

LETTER • OPEN ACCESS

Time to better integrate paleoecological research infrastructures with neoecology to improve understanding of biodiversity long-term dynamics and to inform future conservation

To cite this article: Diego Nieto-Lugilde *et al* 2021 *Environ. Res. Lett.* **16** 095005

View the [article online](#) for updates and enhancements.

You may also like

- [Sedimentation adjacent to naturally eroding and breakwater-protected shorelines in Chesapeake Bay](#)
Cindy M Palinkas, Evamaria W Koch and Nicole Barth
- [Climate and anthropogenic controls on blue carbon sequestration in Hudson River tidal marsh, Piermont, New York](#)
D Peteet, J Nichols, D Pederson et al.
- [The characteristics of a relic steppe of Northeast Asia: refuges of the Pleistocene Mammoth steppe \(an example from the Lower Kolyma area\)](#)
M Shchelchkova, S Davydov, D Fyodorov-Davydov et al.

ENVIRONMENTAL RESEARCH
LETTERS

LETTER

OPEN ACCESS

RECEIVED
28 December 2020REVISED
22 July 2021ACCEPTED FOR PUBLICATION
6 August 2021PUBLISHED
24 August 2021

Original content from
this work may be used
under the terms of the
[Creative Commons
Attribution 4.0 licence](#).

Any further distribution
of this work must
maintain attribution to
the author(s) and the title
of the work, journal
citation and DOI.

Time to better integrate paleoecological research infrastructures
with neoecology to improve understanding of biodiversity
long-term dynamics and to inform future conservationDiego Nieto-Lugilde^{1,*} , Jessica L Blois² , Francisco J Bonet-García¹ , Thomas Giesecke^{3,4} ,
Graciela Gil-Romera^{5,6} and Alistair Seddon^{7,8} ¹ Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de Córdoba, Córdoba, Spain² Department of Life and Environmental Sciences, University of California-Merced, Merced, CA, United States of America³ Department of Palynology and Climate Dynamics, University of Goettingen, Goettingen, Germany⁴ Department of Physical Geography, Faculty Geoscience, Utrecht University, Utrecht, The Netherlands⁵ Department of Geography and Earth Science, Aberystwyth University, Aberystwyth, United Kingdom⁶ Department of Geoenvironmental Processes and Global Change, Instituto Pirenaico de Ecología—CSIC, Zaragoza, Spain⁷ Department of Biological Sciences, University of Bergen, Bergen, Norway⁸ Bjerknes Centre for Climate Research, Bergen, Norway

* Author to whom any correspondence should be addressed.

E-mail: dnieto@uco.es**Keywords:** research infrastructures, paleoecology, neoecology, global changes, climate change, environmental change, biodiversity loss**Abstract**

Anthropogenic pressures are causing a global decline in biodiversity. Successful attempts at biodiversity conservation requires an understanding of biodiversity patterns as well as the drivers and processes that determine those patterns. To deepen this knowledge, neoecologists have focused on studying present-day or recent historical data, while paleoecologists usually study long-term data through the composition of various biological proxies and environmental indicators. By establishing standard protocols or gathering databases, research infrastructures (RIs) have been instrumental to foster exchange and collaboration among scientists within neoecology (e.g. Global Information Biodiversity Facility or National Ecological Observatory Network) and paleoecology (e.g. Paleobiology Database, Neotoma Paleoecology Database or European Pollen Database). However, these two subdisciplines (and their RIs) have traditionally remained segregated although both provide valuable information that combined can improve our understanding of biodiversity drivers and underlying processes, as well as our predictions of biodiversity responses in the future. For instance, integrative studies between paleo- and neoecology have addressed the global challenge of biodiversity loss by validating climate and ecological models, estimating species fundamental niches, understanding ecological changes and trajectories, or establishing baseline conditions for restoration. Supporting and contributing to research infrastructures from both paleo- and neoecology, as well as their further integration, could boost the amount and improve the quality of such integrative studies. We argue this will enable improved capabilities to anticipate the impacts of global change and biodiversity losses. To boost such integration and illustrate our arguments, we (1) review studies integrating paleo- and neoecology to advance in the light of global changes challenge, (2) describe RIs developed in paleoecology, and (3) discuss opportunities for further integration of RIs from both disciplines (i.e. paleo- and neoecology).

1. Introduction

The pace of global change has accelerated since the 1950s, and society currently faces major challenges at the global scale (Steffen *et al* 2005). In fact, humans are potentially causing the sixth mass extinction in the history of life on Earth (Barnosky *et al* 2011, Ceballos *et al* 2015, 2017), and biodiversity loss has been recognized as one of the most relevant challenges that humanity must face in the coming decades (Diaz *et al* 2006, European Commission 2011, Gardner *et al* 2013). Anticipating those changes, especially those affecting biodiversity, has become one of the main goals for scientists from disparate disciplines such as climatology, geology, and/or ecology (Vitousek 1994, Bonan 2008, Heller and Zavaleta 2009, Allan *et al* 2015, Chaudhary and Mooers 2018). However, this global challenge, as many others, is a wicked (Rittel and Webber 1973, DeFries and Nagendra 2017) and multifaceted problem that requires many cooperative efforts if it is to be addressed (Whyte and Thompson 2012). Solving this environmental challenge will require an integrative study of several different interconnected components of the Earth system, which in turn will require interdisciplinary approaches, methods, resources, and efforts.

One of the most intriguing and elusive facets of the global change challenge is understanding the linkages between temporal scales when dealing with biodiversity loss and ecosystem degradation (Bunnell and Huggard 1999, Azae *et al* 2015). Many questions are still unsolved regarding this issue: e.g. To what extent does the past configuration of landscapes affect the current conservation status of species (Kissling *et al* 2012, Eiserhardt *et al* 2015)?; How far into the future should we expect ecological legacies to be influential (Moorhead *et al* 1999)?; To what extent can we use the structure of past ecosystems as analogs for present ones when we try to restore a degraded ecosystem (Suding *et al* 2004, Perring *et al* 2015, Wingard *et al* 2017)?; Can we use hindcasting methods to test the predictive ability of ecological forecasting models under no-analog environments (Maguire *et al* 2015, 2016, Fitzpatrick *et al* 2018)?; Can we anticipate the effects of climate change on biodiversity by understanding past events of biodiversity loss (Willis *et al* 2010, Barnosky *et al* 2011, Willis and MacDonald 2011)? What triggers abrupt and non-linear regime shifts in ecosystems (Ratajczak *et al* 2018)? Rather than providing an exhaustive list of pending work, those questions illustrate the importance of considering different time scales to understand and avoid biodiversity loss and conservation.

Answering these questions, however, requires a deep understanding of biodiversity patterns (e.g. species distributions, community composition and assembly, or macroecological patterns), drivers of change (e.g. geology, climate, fire, or human-induced landscape transformations) and processes

that determine those patterns. Neocologists have traditionally focused on studying current or recent historical processes (intra-annual to decadal or centennial) to address these questions, while paleoecologists have usually studied long-term processes (from decadal to millions of years) through the fossil record. Although this distinction and definition of paleo- and neoecology might be over-simplistic and, in fact, there are multiple exceptions (see Rull 2010, Reitalu *et al* 2014, Jackson and Blois 2015, and references therein), the two fields have traditionally been segregated because of multiple and diverse causes (e.g. differences in samples nature, different jargon, or different journals; see Rull 2010, Reitalu *et al* 2014, Jackson and Blois 2015, and references therein). Nevertheless, ecological elements and processes in the past, present and future are interconnected in a spatio-temporal continuum (Delcourt and Delcourt 1988, Turner *et al* 1989, Reitalu *et al* 2014). Therefore, both disciplines provide valuable information at different and complementary times scales that, combined, have the ability to improve our understanding of biodiversity drivers and underlying processes or improve predictions of biodiversity responses in the future (Rull 2010, Blois *et al* 2013, Williams *et al* 2013, Jackson and Blois 2015, Maguire *et al* 2015). Thus, further integrating these two perspectives is a necessary step towards understanding and anticipating potential ecological changes.

