles et al. 2020). This extinction event drastically altered the course of life on Earth during the Cenozoic, completely rearranging biological communities, promoting the diversification of angiosperms (Vajda and Bercovici 2014) and a shift from slow to fast plant life history strategies (Blonder et al. 2014) and ushering in the age of mammals (Lohaus and Van de Peer 2016). Both the extinction event itself and the postrecovery dynamics had profound impacts on the development of modern biodiversity over the Cenozoic, but the mechanisms facilitating ecological recovery in the aftermath of the impact have been poorly understood.

The fossil record provides valuable information regarding ecosystem restructuring and aftermath of the K–Pg, which was characterized by continental-scale fires, darkness caused by an impact winter that severely restricted photosynthesis, and acid rain (Wilf et al. 2023). It has long been recognized that ferns were some of the first species to colonize the denuded landscapes following this mass extinction, recorded in the sediment record by high values of fern spores known as the *fern spore spike* (e.g., Barreda et al. 2012). The widespread success of ferns in the aftermath of the K–Pg impact and the Mount St. Helens eruption in 1980 CE led Tschudy and colleagues (1984) to classify ferns as *disaster taxa*, because of their high dispersal capability and their ability to withstand stressful environments. For decades, fern spore spikes in the geologic record were interpreted through the lens of competition, despite a growing body of evidence that many ferns act as facilitators in modern-day ecosystems. In a reexamination of the disaster–taxon framework, Azevedo-Schmidt and colleagues (2024) proposed that ferns instead acted as facilitators of community assembly following the K–Pg mass extinction, on the basis of modern-day observations of ferns following a disturbance. Ferns within modern ecosystems provide many facilitative traits that promote ecosystem recovery, including an ability to modify soils by removing heavy metals (Schmitt et al. 2017, Yang et al. 2021), stabilizing substrates (Sanchez-Castillo et al. 2019, Osman et al. 2021, Yang et al. 2021), and increasing soil organic matter and water content (Walker 1994, Zhao et al. 2012, Gallegos et al. 2015, Lyu et al. 2019); they also mediate competition among plants following a disturbance (Brock et al. 2018, Yuan et al. 2019, Yang et al. 2021). Modern fern physiology has shown the high tolerance of ferns within stressful abiotic environments and their adaptability as a group of plants (Anderson 2021) that has colonized nearly all ecosystem types (Azevedo-Schmidt et al. 2024). The cross-temporal approach utilized by Azevedo-Schmidt and

colleagues drew from insights across timescales by applying inferences about mechanisms from neocological research to the observed patterns in the fossil record, leading to an improved understanding of the effects of ferns on ecosystem recovery. By reenvisioning the approach required to create analogous data sets (i.e., replicating paleological methods in modern ecosystems) cross-temporal validation of these ideas can be directly tested opening new lines of inquiry between paleo and neocologists (see the “Collaboration” section).

Megaherbivores (typically defined as herbivores heavier than 1000 kilograms) have long been recognized as ecosystem engineers because of their disproportionate impact on shaping community composition, ecosystem structure, and function relative to their biomass (Owen-Smith 1988, Waldram et al. 2008, Daufresne 2013) and in ways that cannot be replicated by smaller animals (Johnson 2009, Owen-Smith 2016, Hyvarinen et al. 2021). Meanwhile, large species are some of the most threatened on the planet today (Ripple et al. 2015), leading to a growing interest in understanding the ecological consequences of their extirpation. The global extinction of megafauna during the late Pleistocene (Koch and Barnosky 2006), a size-selective event that resulted in the loss of over 50% of large species, provides a natural experiment in understanding the role that large herbivores play on ecological processes (Malhi et al. 2016). Recent methodological advances, including the use of biomarkers such as coprophilous fungi (Perrotti and Van Asperen 2019), fecal sterols (Harrault et al. 2019), and ancient DNA preserved in sediment records (Murchie et al. 2021) have enabled paleoecologists to reconstruct local megaherbivore populations, vegetation composition, and other ecological processes in tandem. Such work has shown that the extinction of large herbivores has been associated with state changes in vegetation composition (Rule 2012, Barnosky et al. 2016), the emergence of novel ecosystems (Gill et al. 2009, 2012), and reductions in plants with fruits adapted for dispersal by endozoochory (Pires et al. 2018, Adeleye et al. 2023). Other research has shown that megaherbivore extinctions changed ecosystem structure and function by increasing woody cover (Doughty et al. 2016), altering the spatial dynamics of nutrient cycling (Doughty et al. 2013), and enhancing global fire regimes (Karp et al. 2021), and they may even have influenced the climate system via vegetation-induced changes in albedo (Doughty et al. 2010) and atmospheric chemistry (Smith et al. 2016).

Studies of megaherbivore impacts on ecosystems are well suited to a temporally wide range of approaches, as has been exemplified by research on megafaunal impacts on Arctic vegetation (Wal 2006, Zimov et al. 2012, Post 2013, Bråthen et al. 2021). Because the proposal of the megafaunal hypothesis to explain the presence of highly productive and biodiverse Arctic ecosystems during the Pleistocene (Zimov et al. 2012, Barrio et al. 2016, Bråthen et al. 2021), researchers have sought to understand the role of megafaunal herbivory on vegetation resilience, in part to evaluate rewilding as a tool to address climate change (Malhi et al. 2016, Olofsson and Post 2018, Beer et al. 2020, Verma et al. 2020). In fact, paleoecological data have been central to discussions of rewilding to restore lost ecological functions that may support biodiversity under global change (Donlan et al. 2006, Svenning et al. 2016, Fordham et al. 2020) and were highlighted as an avenue of neo- and paleoecology collaboration by Kiessling and colleagues (2019). Meanwhile, modern observations and experiments have been foundational to understanding megaherbivore diets (Kartzinel et al. 2015) and the impacts of herbivory (Bakker et al. 2016), allowing for a stronger link between patterns and drivers observed in long-term records. Together, such work is driving a

new understanding of the importance of trophic interactions in structuring ecosystems, both locally and at large spatiotemporal scales.

Fire is an important disturbance that shapes ecological and evolutionary processes across scales (McLaughlan et al. 2020). The fossil record indicates that fire has been a part of Earth’s system since land plants first evolved during the Late Silurian (443 million years ago; Pausas and Keeley 2009). The fossil record indicates that some taxa were already fire specialized by the Late Cretaceous (100–66 million years ago; Keeley et al. 2011), including adaptations such as resprouting, serotiny, germination, and seedling recruitment (Keeley et al. 2011, Pausas and Keeley 2019), which speaks to the deep evolutionary importance of fire. Disturbance is a natural ecosystem process that influences species, populations, and communities by removing biomass, disrupting life histories, and reducing critical resources (Pickett et al. 1989). The paleoecological record expands the concept of disturbances from short-term, localized events (e.g., fire, windthrows) to longer-term perturbations that may express at the continental or global scales (i.e., megadroughts, hyperthermal events; table 1); each alters ecosystems in various ways, depending on their underlying mechanisms (Turner 2010). Many deep-time events may therefore be considered disturbances, providing opportunities to both quantify disturbance regimes (Gaiser et al. 2020) and to understand the impacts of disturbances across timescales. Because fire return intervals are often long (decades to centuries), particularly in forested landscapes, where the trees themselves may live for thousands of years, fire has been a natural focus for integrative work among paleoecology, dendrochronology, and fire ecology (Whitlock et al. 2010).

As fire regimes shift across the globe (O’Donnell et al. 2011, Westerling 2016, Abram et al. 2021, Crist 2023), researchers are increasingly looking to the paleorecord to quantify the drivers and impacts of past fire regimes (Napier and Chipman 2021); meanwhile, neocological research has been critical to understanding the near-term impacts of fire, as well as linking the fossil record of fire to fire histories through modern-process studies. Coop and colleagues (2020) synthesized evidence surrounding fire-driven ecosystem conversion across North America, predicting ecosystem conversion while summarizing uncertainties and proposing key themes for applied research that would support management decisions in cases where prefire forests may not return. One key component of the Coop and colleagues (2020) synthesis was a consideration of spatial and temporal scales. The authors proposed hypothetical ecological outcomes of fire on 1-, 10-, 100-, and 1000-year intervals, merging modern and paleoecological research to identify which systems will display resilience to future changes in fire regimes, the limits to that resilience, and to estimate postfire recovery times. Coop and colleagues (2020) illustrates how researching a fundamental ecological process across temporal scales can help us to address urgent applied issues under global change, such as which ecosystems are susceptible to tipping points and why, the factors and mechanisms that determine the resilience of ecosystems to external perturbations, and how we measure resilience (e.g., Sutherland et al. 2013).

## The future: Improving cross-temporal ecological research and collaboration

As the examples above show, not only do neocology and paleoecology share research agendas, but those agendas are arguably often more effectively advanced when we approach ecology as a

temporally expansive discipline. However, such work has shared many of the same growing pains and challenges of interdisciplinary research (Lin 2008). Given this, it would be fruitful for terrestrial ecologists working across timescales to engage with the work being done within conservation paleobiology (Dietl and Flessa 2011, Louys 2012, Dillon et al. 2023, McClenachan et al. 2024), marine paleontology (Smith et al. 2017), historical ecology (e.g., Bowman et al. 2011), and Indigenous engagement (Larson et al. 2021, Roos et al. 2021, Greenler et al. 2024), which have been leading the way in cross-disciplinary research that explicitly spans timescales.

We aim to make it easier for terrestrial ecologists working across timescales to both communicate and collaborate. Below, we highlight institutional action items that could improve cross-temporal integration by removing language barriers, improving training, and developing research infrastructure.

## Education and training

Perhaps one of the most significant barriers for the integration of the subdisciplines of ecology is the nature of academic training. Paleocologists are more likely to come from a background in Earth sciences, whereas neoecologists tend to come from a life sciences background (Jackson 2001). This has the potential to lead to lost-in-translation scenarios where neo- and paleoecologists encounter disciplinary language barriers rooted in differences in jargon, methodology, analyses, conceptual frameworks, and even data types and scientific norms (Kiessling et al. 2019). Although these differences present a challenge, they also present a unique opportunity to learn, refine, and synthesize shared concepts. In most cases, it's likely that instead of speaking completely different disciplinary languages, the subfields of ecology are just using different dialects to address the same research questions despite temporal differences (figure 1). By integrating people and departments from across ecological subdisciplines, ecology can be better incorporated across temporal scales that aim to answer shared questions. One potential mechanism for this is university research centers or institutes that actively foster cross-temporal collaboration on themes such as climate change, marine science, conservation, or global change.

In 2018, the Ecological Society of America endorsed a curricular framework for undergraduate education in ecology, dubbed the four dimensional ecology education framework (Klemow et al. 2019). This educational framework was designed to ensure that educators incorporate key dimensions of ecology and the scientific process when teaching undergraduate ecology majors. These key dimensions include core ecological concepts, ecological practices, human–environment interactions, and cross-cutting scientific themes. *Core ecological concepts* refers to key concepts that every ecology student should be exposed to, whereas *cross-cutting scientific themes* refers to scientific topics outside of the discipline of ecology that should also be covered, which range from concepts of biology and evolution, to physics. Unfortunately, these core ecological concepts do not cover paleoecology or the concept of ecological change over time. Temporal scales are mentioned in the cross-cutting scientific themes section, but paleoecological methods are not mentioned in the ecological practices section, which details field methods, experimental design, and statistical methods (Klemow et al. 2019). Sediment cores, tree rings, or paleontological deposits that incorporate multiple taxonomic groups, such as tar seeps or caves, are engaging topics for students that could be used to illustrate how the fossil record informs our understanding of ecology and evolution, particularly with regards to

climate change impacts, extinction, and other pressing modern-day topics. The temporal range of ecology spans millions of years; however, there are many concepts from deep-time ecology that are typically underrepresented in classroom settings (Libarkin et al. 2007). Could including exploration of past hothouse worlds inspire new ecologists to think of modern conservation questions in new ways? Or could lessons on geologic history affect how emerging ecologists think about community structure? Although such topics are certainly included in ecological curricula at some institutions, there is always room for growth.

Although it is important to address this temporal disconnect in ecology at the undergraduate level, this issue can be addressed even earlier in a student's education. Primary and secondary education classrooms are a perfect place to begin reinforcing the connectedness of ecological processes through time before impressions about temporal boundaries are even formed. In the United States, the adoption of Next-Generation Science Standards (NGSS; NGSS Lead States 2013) by a majority of public schools means that students are now exposed to concepts such as the fossil record and geologic timescales at an early age; this could help to address previous knowledge gaps, because even college students have been found to struggle with deep-time concepts (Libarkin et al. 2007). The vast timescales of the geologic record are a particular challenge (Trend 2000, Catley and Novak 2009, Czajka and McConnell 2018), which, in turn, exacerbates knowledge gaps in biology, because undergraduate students have been shown to struggle with evolutionary history and understanding the development of the tree of life (Bishop and Anderson 1990, Abraham et al. 2012, Kalinowski et al. 2013). Scale, proportion, and quantity is one of the cross-cutting concepts in the NGSS, and American public school students will now learn not only about the history of the Earth but about how fossil and paleoclimate evidence from sediment records is used to record and understand that history, linking evidence to inference. Children develop foundational scientific understandings at very early ages (Eshach and Fried 2005). Introducing the concept of temporal scale early on could influence the ways students understand past, present, and future ecologies. For example, teachers can use preserved dinosaur trackways to illustrate similarities between modern animal movement and ancient organisms, providing a tangible connection to the past while remaining engaging.

## Collaboration

Integrating data from neo- and paleoecological systems into a unified, cross-temporal framework is also difficult because of different subdisciplinary norms, major methodological differences, and challenges communicating the limitations and opportunities provided by data gathered by those different methods. Methodological differences and misunderstanding of what types of information the deep-time fossil records hold is a large barrier to comparisons across temporal scales (Kiessling et al. 2019). To bridge the gap between modern and deep-time paleoecology, it's necessary to create analogous methods and data sets that are comparable across temporal scales (Rappaciolo and Blois 2019, Nieto-Lugilde et al. 2021, Dillon et al. 2023, Smith et al. 2023). Studies that replicate methodologies across temporal scales bridge our understanding of modern ecosystems in evolutionary time (Azevedo-Schmidt et al. 2022). Specifically, this requires the organization of data in similar formats and units, the use of contemporary observations to test questions that emerge from long-term and geologic data sets, and testing of theories that emerge from contemporary studies using long-term data. Although this work



is challenging to conceptualize, we argue that researchers should start small by familiarizing themselves with the methods being used by their temporal counterparts. Paleocologists should familiarize themselves with neocological methods that are necessary to answer questions related to their research organism, ecosystem, or pattern of study, and neocologists should do the same by diving into the paleontological literature, not only when it comes to using natural archives to reconstruct past ecosystems but also around foundational concepts such as taphonomy and temporal grain and extent. The adaptation of methods will vary across studies, but with each data set, we get closer and closer to creating a more normalized viewpoint of how ecosystems are not truncated by temporal bins.