Research Infrastructures (RIs) may play a critical role in bridging the gap between both disciplines. RIs refer to tools specifically designed to enhance science, providing disparately large services to scientific communities (i.e. from physical infrastructures—experimental sites or facilities—to computational infrastructures—databases and data portals—, but also entities that define and manage standard protocols and/or universal identifiers of samples). Although this term has different meanings around the world, the European Commission has created a definition that properly gathers most of the ‘traits’ of being a RI (European Commission 2017): ‘*research infrastructures are facilities, resources and related services that are used by the scientific community to conduct top-level research in their respective fields and cover major scientific equipment or sets of instruments; knowledge-based resources such as collections, archives or structures for scientific information; enabling information and communication technology-based infrastructures such as grid, computing, software and communication, or any other entity of a unique nature essential to achieve excellence in research*’. This definition might include many initiatives from both neo- (e.g. Long Term Ecological Research networks—LTER—, National Ecological Observatory Network—NEON—, or the Global Biodiversity Information Facility—GBIF—), and paleoecology (e.g. Neotoma Paleocology Database—Neotoma—or Life Earth Consortium). By documenting data and protocols,

improving accessibility to data and analysis, as well as by exchanging and connecting databases and services, RIs might have a primary role in establishing collaborations within and between the two fields (Peters *et al* 2014, Bonet 2016, RISCAGE-project 2017). In our experience, while some of the neocology RIs are widely known and used by scientists from different fields (including paleoecology), paleoecology RIs remain comparatively less known and mostly used only by paleoecologists. However, paleoecology RIs are crucial to reveal insights about the long-term response of biodiversity to environmental and climate changes in the past.

In this manuscript, we aim to encourage integration between paleo- and neocology, through the integration of their RIs. Given the comparatively less popularization and use of paleoecological RIs, we focus on introducing paleoecology and its RIs to a broader audience. To do so, we provide a non-exhaustive review of fruitful studies which have successfully integrated paleo- and neocological data. Using these examples, we aim to describe some cooperation threads between these fields that could be useful to determine the present and future impacts of global change. Then, we describe the past and current initiatives in the paleoecological community to build RIs (i.e. to foster data sharing and collaborative studies), discuss some of their main opportunities and limitations, and suggest further steps to improve integration of paleo- and neocology through RIs. Additionally, for the those unfamiliar with paleoecology, we provide an overview of the nature of paleoecological data and their particularities (Box Paleoecological record) that should be taken into consideration when designing, adapting, connecting, integrating, and/or using RIs that host paleoecological specimens, data, models, or analytical procedures.

2. Integrating ecology and paleoecology: overview and needs

The importance of integrating paleo- and neocology has been recognized since the beginning of the 20th century (Clements 1924, Foster *et al* 1990, Schoonmaker and Foster 1991, Willis and Birks 2006, Willis *et al* 2007, Rull 2010, Reitalu *et al* 2014, Jackson and Blois 2015, and references therein). Indeed, both disciplines are increasingly exchanging theories (e.g. community assembly theories/rules; Jackson and Blois 2015), concepts (e.g. almost all niche-related concepts—realized and fundamental niche or disequilibrium; Veloz *et al* 2012, Nogués-Bravo *et al* 2016, Saarinen and Lister 2016), and/or tools (e.g. species distribution models, time series analyses or multivariate approaches). By combining elements from paleo- and neocology, these integrative studies provide insightful information to understand long term ecological processes and dynamics.

The relationship between biodiversity and climate is scientifically recognized and studied since Humboldt's foundational works (Von Humboldt and Bonpland 2009). This relationship is at the heart of biodiversity responses to global change. Indeed, anticipating those responses increasingly relies on models to predict climate in the future (Global Circulation Models and Regional Climate Models—GCMs and RCMs, respectively; Navarro-Racines *et al* 2020). Because models' predictions to the future cannot be validated, they are frequently hindcasted to past conditions and then validated with paleoecological data (both fossils and environmental proxies). This sort of validation has been, and will be, instrumental in intercomparison projects to quantify model uncertainties and to improve their performance (Pinot *et al* 1999). Similarly, paleoecological information can be used to validate ecological models used to predict biodiversity responses to global changes (Maguire *et al* 2016, Cheddadi *et al* 2017). These sorts of models are usually calibrated using neocological data and then projected into future conditions using climate simulations. These models can also be hindcasted using paleoclimate simulations and then validated against paleoecological records (Alba-Sánchez *et al* 2015). These validations can be used to select best models to calculate future predictions (e.g. Macias-Fauria and Willis 2012) or to quantify model uncertainties (e.g. Garrido-García *et al* 2018).

Fossil records provide the evidence necessary to both infer and study changes in species distribution and/or community composition (e.g. Foster *et al* 1990, Schoonmaker and Foster 1991, Davis 1994, Huntley 1996, Jackson and Overpeck 2000, Williams and Jackson 2007, Rull 2010, Ostling 2012, Jackson and Blois 2015). This information has been used to test ecological theory, such as niche-stability (Veloz *et al* 2012), or test for community assembly rules (Blois *et al* 2014). For instance, Veloz *et al* (2012) compared the climate distributions (based on paleoclimate simulations from GCMs) for fossil-pollen data from the Last Glacial Maximum (21–15 ka bp; LGM) to observed modern pollen assemblages. They found that certain taxa, such as *Fraxinus*, *Ostrya/Carpinus* and *Ulmus*, substantially shifted their realized niches from the late glacial period to present, whereas other taxa, such as *Quercus*, *Picea*, or *Pinus strobus*, had relatively stable realized niches. Consequently, Species Distribution Models (SDMs) for the former taxa had low predictive accuracy when projected to modern climates, despite demonstrating high predictive accuracy for late glacial pollen distributions. For the latter taxa, models tended to have higher predictive accuracy when projected to present. These findings reinforce the point that the realized niche at any time often represents only a subset of the climate conditions in which a taxon can persist and allow the authors to conclude that projections from SDMs into

Box: Paleocological record: nature and structure of the data

Paleoecologists study macro- and microscopic fossils (e.g. shells, bones, spores, plant tissues, pollen, or resistant structures of unicellular organisms), in combination with paleoenvironmental indicators (e.g. sedimentological, geochemical, or tree-ring records), from a particular location (Maguire *et al* 2015) to understand interactions between organisms and between organisms and their environment in the past. Records are usually derived from sedimentary deposits with favorable conditions for preservation of biological samples (e.g. lake bottoms, peat bogs, tar pits, biogenic accumulations as middens). However, they can also be found in archeological deposits or open-air settings. Both macro- and microscopic fossils can provide information about the occurrence (presence, but not absence) and/or relative abundance from a wide range of organisms (table 1). Stable isotopes (as indicators of climatic conditions or diet; Crowley and Samonds 2013) and charcoal (as indicator of fire history or regimes; Clark 1988, Clark *et al* 1998, Power *et al* 2008, Gil-Romera *et al* 2010, Valsecchi *et al* 2013, López-Sáez *et al* 2016, Marlon *et al* 2016) are among the most frequent records of paleoenvironmental conditions.

The strength of fossil data lies in their ability to document biological and ecological patterns on time scales of decades to millions of years; in some cases, as series of continuous records (e.g. microfossils from sedimentary deposits like lakes and marine cores), in others, as discontinuous samples in time (e.g. plant or vertebrate macrofossil remains in discrete alluvial deposits). For instance, continuous deposits (e.g. diatoms, dinoflagellates, pollen and fungal spores), as well as rodent middens, deposits in caves, tar pits, and shallow marine deposits (with marine invertebrates) have been used to study dynamics of ecological communities (Faegri and Iversen 1975, Odgaard 1999, Maguire *et al* 2015). Palynology stands out in this regard since it often provides continuous information about the relative abundances for certain taxa of land plants (see taxonomic biases below). Note that abundances from the paleoecological record are usually relative abundances. Hence, they might be difficult to compare with abundance data from neoecological studies.