Although many universities have ecology departments where neo- and paleoecology researchers coexist, the structure of our institutions can be a barrier to interdisciplinary training and collaboration. Many Quaternary and deep-time paleocologists are housed and trained in geography or Earth science departments, whereas the ecologists may be scattered across departments organized by taxon (e.g., botany or entomology) or the natural resources (e.g., forestry, wildlife biology; Jackson 2001). We think it is significant that most of the authors of the present article (whose expertise spans neocology, Quaternary paleoecology, and deep-time paleontology) have been trained or have a tenure home in ecology departments and have participated in interdisciplinary degree-granting programs designed to address environmental problems. These programs promote interdisciplinary research and offer space and opportunity to dismantle temporal disconnects. Writing groups, working groups, technical workshops, seminar series, and informal gatherings provide a space to talk, listen, and learn across temporal boundaries and have improved the research of all the co-authors here. Ecology departments should make concerted efforts to integrate neo- and paleoecology at all levels, including their faculty, graduate students, undergraduate students, and course content. Funding agencies, such as the National Science Foundation (NSF) and the National Aeronautics and Space Administration (NASA) in the United States, should make concerted efforts to develop programs that encourage cross-temporal collaboration and to train reviewers in evaluating proposals that use such frameworks. Recent programs such as the NSF's Biodiversity on a Changing Planet program may provide a model for funding such research going forward. The NSF Research Coordination Network program could also be a powerful opportunity to bring together researchers from across temporal backgrounds. And for such collaborations to be fruitful, it is imperative to invest in research infrastructure that facilitates cross-temporal research (Flessa and Jackson 2005, Boulton et al. 2005) and comparable data sets (e.g., Goodenough and Webb 2022, Smith et al. 2023).

### Academic community and research infrastructure

Neo- and paleoecologists often attend different scientific conferences, although we note that the Ecological Society of America has elected many Quaternary paleocologists as president in the past, including Paul Sears (1948), Edward Deevey Jr (1969), and Margaret Davis (1987). Deep-time paleocologists tend to opt for geology-focused conferences such as the Geological Society of America's annual meetings. Although there are other conferences, such as those hosted by the International Organisation of Paleobotany and Climate and Biota of the Early Paleogene or the Crossing the Palaeontological–Ecological Gap, they are relatively small

and are held once every 4 years. Such conferences also tend not to include neocological and historical ecology. One conference that does integrate ecological disciplines well is the International Biogeography Society; there is often no divide between talks or symposia that span timescales. Taxon-specific societies, such as the Society of Vertebrate Paleontology, the Botanical Society of America, and American Society of Mammalogists, also appear to have successfully integrated deep-time, Quaternary, and neocological perspectives, likely because of the presence of evolutionary ecologists and systematists; this success record could be built on. Importantly, we should normalize organizing talks by question, taxon, or theme, and not just timescale, to promote cross-temporal discussion; paleocologists working on fire likely have more in common with other fire ecologists than they do with, for example, vertebrate paleontologists.

Integrating cross-temporal perspectives in ecology requires a similar approach to learning any new field or body of knowledge. In addition to reading deeply within the discipline, reading widely across disciplines is critical to building a foundation of temporal approaches and perspectives outside of a single discipline (and, in the age of digital scholarship, it is easier than ever before to access papers in journals with a different temporal framing). Although many geohistorical data sets papers are published in paleoecology-focused journals, we are seeing greater integration with special editions in both the *Proceedings of the National Academy of Sciences* (e.g., McGuire et al. 2023) and *Frontiers in Ecology and Evolution* (Wingard et al. 2024) that have been dedicated to incorporating neo- and paleoecology communities to improve conservation efforts. As with any scientific publication, journal selection is important for making sure the intended audience is reached; however, this may be challenging when research is cross-temporal. When it is unclear where an article should land within the publishing landscape, it can fall between the cracks or end up in interdisciplinary journals, where it may not be integrated into either neo- or paleoecological scholarship (figure 2). Examples of peer-reviewed journals that publish research across temporal bins of ecology are *Ecology*, *BioScience*, the *American Journal of Botany*, *Global Ecology and Biogeography*, *Ecography*, *Ecology Letters*, and *Evolutionary Biology*. Although this list is by no means exhaustive, it is a starting point for researchers who work on temporally complex topics. In addition, the Conservation Paleobiology Network integrates across temporal bins, merging paleontological and historical data with management and restoration efforts. This NSF-funded organization focuses on integration and collaboration with researchers and stakeholders.

Cross-temporal scholarship can take place informally in journal clubs or lab meetings but also in more formal settings, such as classrooms and comprehensive or qualifying exams. As the researcher transitions from reading to writing, the opportunity to evaluate citation practice arises: Do citations cross temporal boundaries, both in terms of the timescales studied and the publication date of the literature? The latter is particularly important, given that much of the foundational literature reflects disciplinary breadth, as was noted above. If the student's work is contemporary, are historical legacies, long-term cycles, or biogeographic processes that may have influenced observed patterns being considered? If the study spans millennial timescales or greater, are modern experimental, theoretical, or observational studies that could deepen understanding of the study system or focal organisms being considered? How much has the field grappled with epistemological questions about the nature of the data and its accompanying assumptions, and how might actualistic, taphonomic, or proof-of-concept studies conducted at different

**Table 3.** To further facilitate collaboration and fill the proposed gap between neo- and paleoecological researchers (figure 2), we provide a checklist of recommended goals and actions.

Goal	Action
Read	Explore texts across disciplines. Exploring widely is critical to building a foundation of temporal approaches and perspectives beyond an ecological subdiscipline.
Citations	Expand the traditional foundational citations typically applied in a subdiscipline. Include the new applications to cross subdiscipline collaboration.
Connect	Peers: Cross-temporal scholarship can take place informally in journal clubs or lab meetings. Professional: Facilitate broader materials in classrooms and comprehensive or qualifying exams. Career: Attend conferences with a wide scope of ecological application.
Organize	Consider the actualistic, taphonomic, or proof-of-concept studies conducted at different temporal scales. Explore the influences of processes influencing the study that are not limited to the study's temporal boundaries.
Methods	Explore epistemological questions about the nature of data and any accompanying assumptions.

Note: These are suggestions on how to engage with other disciplines and span temporal axes in research.

temporal scales influence the results? See table 3 for a full list of suggestions.

As was outlined above, there are a number of pressing questions that would benefit from a cross-temporal approach, particularly as we enter a time of rapid and widespread global changes. As with cross-disciplinary research, fruitful collaborations are more likely if they are approached with curiosity, humility, a willingness to learn, and respect for our colleagues' expertise (especially when methods or paradigms differ). The participants will soon learn that many cross-cutting concepts are widespread across temporal perspectives, but terminology or definitions may shift across subdisciplines. Even in the absence of such barriers, however, different temporal perspectives may shape frameworks about, for example, the relative importance of ecological drivers through time or the degree to which the temporal grain and extent (*sensu* Dornelas et al. 2013) of ecological data may inform approaches to a particular question. In the authors' experience, while working in teams across temporal perspectives, including on the present article, we have found that even when there is mutual respect and clear communication, there will still be moments of confusion, disagreement, or even tension. Such barriers are not insurmountable, however, in working to overcome epistemological tangles, the resulting insights are typically deeper and more rewarding. In the end, ecologists seek to understand the patterns and processes of life on Earth. That history extends nearly 4 billion years; every moment has something to offer our ecological understanding.

## Conclusions

Paleo- and neoecologists ask many of the same questions, engage with the same theories, and produce knowledge relevant to the same practical applications. This should come as no surprise, because the originators of the ecological discipline made no distinctions on the basis of methodology or temporal framings. Although field specialization has led to important conceptual and methodological advancements, the collective project of ecology—to understand the natural world and its workings—will be improved by deepening engagement of ecologists in working across timescales. In his 2016 Recent Advances lecture at the Ecological Society of America Annual Meeting, Quaternary paleoecologist Jack Williams noted that Earth's climate system is moving to a state unlike any in the instrumental record, and that various geological time periods are useful model systems for studying states and rates of climate and ecological change beyond what may be observed in the present, concluding that in a dynamic world, we are all paleoecologists now. Building on that unifying message, it

is also possible to say that as scientists seeking to understand species and their interactions, we're also all ecologists now. Organisms, and their ecosystems are the outcomes of processes spanning the 4.5-billion-year history of the Earth and, therefore, transcend the arbitrary temporal constraints researchers place on them. Collaboration across timescales is eminently possible, as the many publications cited within this article demonstrate. It is our hope that the vision we have presented here inspires a return to our roots as curious, engaged natural historians and that by placing time as a central organizing principle within ecology, our approach will be broader, richer, more inclusive, and more capable of addressing the urgent ecological questions presented by our changing world.

## Acknowledgments

This article was written on Marsh Island in the unceded territory of the Penobscot Nation; we are grateful for their stewardship of these lands, and support them in their ongoing fight for land and water rights. Funding was provided by NASA Exobiology grant no. 80NSSC20K0617 to JLG, NSF CAREER grant no. EAR-1753186 to JLG, NSF Graduate Research Fellowship under grant no. 1840992 to MML, a New England Botanical Society grant to AT, and the Janet Waldron Dissertation Fellowship and American Association of University Women Dissertation Fellowship to KMH. The authors would also like to thank Avery Lamb, Brian McGill, and Jack Williams for early feedback on the manuscript and figures. We would also like to thank the four anonymous reviewers whose feedback greatly strengthened the manuscript. Finally, we'd like to thank Lauryn Hill for the musical styling that prompted us to reimagine the *reeducation* of paleo and neoecology as well as the Beatles who always remind us to *come together*.

## Author contributions

Lauren Azevedo-Schmidt (Conceptualization, Project administration, Supervision, Visualization, Writing - original draft, Writing - review & editing), Madeleine Landrum (Conceptualization, Visualization, Writing - original draft, Writing - review & editing), Meghan M. Spoth (Conceptualization, Visualization, Writing - original draft, Writing - review & editing), Nikhil R. Brocchini (Conceptualization, Visualization, Writing - original draft, Writing - review & editing), Kit M. Hamley (Conceptualization, Visualization, Writing - original draft, Writing - review & editing), Alessandro Mereghetti (Conceptualization, Visualization, Writing - original draft, Writing - review & editing), Andrea J. Tirrell

(Conceptualization, Visualization, Writing - original draft, Writing - review & editing), and Jacquelyn L. Gill (Conceptualization, Funding acquisition, Project administration, Resources, Supervision, Visualization, Writing - original draft, Writing - review & editing)

## Supplemental data

The underlying data used in this article is available at [BIOSCI](#) online.