For certain taxa it is possible to estimate their continuous occurrence by using indirect indicators from other continuous paleo records (e.g. herbivores from dung fungal spores; Gill *et al* 2012, Perrotti and Van Asperen 2019). The study of dynamics for taxa with a discontinuous fossil record requires pooling information from different time periods.

Most fossil records are multivariate, indicating the relative composition and/or the co-occurrence of multiple species in a particular region, allowing both single- and multiple-taxa studies (Maguire *et al* 2015, Nieto-Lugilde *et al* 2018). Although single-taxon fossils (e.g. many macrofossils) are also frequent, they can still be used to infer community composition (e.g. allowing analysis of plant and animal communities altogether) by combining data from different taxa in a particular region and time period (Magri and Palombo 2013, Saarinen and Lister 2016). The increasing availability (Magri and Palombo 2013, Saarinen and Lister 2016) and accessibility (Saarinen and Lister 2016) of fossil data enables pooling information for multiple taxa from different locations and time periods, which strengthen the ability of the fossil record to study multivariate biodiversity patterns through time.

Like all ecological data, fossil records are potentially affected by several types of uncertainty (namely temporal, taxonomic, and taphonomic; Maguire *et al* 2015, Nieto-Lugilde *et al* 2018). For instance, taphonomic uncertainties arise from the geological processes that biological remains undergo since they originate until their fossilized forms are found (movement of the remain, sedimentation and burial, etcetera). Despite these uncertainties, it is possible to make insightful reconstructions about the variability of past landscapes and environments, especially if key features of the fossil record are assessed, quantified, and documented during the analytical process. New developments in proxy-system modelling encourage that each step of the analytical process (i.e. sampling, processing, analyzing, dating, and identifying the samples) are documented so that any uncertainties can be incorporated in either qualitative or quantitative ways (e.g. Jackson 2012, Evans *et al* 2013, Seddon *et al* 2019). In fact, paleoecology has a long tradition in those processes.

Temporal uncertainty is usually high relative to most neoecological observations and most frequently arises from the fact that the age of fossil samples needs to be inferred. Sometimes the fossil samples are dated directly by different dating techniques (e.g. radionuclides of C or U/Th, amino acid racemization, or luminescence dating) depending on the nature of the sample and/or the age. Each technique has its own assumptions and potential biases, which lead to different levels of uncertainty. Age estimates can also be indirect. In these cases, such as pollen grains from sediments, fossils are not directly dated, but age is inferred indirectly through age-depth models based on certain control points (Blaauw 2010). The use of such models implies an increasing level of uncertainty (Blaauw and Christen 2011, Blois *et al* 2011). Sedimentation rates may change through time, affecting the accumulation rates and thus producing non-regular time intervals in sediment cores. Nonetheless, developing reliable age models to the interface between paleo and modern systems might be error prone (Tylmann *et al* 2016, Arias-Ortiz *et al* 2018).

Spatial uncertainty in the fossil record is generally recognized by the fact that the absence of fossil evidence does not indicate the absence of such taxon, because there might not be appropriate conditions for fossilization and/or preservation (Laplana and Sevilla 2013). Although, this challenge of presence-only data is also common in many present-day biodiversity datasets, the additional uncertainties, and limitations of the paleoecological datasets make it more difficult to circumvent. Furthermore, fossil samples might be affected by taphonomic processes due to erosion, topographical changes, tectonic plate dynamics and/or animal and human action (Varela *et al* 2011, Martín-Perea *et al* 2019). Fossil remains can often be incomplete or degraded, making identification difficult. In other cases, like pollen grains, fossil remains are identified at higher taxonomic levels (e.g. genus or family; Rull 2012) because they are morphologically similar or do not provide enough information to distinguish between taxonomic units (Alba-Sánchez *et al* 2010). Other taphonomic uncertainties arise because different organisms fossilize and preserve differently, leading to a positive bias towards those groups with better preservation (Behrensmeyer *et al* 2000). Furthermore, pollen grains do not linearly correlate with vegetation abundance. For instance, *Pinus* can disperse very long distances before deposition, blurring the signal of the local taxon occurrence (Bunting *et al* 2004, Broström *et al* 2016, Hicks 2001, Lisitsyna *et al* 2012, Goring *et al* 2013). Factors like weather, pollen morphology, depositional basin size, and especially pollen productivity affect such uncertainty (Davis 2000, Bunting *et al* 2004, Sugita 2007b, Sugita 2007a, Hellman *et al* 2009, Bunting *et al* 2013).

Table 1. Main taxonomic groups recorded in the fossil record and references to examples of studies that report fossil for such groups.

| Taxon | Example studies |
|-------------------------------------|-------------------------------|
| Diatoms | Roberts <i>et al</i> (2015) |
| Dinoflagellates | Kenfack <i>et al</i> (2012) |
| Fishes | Stewart and Rufolo (2020) |
| Tetrapods | Lakin and Longrich (2019) |
| Aquatic and land plants | Pisarcic <i>et al</i> (2003) |
| Fungi: from spores and/or sporocarp | Jackson (1994) |
| Cladocera | Novakova <i>et al</i> (2013) |
| Foraminifera | Uthicke <i>et al</i> (2012) |
| Ostracods | Von Barga <i>et al</i> (2016) |
| Chironomids | Brooks (2006) |
| Cyanobacteria | Golubic and Seong-Joo (1999) |
| Molluscs | D'Amico <i>et al</i> (2014) |

future climate conditions that are based solely on contemporary realized distributions are potentially misleading for assessing the vulnerability of species to future climate change.

Paleoecological information has also been used to fit multitemporal models, with the aim of better estimating the fundamental niche and partially

circumventing shifted-realized niches (Nogués-Bravo 2009). In this vein, Nogués-Bravo *et al* (2016) projected changes in abundance and conservation status under a climate warming scenario for 187 plant taxa using niche-based models calibrated with paleorecords for the last 21 000 years. Incorporating long-term data into niche-based models increased the magnitude of projected changes for abundance and community turnover. Those larger projected changes translated into different, and often more threatened, projected conservation status for declining taxa, compared with traditional and single-time approaches. Interestingly, they also found that few models predicted total disappearance of taxa, suggesting that these taxa are resilient if climate is the only extinction driver. These findings demonstrate how linking paleorecords and forecasting techniques have the potential to improve conservation assessments and inform future conservation measures. Furthermore, information derived from paleorecords can help to improve environmental management and decision making. For instance, information from paleolimnological studies has been proposed to select reference sites and determine reference conditions in those sites to define current aquatic ecosystem statuses and restoration goals in the light of the European Union

Water Framework Directive (Bennion and Battarbee 2007).

Paleoecological information can also help to understand biodiversity dynamics and responses to climate and anthropic changes (e.g. Garrido-García *et al* 2018, Gaüzère *et al* 2020). For instance, Lozano *et al* (2016) studied how hominin species affected large mammals' interactions during the Early and Middle Pleistocene in Western Eurasia, by constructing and analyzing paleo food-webs from the archaeo-paleontological records. Pleistocene food webs shared basic features with modern food webs, although several parameters differed significantly. Very interestingly, the results also highlight the central position of hominins in the trophic web, modifying energy fluxes. Other studies have identified the effect of human pressure on many other aspects of paleobiodiversity, like body size (Faurby and Svenning 2016) or equilibrium in plant functional trait responses to climate (Gaüzère *et al* 2020).