## References cited

- Abraham JK, Perez KE, Downey N, Herron JC, Meir E. 2012. Short lesson plan associated with increased acceptance of evolutionary theory and potential change in three alternate conceptions of macroevolution in undergraduate students. *CBE—Life Sciences Education* 11: 152–164.
- Abram NJ, et al. 2021. Connections of climate change and variability to large and extreme forest fires in Southeast Australia. *Communications Earth and Environment* 2: 8. <https://doi.org/10.1038/s43247-020-00065-8>.
- Adeleye MA, Andrew SC, Gallagher R, Kaars SVD, Deckker PD, Hua Q, Haberle SG. 2023. On the timing of megafaunal extinction and associated floristic consequences in Australia through the lens of functional palaeoecology. *Quaternary Science Reviews* 316: 108263. <https://doi.org/10.1016/j.quascirev.2023.108263>.
- Anderson OR. 2021. Physiological ecology of ferns: Biodiversity and conservation perspectives. *International Journal of Biodiversity and Conservation* 13: 49–63.
- Ash JD, Givnish TJ, Waller DM. 2017. Tracking lags in historical plant species' shifts in relation to regional climate change. *Global Change Biology* 23: 1305–1315. <https://doi.org/10.1111/gcb.13429>.
- Azevedo-Schmidt L, Meineke EK, Currano ED. 2022. Insect herbivory within modern forests is greater than fossil localities. *Proceedings of the National Academy of Sciences* 119: e2202852119. <https://doi.org/10.1073/pnas.2202852119>.
- Azevedo-Schmidt L, Currano ED, Dunn RE, Gjieli E, Pittermann J, Sessa E, Gill JL. 2024. Ferns as facilitators of community recovery following biotic upheaval. *BioScience* 74: 322–332.
- Bakker ES, Gill JL, Johnson CN, Vera FWM, Sandom CJ, Asner GP, Svenning J-C. 2016. Combining paleo-data and modern enclosure experiments to assess the impact of megafauna extinctions on Woody vegetation. *Proceedings of the National Academy of Sciences* 113: 847–855. <https://doi.org/10.1073/pnas.1502545112>.
- Barak RS, Hipp AL, Cavender-Bares J, Pearse WD, Hotchkiss SC, Lynch EA, Callaway JC, Calcote R, Larkin DJ. 2016. Taking the long view: Integrating recorded, archeological, paleoecological, and evolutionary data into ecological restoration. *International Journal of Plant Sciences* 177: 90–102.
- Barnosky AD, Lindsey EL, Villavicencio NA, Bostelmann E, Hadly EA, Wanket J, Marshall CR. 2016. Variable impact of late-quaternary megafaunal extinction in causing ecological State shifts in North and South America. *Proceedings of the National Academy of Sciences* 113: 856–861. <https://doi.org/10.1073/pnas.1505295112>.
- Barreda VD, Cúneo NR, Wilf P, Currano ED, Scasso RA, Brinkhuis H. 2012. Cretaceous/paleogene floral turnover in Patagonia: Drop in diversity, low extinction, and a classopollis spike. *PLOS ONE* 7: e52455. <https://doi.org/10.1371/journal.pone.0052455>.
- Barrio IC, Hik DS, Jónsdóttir IS, Bueno CG, Mörsdorf MA, Ravolainen VT. 2016. Herbivory network: An international, collaborative effort to study herbivory in Arctic and alpine ecosystems. *Polar Science* 10: 297–302. <https://doi.org/10.1016/j.polar.2016.03.001>.
- Beer C, Zimov N, Olofsson J, Porada P, Zimov S. 2020. Protection of permafrost soils from thawing by increasing herbivore density. *Scientific Reports* 10: 4170. <https://doi.org/10.1038/s41598-020-60938-y>.
- Bennington BJ, Aronson. 2012. Reconciling scale in paleontological and neontological data: Dimensions of time, space, and taxonomy. Pages 39–67 in Louys J, ed. *Paleontology in Ecology and Conservation*. Springer. <https://doi.org/10.1007/978-3-642-25038-5>.
- Bennington JB, et al. 2009. Critical issues of scale in paleoecology. *PALAIOS* 24: 1–4. <https://doi.org/10.2110/palo.2009.S01>.
- Birks HJB. 2012. Ecological palaeoecology and conservation biology: Controversies, challenges, and compromises. *International Journal of Biodiversity Science, Ecosystem Services and Management* 8: 292–304. <https://doi.org/10.1080/21513732.2012.701667>.
- Birks HJB. 2019. Contributions of quaternary botany to modern ecology and biogeography. *Plant Ecology and Diversity* 12: 1646831. [www.tandfonline.com/doi/metrics/10.1080/17550874.2019.1646831?scroll=top](http://www.tandfonline.com/doi/metrics/10.1080/17550874.2019.1646831?scroll=top)
- Bishop BA, Anderson CW. 1990. Student conceptions of natural selection and its role in evolution. *Journal of Research in Science Teaching* 27: 415–427.
- Blonder B, Royer DL, Johnson KR, Miller I, Enquist BJ. 2014. Plant ecological strategies shift across the Cretaceous–Paleogene boundary. *PLOS Biology* 12: e1001949.
- Boulton AJ, Panizzon D, Prior J. 2005. Explicit knowledge structures as a tool for overcoming obstacles to interdisciplinary research. *Conservation Biology* 19: 2026–2029.
- Boulton CA, Belcher CM. 2019. A novel approach for predicting the probability of ignition of palaeofires using fossil leaf assemblages. *Palaeontology* 62: 715–730. <https://doi.org/10.1111/pala.12417>.
- Bowman DMJS, et al. 2011. The human dimension of fire regimes on Earth. *Journal of Biogeography* 38: 2223–2236. <https://doi.org/10.1111/j.1365-2699.2011.02595.x>.
- Brâthen KA, Pugnaire FI, Bardgett RD. 2021. The paradox of forbs in grasslands and the legacy of the Mammoth steppe. *Frontiers in Ecology and the Environment* 19: 584–592. <https://doi.org/10.1002/fee.2405>.
- Braun EL. 1947. Development of the deciduous forests of Eastern North America. *Ecological Monographs* 17: 211–219. <https://doi.org/10.2307/1943265>.
- Brock JMR, Perry GLW, Burkhardt T, Burns BR. 2018. Forest seedling community response to understorey filtering by tree ferns. *Journal of Vegetation Science* 29: 887–897. <https://doi.org/10.1111/jvs.12671>.
- Brusatte SL, et al. 2015. The Extinction of the Dinosaurs. *Biological Reviews* 90: 628–642. <https://doi.org/10.1111/brv.12128>.
- Buma B, et al. 2019. The value of linking paleoecological and neoecological perspectives to understand spatially-explicit ecosystem resilience. *Landscape Ecology* 34: 17–33. <https://doi.org/10.1007/s10980-018-0754-5>.
- Burke KD, Williams JW, Chandler MA, Haywood AM, Lunt DJ, Otto-Bliesner BL. 2018. Pliocene and eocene provide best analogs for near-future climates. *Proceedings of the National Academy of Sciences* 115: 13288–13293. <https://doi.org/10.1073/pnas.1809600115>.
- Catley KM, Novak LR. 2009. Digging deep: Exploring college students' knowledge of macroevolutionary time. *Journal of Research in Science Teaching* 46: 311–332.
- Cloud PE. 1959. Paleoecology: Retrospect and prospect. *Journal of Paleontology* 33: 926–962.
- Colles A, Hsiang Liow L, Prinzing A. 2009. Are specialists at risk under environmental change? Neoecological, paleoecological, and phylogenetic approaches. *Ecology Letters* 12: 849–863.
- Coop JD, et al. 2020. Wildfire-driven forest conversion in Western North American landscapes. *BioScience* 70: 659–673. <https://doi.org/10.1093/biosci/biaa061>.

- Cowie RH, Bouchet P, Fontaine B. 2022. The sixth mass extinction: Fact, fiction, or speculation? *Biological Reviews* 97: 640–663. <https://doi.org/10.1111/brv.12816>.
- Cowles HC. 1899. The ecological relations of the vegetation on the Sand Dunes of Lake Michigan, part I: Geographical relations of the dune floras. *Botanical Gazette* 27: 95–117. <https://doi.org/10.1086/327796>.
- Crist MR. 2023. Rethinking the focus on forest fires in federal wildland fire management: Landscape patterns and trends of non-forest and forest burned area. *Journal of Environmental Management* 327: 116718. <https://doi.org/10.1016/j.jenvman.2022.116718>.
- Cusser S, Bahlai C, Swinton SM, Robertson GP, Haddad NM. 2020. Long-term research avoids spurious and misleading trends in sustainability attributes of No-till. *Global Change Biology* 26: 3715–3725. <https://doi.org/10.1111/gcb.15080>.
- Cusser S, Helms J, Bahlai CA, Haddad NM. 2021. How long do population level field experiments need to be? Utilising data from the 40-year-old LTER Network. *Ecology Letters* 24: 1103–1111. <https://doi.org/10.1111/ele.13710>.
- Czajka CD, McConnell D. 2018. An exploratory study examining undergraduate geology students' conceptions related to geologic time and rates. *Journal of Geoscience Education* 66: 231–245.
- Daufresne T. 2013. Megafauna as a nutrient pump. *Nature Geoscience* 6: 679–680. <https://doi.org/10.1038/ngeo1932>.
- Delcourt HR, Delcourt PA. 1988. Quaternary landscape ecology: Relevant scales in space and time. *Landscape Ecology* 2: 23–44.
- Dietl GP. 2016. Brave new world of conservation paleobiology. *Frontiers in Ecology and Evolution* 4: 21. <https://doi.org/10.3389/fevo.2016.00021>.
- Dietl GP, Flessa KW. 2011. Conservation paleobiology: Putting the dead to work. *Trends in Ecology and Evolution* 26: 30–37. <https://doi.org/10.1016/j.tree.2010.09.010>.
- Dillon EM, et al. 2023. Challenges and directions in Analytical paleobiology. *Paleobiology* 49: 377–393. <https://doi.org/10.1017/pab.2023.3>.
- DiMichele WA, Behrensmeyer AK, Olszewski TD, Labandeira CC, Pandolfi JM, Wing SL, Bobe R. 2004. Long-term stasis in ecological assemblages: Evidence from the fossil record. *Annual Review of Ecology, Evolution, and Systematics* 35: 285–322. <https://doi.org/10.1146/annurev.ecolsys.35.120202.110110>.
- Donlan CJ, et al. 2006. Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *American Naturalist* 168: 660–681.
- Dornelas M, et al. 2013. Quantifying temporal change in biodiversity: Challenges and opportunities. *Proceedings of the Royal Society B* 280: 20121931. <https://doi.org/10.1098/rspb.2012.1931>.
- Doughty CE, Wolf A, Field CB. 2010. Biophysical feedbacks between the Pleistocene megafauna extinction and climate: The first human-induced global warming? *Geophysical Research Letters* 37: 2010GL043985. <https://doi.org/10.1029/2010GL043985>.
- Doughty CE, Wolf A, Malhi Y. 2013. The legacy of the pleistocene megafauna extinctions on nutrient availability in Amazonia. *Nature Geoscience* 6: 761–764. <https://doi.org/10.1038/ngeo1895>.
- Doughty CE, et al. 2016. Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography* 39: 194–203. <https://doi.org/10.1111/ecog.01587>.
- Eshach H, Fried MN. 2005. Should science be taught in early childhood?. *Journal of Science Education and Technology* 14: 315–336.
- Estes L, Elsen PR, Treuer T, Ahmed L, Caylor K, Chang J, Choi JJ, Ellis EC. 2018. The spatial and temporal domains of modern ecology. *Nature Ecology and Evolution* 2: 819–826. <https://doi.org/10.1038/s41559-018-0524-4>.
- Fenton CL. 1935. Viewpoints and objects of paleoecology. *Journal of Paleontology* 9: 63–78.
- Flessa KW, Jackson ST. 2005. Forging a common agenda for ecology and paleoecology. *BioScience* 55: 1030. [https://doi.org/10.1641/0006-3568\(2005\)055\[1030:FACAFE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[1030:FACAFE]2.0.CO;2).
- Fordham DA, et al. 2020. Using paleo-archives to safeguard biodiversity under climate change. *Science* 369: eabc5654. <https://doi.org/10.1126/science.abc5654>.
- Foster DR, Schoonmaker PK, Pickett STA. 1990. Insights from paleoecology to community ecology. *Trends in Ecology and Evolution* 5: 119–122.
- Gaiser EE, et al. 2020. Long-term ecological research and evolving frameworks of disturbance ecology. *BioScience* 70: 141–156. <https://doi.org/10.1093/biosci/biz162>.
- Gallegos SC, Hensen I, Saavedra F, Schleuning M. 2015. Bracken fern facilitates tree seedling recruitment in tropical fire-degraded habitats. *Forest Ecology and Management* 337: 135–143. <https://doi.org/10.1016/j.foreco.2014.11.003>.
- Gavin DG, et al. 2014. Climate refugia: Joint inference from fossil records, species distribution models and phylogeography. *New Phytologist* 204: 37–54. <https://doi.org/10.1111/nph.12929>.
- Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* 326: 1100–1103. <https://doi.org/10.1126/science.1179504>.
- Gill JL, Williams JW, Jackson ST, Donnelly JP, Schellinger GC. 2012. Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio. *Quaternary Science Reviews* 34: 66–80.
- Goodenough AE, Webb JC. 2022. Learning from the past: Opportunities for advancing ecological research and practice using palaeoecological data. *Oecologia* 199: 275–287. <https://doi.org/10.1007/s00442-022-05190-z>.
- Greenler SM, et al. 2024. Blending Indigenous and Western science: Quantifying cultural burning impacts in Karuk Aboriginal Territory. *Ecological Applications* 34: e2973.
- Groff DV, McDonough MacKenzie C, Pier JQ, Shaffer AB, Dietl GP. 2023. Knowing but not doing: Quantifying the research-implementation gap in conservation paleobiology. *Frontiers in Ecology and Evolution* 11: 1058992. <https://doi.org/10.3389/fevo.2023.1058992>.
- Harrault L, Milek K, Jardé E, Jeanneau L, Derrien M, Anderson DG. 2019. Faecal biomarkers can distinguish specific mammalian species in modern and past environments. *PLOS ONE* 14: e0211119. <https://doi.org/10.1371/journal.pone.0211119>.
- Hunter ML, Jr, Jacobson GL, Jr, Webb T. 1988. Paleoecology and the course-filter approach to maintaining biological diversity. *Conservation Biology* 2: 375–385.
- Hyvarinen O, Beest MT, Roux EL, Kerley G, De Groot E, Vinita R, Cromsigt JPM. 2021. Megaherbivore impacts on ecosystem and Earth system functioning: The current State of the science. *Ecography* 44: 1579–1594. <https://doi.org/10.1111/ecog.05703>.
- Jablonski D, Sepkoski J, Jr. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77: 1367–1378.
- Jackson ST. 2001. Integrating ecological dynamics across timescales: Real-time, Q-time, and deep-time. *Palaeos* 16: 1–2.
- Jackson ST. 2012. Representation of flora and vegetation in quaternary fossil assemblages: Known and unknown knowns and unknowns. *Quaternary Science Reviews* 49: 1–15.
- Jackson ST, Blois JL. 2015. Community ecology in a changing environment: Perspectives from the quaternary. *Proceedings of the National Academy of Sciences* 112: 4915–4921. <https://doi.org/10.1073/pnas.1403664111>.