While the previous studies exemplify the use of paleoecological information with neoecological theories and tools, they are biased towards relatively recent time periods (mostly the Quaternary, and most specifically the Pleistocene and the Holocene). However, paleoecological information from distant periods in the past (millions of years ago) are also crucial to analyze and understand current and future patterns and responses of biodiversity. For instance, advances in molecular methods are allowing to analyze whole genomes, which enables to estimate phylogenies with unprecedented levels of confidence (Armstrong *et al* 2020). Furthermore, analytical methods have been developed to ensemble multiple phylogenies in megatrees, which increase the taxonomic breadth of phylogenies to cover the whole tree of life (Redelings and Holder 2017). However, dated fossils remain essential to constrain nodes' ages in all those phylogenetic trees (Anderson *et al* 2005, Beck 2008). Age calibrated trees are crucial to estimate speciation and extinction rates, as well as phylogenetic diversity, becoming essential for most eco-evolutionary studies.

The previous links between paleo and neoecology illustrate the relevance of such integrative studies and how they can advance the biodiversity loss and conservation agenda. However, this agenda is far from complete and there remain several areas of research that can benefit from further integration and advance in the study of ecological processes and dynamics within the context of long temporal scales (table 2).

3. RIs in paleoecology: state of the art

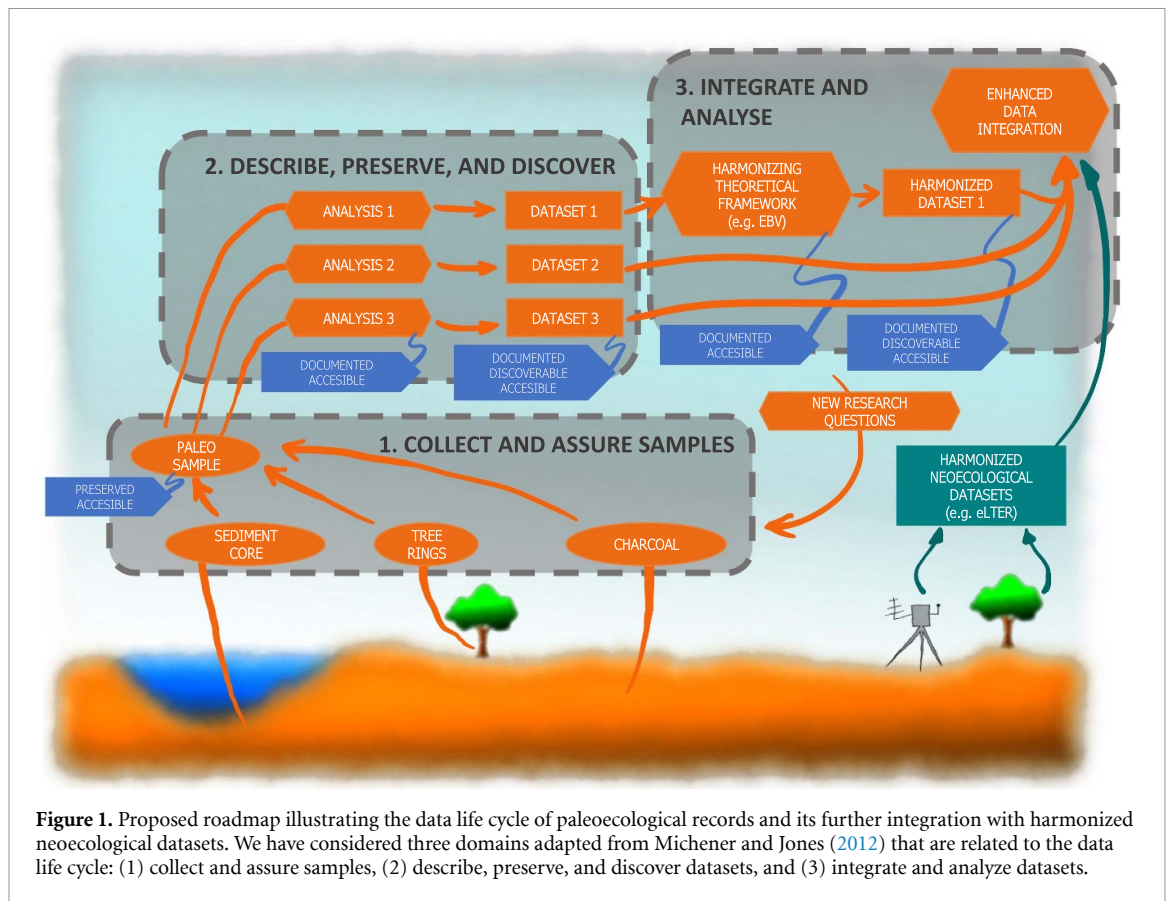
A stronger integration between paleo- and neoecology could help to circumvent limitations from both fields (e.g. temporal extent and data biases; Alba-Sánchez *et al* 2010, Williams *et al* 2013, Maguire *et al* 2015). More importantly, RIs could play an

Table 2. Research areas where a better integration between paleo- and neoecology can be relevant to address the global challenge of biodiversity loss and conservation.

| Research topic | References |
|--|--|
| Validating paleoclimate simulations by hindcasting models to the past and comparing them with fossil evidence of climate change | Gaard <i>et al</i> (2014) |
| Testing ecological theory and/or validating forecasting models | Veloz <i>et al</i> (2012) and Maguire <i>et al</i> (2016) |
| Expanding and improving estimates of species' ecological niches | Nogués-Bravo (2009) |
| Setting conservation baselines (e.g. pre-anthropogenic species distributions) | Grace <i>et al</i> (2019) |
| Determining the extent of historical vs. novel ecosystems, as well as ecosystem resistance, resilience, and dynamics | Froyd and Willis (2008), Lindbladh <i>et al</i> (2013), and Barnosky <i>et al</i> (2017) |
| Better understanding the multitemporal biodiversity and ecosystem responses to climate and other global changes | Willis and Birks (2006) and Jackson and Sax (2010) |
| Setting temporal constraints when calibrating phylogenetic trees and incorporating explicitly the fourth dimension in eco-evolutionary studies | Donoghue and Benton (2007) |

important role in boosting such integration by ensuring all stages involved in successful management and preservation of data for use and reuse (a data life cycle; Michener and Jones 2012) in paleoecology. Paleoecological community has developed their own set of RIs to cover different parts of the cycle (see below in this section). We propose a tentative roadmap illustrating the data life cycle of paleoecological records (figure 1) that integrate all possible actions of the cycle in three main stages: (1) collect and assure samples, (2) describe, preserve, and discover, and (3) integrate and analyze.

Standardized methods and protocols to collect, store, preserve, and document fossil records are well developed, some of them with long histories that trace to the foundations of their disciplines (e.g. fossil pollen; Faegri and Iversen 1950). Most frequently, paleoecological samples (e.g. fossils) are preserved in museums and biological collections (Jagt *et al* 2006), while others (e.g. sediment cores) are preserved in facilities of research institutions (Sampéris *et al* 2013). The International Geo Sample Number (IGSN) provides a system to assign unique identifiers to geological samples in order to locate, identify, and cite physical samples (including fossils



and paleoecological samples) with confidence, which is utterly relevant to ensure accessibility of those samples. Despite IGSN being established in 2011, it has already issued more than 7 million identifiers. Several organizations (e.g. European and American Geosciences Unions; EGU/AGU) recommend reporting IGSN for samples in their publications (e.g. poster sessions in AGU conferences and articles in AGU journals). Furthermore, important data repositories, like Pangaea (www.pangaea.de) or Neotoma DB (see below in this section), include fields for IGSN in their data structure. Hence, the first stage of the data life cycle of paleoecological records (figure 1) is well established and implemented. However, a wider use of the IGSN, by more journals and data repositories adopting the IGSN and making it mandatory, could improve the accessibility of samples.

Similarly, methods and protocols to analyze paleoecological samples and produce useful information (e.g. depth-age models and sedimentation rates, microorganisms/charcoal counts, or isotope ratios) are generally well developed and standardized. Furthermore, there is also a long tradition in the paleosciences to build databases that store, preserve, and share this processed information (see table 3 for some of the main paleoecological databases). For instance, in the 1980s, several databases, like the European Pollen Database (EPD) or the North American Pollen Database (NAPD) emerged to preserve and share Quaternary

pollen data at continental scales (Pollen Database Administration 2007, Fyfe *et al* 2009, Grimm *et al* 2018). More recently, these initiatives have been complemented with the development of more databases covering different taxonomic groups/proxies and/or temporal scales and resolutions (e.g. paleobiology Database—PBDB—Global Charcoal Database), database aggregations (e.g. Neotoma), data repositories (e.g. Pangaea), or metadatabases (compiled during the execution of research projects; e.g. Past Global Changes metadatabases). Although some paleoecological subfields might lack such developments, overall, the second stage of the data life cycle of paleoecological records (figure 1) is also well advanced and implemented.

The paleosciences also have a long tradition of collaborative and integrative projects and initiatives. For instance, in 1991 the National Science Foundation funded the Past Global Changes project (www.pastglobalchanges.org), which encourages international and interdisciplinary collaborations to understand the Earth's past environment, in order to obtain better predictions of future climate and environment and inform strategies for sustainability. More recent developments include the Earth Life Consortium (<http://earthlifeconsortium.org>; Uhen *et al* 2018) or the EarthCube community (www.earthcube.org), which have common and overlapping objectives. The Earth Life Consortium aims to develop an Application Programming Interface

Table 3. Some of the more relevant and comprehensive paleoecological databases in terms of spatial, temporal, or taxonomic extent.

| Name | Hyper-link | Scope |
|---|--|---|
| European Pollen Database (EPD) | www.europeanpollen-database.net | Store information of palynological remains (e.g. pollen, spores, charcoal, etc) from Eurasia during the Pleistocene and Holocene. |
| Neotoma Database | www.neotomadb.org | Gather and store all sort of paleoecological data (i.e. pollen, spores, mammals, beetles, ostracods, diatoms, isotopes, etc) at global scale encompassing the Pliocene and Quaternary. |
| Paleobiology Database (PBDB) | paleobiodb.org | Store data of fossil from all taxonomic groups at global scale from all geological time periods. |
| Neomap Database | www.ucmp.berkeley.edu/miomap | Store data of fossil mammals from North America during the Miocene. |
| New and Old Worlds (NOW) Database | www.helsinki.fi/science/now | Store data of fossils of terrestrial mammals at global scale during the Cenozoic. |
| EDNA Fossil Insects Database | edna.palass-hosting.org | Store data of insects at global scale during the Paleozoic, Mesozoic, and Cenozoic. |
| Pangaea Data repository | www.pangaea.de | Archive, publish and distribute georeferenced data from earth system research. |
| PAGES databases and metadatabases - e.g. Global Charcoal Database | www.pastglobalchanges.org/my-pages/data - e.g. www.paleofire.org/index.php | Facilitate activities that address past changes in the Earth System in a quantitative and process-oriented way in order to improve predictions of future climate and environment, and inform strategies for sustainability. Working groups in PAGES have developed databases and metadatabases to support their projects. |

(API) to interconnect and interoperate databases (i.e. Neotoma and the PBDB). EarthCube is more ambitious and aims to boost data science, integration, and collaboration across the geosciences by developing many types of cyberinfrastructures (and not only APIs to interoperate databases). Two of the main outcomes from EarthCube activities are the LinkedEarth (<http://linked.earth>; Emile-Geay *et al* 2018) and the Linked paleo Data (<http://lipd.net>; McKay and Emile-Geay 2018) projects. LinkedEarth aims to better organize and share Earth Science data, especially paleoclimate information, through curation, developing standards to store and share paleodata, and crafting tools to analyze those data; Linked paleo Data aims to develop the framework (which includes data structure, API, and tools) necessary to reach the goals of LinkedEarth. While APIs and cyberinfrastructures would allow a decentralized interoperability of databases, databases like Neotoma have started to centralize and aggregate other databases (e.g. the EPD has started the migration into Neotoma). Note that all these initiatives (developments and databases aggregations) contribute to the third stage of the data life cycle of paleoecological records (figure 1) but remain limited to the paleoscience domain. The enhancing Paleontological and Neontological Data Discovery API (ePANDDA; <https://epandda.org>), a project in active development, has developed an API that connects data from the paleo and neocological domains. More specifically, it interconnects the PBDB, iDigpaleo (www.idigpaleo.org), and iDigBio (www.idigbio.org). In line with the integration of paleo- and neocological data, some of the paleo-databases have been integrated with

present-day database aggregators (e.g. the PBDB has been connected to GBIF).

4. Opportunities from closer integration

Most of the past and current initiatives occurring within the paleoecological community have a strong resemblance to the process followed by neoecologists when building RIs: e.g. definition of protocols and standards, data harmonization, use of metadata standards. The former suggests that paleoscience could benefit from a higher-level RI that organizes and coordinates all these initiatives. In fact, this gap has been partially filled by certain scientific initiatives like Past Global Changes (www.pastglobalchanges.org/) or Earth Life Consortium (<http://earthlifec consortium.org>). Realizing this gap, a recent white paper was submitted to the National Science Foundation (USA) to create a paleoecological cyberinfrastructure (Williams *et al* 2017). Nevertheless, the approval of this proposal would cover only part of the data life cycle. Alternatively, paleoecological RIs (i.e. data, procedures, analysis, and services) could also be directly integrated with neoecological RIs. In any case, further steps in the development of paleoecology RIs, should be made in a flexible and integrative approach that enable close collaborations and interoperability with neoecological RIs to elicit a stronger integration of both fields.

Regardless of the route taken, we describe next some of the aspects in which such integration can benefit both paleo- and neoecology and their RIs in terms of the three main stages of the data life cycle.

4.1. Collect and assure samples and data

Although protocols and standards for collecting and assuring paleoecological samples are well developed and established, RIs could foster harmonization by forcing to review, or create, if necessary, protocols and methods. Those protocols should cover collecting and assuring samples but also storing and curating information. Such RI would promote such protocols and methods (e.g. IGSN) among the participating entities, which would in turn ensure that samples are correctly stored, preserved and located, while data are correct, properly documented, searchable, and easily accessible. Integrating paleoecology with neocological RIs would have the additional advantage of sharing experience with other infrastructures also concerned with curation of samples (e.g. NEON biorepository; www.neonscience.org/data/neon-biorepository).

4.2. Describe, preserve, discover

Here, we see at least three main areas to develop for the integration of paleoecology and neocology and their RIs: (1) promoting the use of standards, (2) improving/completing paleoecological databases, and (3) increasing the discoverability and accessibility of paleoecological data.

Like the first stage of the data life cycle, RIs should promote the use of standards for describing, preserving, and discovering paleoecological data. This would require increasing the participation of the paleoecological community in the international initiatives defining Biodiversity Information Standards (e.g. www.tdwg.org) to consider and incorporate the peculiarities of the paleoecological information (e.g. modifying the Darwin Core, a standard to facilitate the sharing of information about biological diversity, according to modifications proposed from the Earth Life Consortium).