- Johnson CN. 2009. Ecological consequences of late quaternary extinctions of megafauna. *Proceedings of the Royal Society B* 276: 2509–2519. <https://doi.org/10.1098/rspb.2008.1921>.
- Kalinowski ST, Leonard MJ, Andrews TM, Litt AR. 2013. Six classroom exercises to teach natural selection to undergraduate biology students. *CBE—Life Sciences Education* 12: 483–493.
- Karp AT, Faith JT, Marlon JR, Staver AC. 2021. Global response of fire activity to late quaternary grazer extinctions. *Science* 374: 1145–1148. <https://doi.org/10.1126/science.abj1580>.
- Kartzinel TR, Chen PA, Coverdale TC, Erickson DL, Kress WJ, Kuzmina ML, Rubenstein DI, Wang W, Pringle RM. 2015. DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proceedings of the National Academy of Sciences* 112: 8019–8024. <https://doi.org/10.1073/pnas.1503283112>.
- Keeley JE, Pausas JG, Rundel PW, Bond WJ, Bradstock RA. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406–411. <https://doi.org/10.1016/j.tplants.2011.04.002>.
- Kelley PH, Fastoversusky DE, Wilson MA, Laws RA, Raymond A, Bickford ME. 2013. From paleontology to paleobiology: A half-century of progress in understanding life history. *Geological Society of America Special Paper* 500: 191–232.
- Kiessling W, Raja NB, Roden VJ, Turvey ST, Saupe EE. 2019. Addressing priority questions of conservation science with palaeontological data. *Philosophical Transactions of the Royal Society B* 374: 20190222. <https://doi.org/10.1098/rstb.2019.0222>.
- Klemow K, Berkowitz A, Cid C, Middendorf G. 2019. Improving ecological education through a four-dimensional framework. *Frontiers in Ecology and the Environment* 17: 71–71. <https://doi.org/10.1002/fee.2013>.
- Koch PL, Barnosky AD. 2006. Late quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics* 37: 215–250.
- Larson ER, Kipfmüller KF, Johnson LB. 2021. People, fire, and pine: Linking human agency and landscape in the boundary waters canoe area wilderness and beyond. *Annals of the American Association of Geographers* 111: 1–25.
- Libarkin JC, Kurdziel JP, Anderson SW. 2007. College student conceptions of geological time and the disconnect between ordering and scale. *Journal of Geoscience Education* 55: 413–422.
- Lin H. 2008. Opportunities and challenges for interdisciplinary research and education. *Journal of Natural Resources and Life Sciences Education* 37: 83–91.
- Lockwood R. 2008. Beyond the big five: Extinctions as experiments in the history of life. *Paleontological Society Papers* 14: 249–270.
- Lohaus R, Van De Peer Y. 2016. Of dups and dinos: Evolution at the K/pg boundary. *Current Opinion in Plant Biology* 30: 62–69. <https://doi.org/10.1016/j.pbi.2016.01.006>.
- Louys J, ed. 2012. *Paleontology in Ecology and Conservation*. Springer. <https://doi.org/10.1007/978-3-642-25038-5>.
- Lyu M, Xie J, Giardina CP, Vadeboncoeur MA, Feng X, Wang M, Ukonmaanaho L, Lin T-C, Kuznyakov Y, Yang Y. 2019. Understorey ferns alter soil carbon chemistry and increase carbon storage during reforestation with native pine on previously degraded sites. *Soil Biology and Biochemistry* 132: 80–92. <https://doi.org/10.1016/j.soilbio.2019.02.004>.
- Malhi Y, Doughty CE, Galetti M, Smith FA, Svenning J-C, Terborgh JW. 2016. Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proceedings of the National Academy of Sciences* 113: 838–846. <https://doi.org/10.1073/pnas.1502540113>.
- Manzano S, Julier ACM, Dirk CJ, Razafimanantsoa AHI, Samuels I, Petersen H, Gell P, Hoffman MT, Gillson L. 2020. Using the past to manage the future: The role of palaeoecological and long-term data in ecological restoration. *Restoration Ecology* 28: 1335–1342. <https://doi.org/10.1111/rec.13285>.
- McClenachan L, et al. 2024. Global research priorities for historical ecology to inform conservation. *Endangered Species Research* 54: 285–310.
- McGuire JL, Michelle Lawing A, Díaz S, Stenseth NC. 2023. The past as a lens for biodiversity conservation on a dynamically changing planet. *Proceedings of the National Academy of Sciences* 120: e2201950120. <https://doi.org/10.1073/pnas.2201950120>.
- McLauchlan KK, Higuera PE, Miesel J, Rogers BM, Schweitzer J, Shuman JK, Tepley AJ, et al. 2020. Fire as a fundamental ecological process: Research advances and frontiers. *Journal of Ecology* 108: 2047–2069. <https://doi.org/10.1111/1365-2745.13403>.
- Munguia P, Ojanguren AF. 2015. Bridging the gap in marine and terrestrial studies. *Ecosphere* 6: 1–4. <https://doi.org/10.1890/ES14-00231.1>.
- Murchie TJ, et al. 2021. Optimizing extraction and targeted capture of ancient environmental DNA for reconstructing past environments using the PalaeoChip Arctic-1.0 bait-set. *Quaternary Research* 99: 305–328. <https://doi.org/10.1017/qua.2020.59>.
- Napier JD, Chipman M. 2021. Emerging palaeoecological frameworks for elucidating plant dynamics in response to fire and other disturbance. *Global Ecology and Biogeography* 31: 138–154.
- NGSS Lead States. 2013. *Next Generation Science Standards: For States, by States*. National Academies Press.
- Nieto-Lugilde D, Blois JL, Bonet-García FJ, Giesecke T, Gil-Romera G, Seddon A. 2021. Time to better integrate paleoecological research infrastructures with neocology to improve understanding of biodiversity long-term dynamics and to inform future conservation. *Environmental Research Letters* 16: 095005. <https://doi.org/10.1088/1748-9326/ac1b59>.
- O'Donnell AJ, Boer MM, Lachlan McCaw W, Grierson PF. 2011. Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia: Vegetation and landscape connectivity control wildfire intervals. *Journal of Biogeography* 38: 112–124. <https://doi.org/10.1111/j.1365-2699.2010.02381.x>.
- Olofsson J, Post E. 2018. Effects of large herbivores on tundra vegetation in a changing climate, and implications for rewilding. *Philosophical Transactions of the Royal Society B* 373: 20170437. <https://doi.org/10.1098/rstb.2017.0437>.
- Osman N, Dorairaj D, Halim A, Zelan NIA, Rashid MAA, Zakaria RM. 2021. Dynamics of plant ecology and soil conservation: Implications for cut-slope protection. *Acta Oecologica* 111: 103744. <https://doi.org/10.1016/j.actao.2021.103744>.
- Owen-Smith NR. 1988. *Megaherbivores: the Influence of Very Large Body Size on Ecology*. Cambridge University Press.
- Owen-Smith NR. 2016. Pleistocene extinctions: The pivotal role of megaherbivores. *Paleobiology* 13: 351–362.
- Pausas JG, Keeley JE. 2009. A burning story: The role of fire in the history of life. *BioScience* 59: 593–601. <https://doi.org/10.1525/bio.2009.59.7.10>.
- Perrotti AG, Van Asperen E. 2019. Dung fungi as a proxy for megaherbivores: Opportunities and limitations for archaeological applications. *Vegetation History and Archaeobotany* 28: 93–104. <https://doi.org/10.1007/s00334-018-0686-7>.
- Perry GLW, Brazier RE, Wilmshurst JM. 2021. The role of paleoecology in understanding landscape-level ecosystem dynamics. Pages 384–397 in Francis RA, Millington JDA, Perry GLW Minor ES, eds. *The Routledge Handbook of Landscape Ecology*. Routledge.
- Pickett STA, Kolasa J, Armesto JJ, Collins SL. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* 54: 129. <https://doi.org/10.2307/3565258>.