RIs can also help to improve and complete paleoecological databases. For many biological groups (like vertebrate fossils), the actual specimens are housed in museums with their own databases, which may or may not be easily exposed to the public or available for integration. Nonetheless, RIs are powerful agents to articulate institutions (see GBIF articulating more than a thousand of institutions around the world) and databases, which could help to mobilize all those museum records into the existing databases or the corresponding cyberinfrastructures (like GBIF itself). In this line, iDigBio is trying to mobilize specimens from both present-day and paleo collections. Of course, incorporating data into databases is not easy and serious difficulties are expected. For instance, the difficulty of incorporating taxonomic updates to data from legacy and/or institutional databases. Because these problems are not trivial, RIs should increase the participation of paleoscientists in current

initiatives dealing with taxonomic backbones (e.g. www.itis.gov) for present-day biodiversity. Furthermore, the use of common standards, apart from improving the description, preservation, and discoverability of the data (see above), should ease the combination and integration of paleoecological databases.

Although some paleoecological fields and databases have a long history of data sharing, many others are difficult to find and access. However, most of them (if not all) might be little known and/or difficult to use by non-experts. These aspects could be partially solved by creating or improving data portals where datasets and metadata are searchable, citable (via DOIs), and downloadable. Again, data contained in these portals should be compliant with international standards commonly used to document ecological and biodiversity data (e.g. Ecological Metadata Language, Darwin Core, etcetera). Furthermore, the existing databases and catalogs could be integrated into other initiatives like eLTER (www.lter-europe.net) or DataONE (www.dataone.org).

4.3. Integrate and analyze

Regarding the last stage of the data life cycle, we recognize at least two areas of interest for paleoecology. First, RIs could coordinate the implementation of standards and protocols to facilitate/automate data homogenization and standardization, which would elicit the harmonization of data among paleoecological fields (e.g. request data from pollen and diatoms for the same region and time in a single query). RIs would also help to develop tools that allow documenting workflows (e.g. statistical analysis or hindcasting and forecasting models; Bonet *et al* 2014), which could also be advanced with the integration of paleoecological workflows into Virtual Labs within LifeWatch ERIC (www.lifewatch.eu). Such workflows should be made with paleo- and neocology integration and interoperability in mind (e.g. getting paleo- and present-day data for a specific region in a single query). This would require database integration to overcome the numerous challenges described here. For instance, current neocological databases and RIs cannot tackle spatial, temporal, and taxonomical uncertainties that are idiosyncratic to paleoecological data (see Box Paleoecological record); whilst discrepancies in taxonomic nomenclatures between paleo- and neocological fields need to be addressed and resolved. Paleoecology could also join existing theoretical frameworks for indicators of biodiversity, like the essential biodiversity variables (e.g. <https://geobon.org/ebvs>; Pereira *et al* 2013). By generalizing beyond individual species data, these frameworks might provide an alternative to circumvent part of the issues in paleo- and neocological databases integration.

4.4. Networking activities

Finally, and regardless of the data life cycle, promoting networking activities is at the heart of RIs. Among the countless opportunities, we highlight the possibility to access to paleoecological facilities (e.g. laboratories, sampling sites, etcetera) through transnational activities, like the free access to RIs' facilities supported by the European Union (<https://ec.europa.eu/research/infrastructures/index.cfm?pg=access>). eLTER, EMSO, ACTRIS-2, INTERACT, AQUACOSM are several examples of European RIs that share their facilities and in which certain paleoecological facilities might fit. Furthermore, RIs can create training programs in the network of research facilities. These programs could train from other paleoecological fields as well as non-paleoecologists regarding appropriate paleoecological methods and work (i.e. collect, process, and analyze) with samples. These programs would reinforce all the initiatives from the RI regarding the data life cycle, but most importantly, it would bridge the gap between paleo- and neocology.

Taken together, all the previous confirms, not only that there is a potential for paleoecology being part of the environmental RI's ecosystem, but that environmental RI would benefit from that movement (i.e. a win-win situation). A lot of work has been advanced from both the paleo- and neocological community, but there is still plenty of work to be done. However, the importance of such integration to facing global challenges really deserves the attempt.

Data availability statement

No new data were created or analyzed in this study.

Acknowledgments

We thank John W Williams (U of Wisconsin) and three anonymous reviewers for their insightful comments and suggestions that helped to improve the manuscript. This research was sponsored by European Union Horizon 2020 Grant No. 654131 'COOP+: Cooperation of Research Infrastructures to address global challenges in the environmental field'. Diego Nieto-Lugilde is funded by projects Med-Refugia RTI2018-101714-B-I00 (*Ministerio de Ciencia e Innovación. Gobierno de España*) and Relict-Flora2 B-RNM-404-UGR18 (*Consejería de Economía, Innovación, Ciencia y Empleo. Junta de Andalucía*). Graciela Gil-Romera is funded by the DFG project FOR 2358.

ORCID iDs

Diego Nieto-Lugilde  <https://orcid.org/0000-0003-4135-2881>

Jessica L Blois  <https://orcid.org/0000-0003-4048-177X>

Francisco J Bonet-García  <https://orcid.org/0000-0002-4627-1442>

Thomas Giesecke  <https://orcid.org/0000-0002-5132-1061>

Graciela Gil-Romera  <https://orcid.org/0000-0001-5726-2536>

Alistair Seddon  <https://orcid.org/0000-0002-8266-0947>

References

- Alba-Sánchez F, López-Sáez J A, Nieto-Lugilde D and Svenning J-C 2015 Long-term climate forcings to assess vulnerability in North Africa dry argan woodlands *Appl. Veg. Sci.* **18** 283–96
- Alba-Sánchez F, López-Sáez J A, Pando B B, Linares J C, Nieto-Lugilde D and López-Merino L 2010 Past and present potential distribution of the Iberian Abies species: a phytogeographic approach using fossil pollen data and species distribution models *Divers. Distrib.* **16** 214–28
- Allan E et al 2015 Land use intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional composition *Ecol. Lett.* **18** 834–43
- Anderson C L, Bremer K and Friis E M 2005 Dating phylogenetically basal eudicots using rbcL sequences and multiple fossil reference points *Am. J. Bot.* **92** 1737–48
- Arias-Ortiz A, Masqué P, Garcia-Orellana J, Serrano O, Mazarrasa I, Marbà N, Lovelock C E, Lavery P S and Duarte C M 2018 Reviews and syntheses: ²¹⁰Pb-derived sediment and carbon accumulation rates in vegetated coastal ecosystems—setting the record straight *Biogeosciences* **15** 6791–818
- Armstrong J et al 2020 Progressive Cactus is a multiple-genome aligner for the thousand-genome era *Nature* **587** 246–51
- Azaele S, Maritan A, Cornell S J, Suweis S, Banavar J R, Gabriel D and Kunin W E 2015 Towards a unified descriptive theory for spatial ecology: predicting biodiversity patterns across spatial scales *Methods Ecol. Evol.* **6** 324–32
- Barnosky A D et al 2011 Has the Earth's sixth mass extinction already arrived? *Nature* **471** 51–7
- Barnosky A D et al 2017 Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems *Science* **355** eaah4787
- Beck R M D 2008 A dated phylogeny of marsupials using a molecular supermatrix and multiple fossil constraints *J. Mammal.* **89** 175–89
- Behrensmeyer A K, Kidwell S M and Gastaldo R A 2000 Taphonomy and paleobiology *Paleobiology* **26** 103–47
- Bennion H and Battarbee R 2007 The European Union water framework directive: opportunities for palaeolimnology *J. Paleolimnol.* **38** 285–95
- Blaauw M 2010 Methods and code for 'classical' age-modelling of radiocarbon sequences *Quat. Geochronol.* **5** 512–8
- Blaauw M and Christen J A 2011 Flexible paleoclimate age-depth models using an autoregressive gamma process *Bayesian Anal.* **6** 457–74
- Blois J L et al 2014 A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary *Ecography* **37** 1095–108
- Blois J L, Williams J W, Grimm E C, Jackson S T and Graham R W 2011 A methodological framework for assessing and reducing temporal uncertainty in paleovegetation mapping from late-Quaternary pollen records *Quat. Sci. Rev.* **30** 1926–39
- Blois J L, Zarnetske P L, Fitzpatrick M C and Finnegan S 2013 Climate change and the past, present, and future of biotic interactions *Science* **341** 499–504
- Bonan G B 2008 Forests and climate change: forcings, feedbacks, and the climate benefits of forests *Science* **320** 1444–9

- Bonet F J 2016 COOP+ project: fostering systematic global cooperation among international Research Infrastructures *ENVRplus Newsletter #2* 1–2
- Bonet F J, Pérez-Pérez R, Benito B M, De Albuquerque F S and Zamora R 2014 Documenting, storing, and executing models in Ecology: a conceptual framework and real implementation in a global change monitoring program *Environ. Model. Softw.* **52** 192–9
- Brooks S J 2006 Fossil midges (Diptera: chironomidae) as palaeoclimatic indicators for the Eurasian region *Quat. Sci. Rev.* **25** 1894–910
- Broström A, Sugita S, Gaillard M-J and Pilesjö P 2016 Estimating the spatial scale of pollen dispersal in the cultural landscape of southern Sweden *The Holocene* **15** 252–62
- Bunnell F L and Huggard D J 1999 Biodiversity across spatial and temporal scales: problems and opportunities *For. Ecol. Manage.* **115** 113–26
- Bunting M J, Farrell M, Broström A, Hjelle K L, Mazier F, Middleton R, Nielsen A B, Rushton E, Shaw H and Twiddle C L 2013 Palynological perspectives on vegetation survey: a critical step for model-based reconstruction of Quaternary land cover *Quat. Sci. Rev.* **82** 41–55
- Bunting M J, Gaillard M-J, Sugita S, Middleton R and Broström A 2004 Vegetation structure and pollen source area *Holocene* **14** 651–60
- Ceballos G, Ehrlich P R, Barnosky A D, García A, Pringle R M and Palmer T M 2015 Accelerated modern human-induced species losses: entering the sixth mass extinction *Sci. Adv.* **1** e1400253
- Ceballos G, Ehrlich P R and Dirzo R 2017 Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines *Proc. Natl Acad. Sci.* **114** E6089–96
- Chaudhary A and Mooers A O 2018 Terrestrial vertebrate biodiversity loss under future global land use change scenarios *Sustainability* **10** 2764
- Cheddadi R et al 2017 Microrefugia, climate change, and conservation of cedrus atlantica in the Rif mountains, morocco *Front. Ecol. Evol.* **5** 114
- Clark J S 1988 Particle motion and the theory of charcoal analysis: source area, transport, deposition, and sampling *Quat. Res.* **30** 67–80
- Clark J S, Lynch J, Stocks B J and Goldammer J G 1998 Relationships between charcoal particles in air and sediments in west-central Siberia *Holocene* **8** 19–29
- Clements F E 1924 *Methods and Principles of Paleo-Ecology* (Washington, DC: Carnegie Institution of Washington)
- Crowley B E and Samonds K E 2013 Stable carbon isotope values confirm a recent increase in grasslands in northwestern Madagascar *Holocene* **23** 1066–73
- D’Amico C, Esu D and Magnatti M 2014 Land mollusc palaeocommunity dynamics related to palaeoclimatic changes in the Upper Pleistocene alluvial deposits of Marche Apennines (central Italy) *Italian J. Geosci.* **133** 235–48
- Davis M B 1994 Ecology and paleoecology begin to merge *Trends Ecol. Evol.* **9** 357–8
- Davis M B 2000 Palynology after Y2K—understanding the source area of pollen in sediments *Annu. Rev. Earth Planet. Sci.* **28** 1–18
- DeFries R and Nagendra H 2017 Ecosystem management as a wicked problem *Science* **356** 265–70
- Delcourt H R and Delcourt P A 1988 Quaternary landscape ecology: relevant scales in space and time *Landsc. Ecol.* **2** 23–44
- Díaz S, Fargione J, Chapin III F S and Tilman D 2006 Biodiversity loss threatens human well-being *PLoS Biol.* **4** e277
- Donoghue P C J and Benton M J 2007 Rocks and clocks: calibrating the Tree of Life using fossils and molecules *Trends Ecol. Evol.* **22** 424–31
- Eiserhardt W L, Borchsenius F, Sandel B, Kissling W D and Svenning J-C 2015 Late Cenozoic climate and the phylogenetic structure of regional conifer floras world-wide *Glob. Ecol. Biogeogr.* **24** 1136–48
- Emile-Geay J, Khider D, McKay N P, Gil Y, Garijo D and Ratnakar V 2018 LinkedEarth: supporting paleoclimate data standards and crowd curation *Past. Glob. Change Mag.* **26** 2
- European Commission 2011 *Our Life Insurance, Our Natural Capital: An EU Biodiversity Strategy to 2020: Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions* (available at: http://ec.europa.eu/environment/nature/biodiversity/comm2006/pdf/EP_resolution_april2012.pdf)
- European Commission 2017 About research infrastructures *Infrastructures—Research and Innovation* (available at: <https://ec.europa.eu/research/infrastructures/index.cfm?pg=about>)
- Evans M N, Tolwinski-Ward S E, Thompson D M and Anchukaitis K J 2013 Applications of proxy system modeling in high resolution paleoclimatology *Quat. Sci. Rev.* **76** 16–28
- Faegri K and Iversen J 1950 *Textbook of Modern Pollen Analysis* (Ejnar Munksgaard, Copenhagen: Hafner Pub. Co.)
- Faegri K and Iversen J 1975 *Textbook of Pollen Analysis* (Munksgaard, Copenhagen: Hafner Pub. Co.)
- Faurby S and Svenning J-C 2016 Resurrection of the Island rule: human-driven extinctions have obscured a basic evolutionary pattern *Am. Nat.* **187** 812–20
- Fitzpatrick M C, Blois J L, Williams J W, Nieto-Lugilde D, Maguire K C and Lorenz D J 2018 How will climate novelty influence ecological forecasts? Using the Quaternary to assess future reliability *Glob. Change Biol.* **24** 3575–86
- Foster D, Schoonmaker P and Pickett S 1990 Insights from paleoecology to community ecology *Trends Ecol. Evol.* **5** 119–22
- Froyd C A and Willis K J 2008 Emerging issues in biodiversity & conservation management: the need for a palaeoecological perspective *Quat. Sci. Rev.* **27** 1723–32
- Fyfe R M et al 2009 The European Pollen Database: past efforts and current activities *Veget. Hist. Archaeobot.* **18** 417–24
- Gardner T A et al 2013 Biodiversity offsets and the challenge of achieving no net loss *Conserv. Biol.* **27** 1254–64
- Garrido-García J A, Nieto-Lugilde D, Alba-Sánchez F and Soriguer R C 2018 Agricultural intensification during the Late Holocene rather than climatic aridification drives the population dynamics and the current conservation status of *Microtus cabreræ*, an endangered Mediterranean rodent *J. Biogeogr.* **45** 448–60
- Gaüzère P, Iversen L L, Seddon A W R, Violle C and Blonder B 2020 Equilibrium in plant functional trait responses to warming is stronger under higher climate variability during the Holocene *Glob. Ecol. Biogeogr.* **29** 2052–66
- Gil-Romera G, Carrión J S, Pausas J G, Sevilla-Callejo M, Lamb H F, Fernández S and Burjachs F 2010 Holocene fire activity and vegetation response in South-Eastern Iberia *Quat. Sci. Rev.* **29** 1082–92
- Gill J L, Williams J W, Jackson S T, Donnelly J P and Schellinger G C 2012 Climatic and megaherbivory controls on late-glacial vegetation dynamics: a new, high-resolution, multi-proxy record from Silver Lake, Ohio *Quat. Sci. Rev.* **34** 66–80
- Golubic S and Seong-Joo L 1999 Early cyanobacterial fossil record: preservation, palaeoenvironments and identification *Eur. J. Phycol.* **34** 339–48
- Goring S, Lacourse T, Pellatt M G and Mathewes R W 2013 Pollen assemblage richness does not reflect regional plant species richness: a cautionary tale *J. Ecol.* **101** 1137–45
- Grace M, Akçakaya H R, Bennett E, Hilton-Taylor C, Long B, Milner-Gulland E J, Young R and Hoffmann M 2019 Using historical and palaeoecological data to inform ambitious species recovery targets *Phil. Trans. R. Soc. B* **374** 20190297
- Grimm E C, Blois J L, Giesecke T, Graham R W, Smith A J and Williams J W 2018 Constituent databases and data stewards in the Neotoma Paleocology Database: history, growth, and new directions *Past. Glob. Change Mag.* **26** 4–5