- Pires APF, Amaral AG, Padgurschi MCG, Joly CA, Scarano FR. 2018. Biodiversity research still falls short of creating links with ecosystem services and Human well-being in a global hotspot. *Ecosystem Services* 34: 68–73. <https://doi.org/10.1016/j.ecoser.2018.10.001>.
- Post E. 2013. Erosion of community diversity and stability by herbivore removal under warming. *Proceedings of the Royal Society B: Biological Sciences* 280: 20122722.
- Price SA, Schmitz L. 2016. A promising future for integrative biodiversity research: An increased role of scale-dependency and functional biology. *Philosophical Transactions of the Royal Society B* 371: 20150228. <https://doi.org/10.1098/rstb.2015.0228>.
- Rappaciolo G, Blois JL. 2019. Understanding ecological change across large spatial, temporal and taxonomic scales: Integrating data and methods in light of theory. *Ecography* 47: 1247–1266.
- Ripple WJ, et al. 2015. Collapse of the world's largest herbivores. *Science Advances* 1: e1400103. <https://doi.org/10.1126/sciadv.1400103>.
- Roos CI, et al. 2021. Native American fire management at an ancient wildland–urban interface in the Southwest United States. *Proceedings of the National Academy of Sciences* 118: e2018733118.
- Rudwick MJS. 1998. Lyell and the Principles of Geology. *Geological Society*.
- Rule S. 2012. The aftermath of megafauna extinction: Ecosystem transformation in Pleistocene Australia. *Science* 335: 1483.
- Rull V. 2010. Ecology and palaeoecology: Two approaches, one objective. *Open Ecology Journal* 3: 1–5. <https://doi.org/10.2174/1874213001003020001>.
- Sanchez-Castillo L, Kosugi K, Masaoka N, Kubota T. 2019. Ecological characteristics of fern species for slope conservation. *Journal of Mountain Science* 16: 504–515.
- Schmitt M, Mehlreter K, Sundue M, Testo W, Watanabe T, Jansen S. 2017. The evolution of aluminum accumulation in ferns and lycophytes. *American Journal of Botany* 104: 573–583. <https://doi.org/10.3732/ajb.1600381>.
- Schulte P, et al. 2010. The Chicxulub asteroid impact and mass extinction at the Cretaceous–Paleogene boundary. *Science* 327: 1214–1218. <https://doi.org/10.1126/science.1177265>.
- Seddon AWR, et al. 2014. Looking forward through the past: Identification of 50 priority research questions in palaeoecology. *Journal of Ecology* 102: 256–267. <https://doi.org/10.1111/1365-2745.12195>.
- Sepkoski D. 2005. Stephen Jay Gould, Jack Sepkoski, and the “quantitative revolution” in American paleobiology. *Journal of the History of Biology* 38: 209–237.
- Silvertown J, et al. 2010. Environmental myopia: A diagnosis and a remedy. *Trends in Ecology and Evolution* 25: 556–561. <https://doi.org/10.1016/j.tree.2010.06.015>.
- Smith FA, Boyer AG. 2012. Losing time? Incorporating a deeper temporal perspective into modern ecology. *Frontiers of Biogeography* 4: F5FBG12562.
- Smith FA, Hammond JI, Balk MA, Elliott SM, Kathleen Lyons S, Pardi MI, Tomé CP, Wagner PJ, Westover ML. 2016. Exploring the influence of ancient and historic megaherbivore extirpations on the global methane budget. *Proceedings of the National Academy of Sciences* 113: 874–879. <https://doi.org/10.1073/pnas.1502547112>.
- Smith JA, Durham SR, Dietl GP. 2017. Conceptions of long-term data among marine conservation biologists and what conservation paleobiologists need to know. Pages 23–54 in Tyler CL Schneider CL, eds. *Marine Conservation Paleobiology*. Springer.
- Smith J, et al. 2023. BioDeepTime: A database of biodiversity time series for modern and fossil assemblages. *Global Ecology and Biogeography* 32: 1680–1689. <https://doi.org/10.1111/geb.13735>.
- Stiles E, Wilf P, Iglesias A, Gandolfo MA, Rubén Cúneo N. 2020. Cretaceous–Paleogene plant extinction and recovery in Patagonia. *Paleobiology* 46: 445–469. <https://doi.org/10.1017/pab.2020.45>.
- Sutherland WJ, et al. 2013. Identification of 100 fundamental ecological questions. *Journal of Ecology* 101: 58–67. <https://doi.org/10.1111/1365-2745.12025>.
- Svenning J-C, et al. 2016. Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proceedings of the National Academy of Sciences* 113: 898–906. <https://doi.org/10.1073/pnas.1502556112>.
- Trend R. 2000. Conceptions of geological time among primary teacher trainees, with reference to their engagement with geoscience, history, and science. *International Journal of Science Education* 22: 539–555.
- Tschudy RH, Pillmore CL, Orth CJ, Gilmore JS, Knight JD. 1984. Disruption of the terrestrial plant ecosystem at the Cretaceous–tertiary boundary, Western Interior. *Science* 225: 1030–1032.
- Turner MG. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91: 2833–2849. <https://doi.org/10.1890/10-0097.1>.
- Turner MG, O'Neill RV, Gardner RH, Milne BT. 1989. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* 3: 153–162. <https://doi.org/10.1007/BF00131534>.
- Vajda V, Bercovici A. 2014. The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: A template for other extinction events. *Global and Planetary Change* 122: 29–49. <https://doi.org/10.1016/j.gloplacha.2014.07.014>.
- Verma M, Bühne HS, Lopes M, Ehrlich D, Sokovnina S, Hofhuis SP, Petorelli N. 2020. Can reindeer husbandry management slow down the shrubification of the Arctic? *Journal of Environmental Management* 267: 110636. <https://doi.org/10.1016/j.jenvman.2020.110636>.
- Wal R. 2006. Do herbivores cause habitat degradation or vegetation State transition? Evidence from the Tundra. *Oikos* 114: 177–186. <https://doi.org/10.1111/j.2006.0030-1299.14264.x>.
- Waldram MS, Bond WJ, Stock WD. 2008. Ecological engineering by a mega-grazer: White rhino impacts on a South African Savanna. *Ecosystems* 11: 101–112. <https://doi.org/10.1007/s10021-007-9109-9>.
- Walker LR. 1994. Effects of fern thickets on woodland development on landslides in Puerto Rico. *Journal of Vegetation Science* 5: 525–532. <https://doi.org/10.2307/3235979>.
- Westerling ALR. 2016. Increasing Western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society B* 371: 20150178. <https://doi.org/10.1098/rstb.2015.0178>.
- Whitlock C, Higuera PE, McWethy DB, Briles CE. 2010. Paleocological perspectives on fire ecology: Revisiting the fire-regime concept. *Open Ecology Journal* 3: 6–23.
- Wilf P, Carvalho MR, Stiles E. 2023. The end-Cretaceous plant extinction: Heterogeneity, ecosystem transformation, and insights for the future. *Extinction* 1: 1–10.
- Willis KJ, Bailey RM, Bhagwat SA, Birks HJB. 2010. Biodiversity baselines, thresholds and resilience: Testing predictions and assumptions using palaeoecological data. *Trends in Ecology and Evolution* 25: 583–591. <https://doi.org/10.1016/j.tree.2010.07.006>.
- Wingard GL, Schneider C, Dietl GP, Fordham D, eds. 2024. Integrating Conservation Biology and Paleobiology to Manage Biodiversity and Ecosystems in a Changing World. *Frontiers Media*. <https://doi.org/10.3389/978-2-8325-5085-4>.
- Wolkovich EM, Cook BI, McLauchlan KK, Davies TJ. 2014. Temporal ecology in the Anthropocene. Edited by Franck Courchamp. *Ecology Letters* 17: 1365–1379. <https://doi.org/10.1111/ele.12353>.
- Yang L, Huang Y, Vieira Lima L, Sun Z, Liu M, Wang J, Liu N, Ren H. 2021. Rethinking the ecosystem functions of dicranopteris, a widespread genus of ferns. *Frontiers in Plant Science* 11: 581513. <https://doi.org/10.3389/fpls.2020.581513>.

- Yasuhara M, Tittensor DP, Hillebrand H, Worm B. 2015. Combining marine macroecology and palaeoecology in understanding biodiversity: Microfossils as a model. *Biological Reviews* 92: 199–215.
- Yates KL, et al. 2018. Outstanding challenges in the transferability of ecological models. *Trends in Ecology and Evolution* 33: 790–802. <https://doi.org/10.1016/j.tree.2018.08.001>.
- Yuan S, Liu N, Ren H, Zhang H, Wang J. 2019. Do pioneer species enhance early performance of native species in subtropical shrublands? An examination involving six native species in South China. *Community Ecology* 20: 53–63. <https://doi.org/10.1556/168.2019.20.1.6>.
- Zhao J, Wan S, Li Z', Shao Y, Xu G, Liu Z, Zhou L, Fu S. 2012. Dicranopteris-dominated understory as major driver of intensive forest ecosystem in humid subtropical and tropical region. *Soil Biology and Biochemistry* 49: 78–87. <https://doi.org/10.1016/j.soilbio.2012.02.020>.
- Zimov SA, Zimov NS, Tikhonov AN, Chapin FS. 2012. Mammoth Steppe: A high-productivity phenomenon. *Quaternary Science Reviews* 57: 26–45. <https://doi.org/10.1016/j.quascirev.2012.10.005>.

---

**Received:** August 28, 2023. **Revised:** September 17, 2024. **Accepted:** September 30, 2024

© The Author(s) 2024. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact [journals.permissions@oup.com](mailto:journals.permissions@oup.com)