- Heller N E and Zavaleta E S 2009 Biodiversity management in the face of climate change: a review of 22 years of recommendations *Biol. Conserv.* **142** 14–32
- Hellman S, Bunting M J and Gaillard M-J 2009 Relevant Source Area of Pollen in patchy cultural landscapes and signals of anthropogenic landscape disturbance in the pollen record: a simulation approach *Rev. Palaeobot. Palynol.* **153** 245–58
- Hicks S 2001 The use of annual arboreal pollen deposition values for delimiting tree-lines in the landscape and exploring models of pollen dispersal *Rev. Palaeobot. Palynol.* **117** 1–29
- Huntley B 1996 Quaternary palaeoecology and ecology *Quat. Sci. Rev.* **15** 591–606
- Jackson S T 2012 Representation of flora and vegetation in Quaternary fossil assemblages: known and unknown knowns and unknowns *Quat. Sci. Rev.* **49** 1–15
- Jackson S T and Blois J L 2015 Community ecology in a changing environment: perspectives from the Quaternary *Proc. Natl Acad. Sci.* **112** 4915–21
- Jackson S T and Overpeck J T 2000 Responses of plant populations and communities to environmental changes of the late Quaternary *Paleobiology* **26** 194–220
- Jackson S T and Sax D F 2010 Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover *Trends Ecol. Evol.* **25** 153–60
- Jackson S T 1994 Pollen and spores in Quaternary lake sediments as sensors of vegetation composition: theoretical models and empirical evidence *Sedimentation of Organic Particles* ed Traverse A (Cambridge: Cambridge University Press) pp 253–86
- Jagt J W M, Van Bakel B W M, Fraaije R H B and Neumann C 2006 *In situ* fossil hermit crabs (Paguroidea) from northwest Europe and Russia: preliminary data on new records *Revista Mexicana De Ciencias Geológicas* **23** 364–9
- Kenfack P L, Ngaha P R N, Ekodeck G E, Ngueutchoua G, Kenfack P L, Ngaha P R N, Ekodeck G E and Ngueutchoua G 2012 Fossils dinoflagellates from the Northern Border of the douala sedimentary sub-basin (South-West Cameroon): age assessment and paleoecological interpretations *Geosciences* **2** 117–24
- Kissling W D, Baker W J, Balslev H, Barfod A S, Borchsenius F, Dransfield J, Govaerts R and Svenning J-C 2012 Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage *Glob. Ecol. Biogeogr.* **21** 909–21
- Lakin R J and Longrich N R 2019 Juvenile spinosaurs (Theropoda: spinosauridae) from the middle Cretaceous of Morocco and implications for spinosaur ecology *Cretaceous Res.* **93** 129–42
- Laplana C and Sevilla P 2013 Documenting the biogeographic history of *Microtus cabrerai* through its fossil record *Mammal Rev.* **43** 309–22
- Lindbladh M, Fraver S, Edvardsson J and Felton A 2013 Past forest composition, structures and processes—How paleoecology can contribute to forest conservation *Biol. Conserv.* **168** 116–27
- Lisitsyna O V, Hicks S and Huusko A 2012 Do moss samples, pollen traps and modern lake sediments all collect pollen in the same way? A comparison from the forest limit area of northernmost Europe *Veget. Hist. Archaeobot.* **21** 187–99
- López-Sález J A, Abel-Schaad D, Robles-López S, Pérez-Díaz S, Alba-Sánchez F and Nieto-Lugilde D 2016 Landscape dynamics and human impact on high-mountain woodlands in the western Spanish Central System during the last three millennia *J. Archaeol. Sci.: Rep.* **9** 203–18
- Lozano S, Mateos A and Rodríguez J 2016 Exploring paleo food-webs in the European Early and Middle Pleistocene: a network analysis *Quat. Int.* **413** 44–54
- Macías-Fauria M and Willis K J 2012 Landscape planning for the future: using fossil records to independently validate bioclimatic envelope models for economically valuable tree species in Europe *Glob. Ecol. Biogeogr.* **22** 318–33
- Magri D and Palombo M R 2013 Early to Middle Pleistocene dynamics of plant and mammal communities in South West Europe *Quat. Int.* **288** 63–72
- Maguire K C, Nieto-Lugilde D, Blois J L, Fitzpatrick M C, Williams J W, Ferrier S and Lorenz D J 2016 Controlled comparison of species- and community-level models across novel climates and communities *Proc. R. Soc. B* **283** 20152817
- Maguire K C, Nieto-Lugilde D, Fitzpatrick M C, Williams J W and Blois J L 2015 Modeling species and community responses to past, present, and future episodes of climatic and ecological change *Annu. Rev. Ecol. Evol. Syst.* **46** 343–68
- Marlon J R *et al* 2016 Reconstructions of biomass burning from sediment-charcoal records to improve data–model comparisons *Biogeosciences* **13** 3225–44
- Martín-Perea D, Fesharaki O, Domingo M S, Gamboa S and Hernández Fernández M 2019 Messor barbarus ants as soil bioturbators: implications for granulometry, mineralogical composition and fossil remains extraction in Somosaguas site (Madrid basin, Spain) *CATENA* **172** 664–77
- McKay N P and Emile-Geay J 2018 Linked Paleo Data: a resource for open, reproducible, and efficient paleoclimatology *Past. Glob. Change Mag.* **26** 71
- Michener W K and Jones M B 2012 Ecoinformatics: supporting ecology as a data-intensive science *Trends Ecol. Evol.* **27** 85–93
- Moorhead D L, Doran P T, Fountain A G, Lyons W B, Mcknight D M, Priscu J C, Virginia R A and Wall D H 1999 Ecological legacies: impacts on ecosystems of the McMurdo dry valleys *BioScience* **49** 1009–19
- Navarro-Racines C, Tarapues J, Thornton P, Jarvis A and Ramirez-Villegas J 2020 High-resolution and bias-corrected CMIP5 projections for climate change impact assessments *Sci. Data* **7** 7
- Nieto-Lugilde D, López-Sález J A and Alba-Sánchez F 2018 Estudiando los determinantes de la composición de comunidades y sus dinámicas en el pasado incorporando información filogenética y funcional al registro fósil *Rev. Ecosistemas* **27** 52–61
- Nogués-Bravo D, Veloz S, Holt B G, Singarayer J, Valdes P, Davis B, Brewer S C, Williams J W and Rahbek C 2016 Amplified plant turnover in response to climate change forecast by Late Quaternary records *Nat. Clim. Change* **6** 1115–9
- Nogués-Bravo D 2009 Predicting the past distribution of species climatic niches *Glob. Ecol. Biogeogr.* **18** 521–31
- Novakova K, Van Hardenbroek M and Van Der Knaap W O 2013 Response of subfossil Cladocera in Gerzensee (Swiss Plateau) to early Late Glacial environmental change *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **391** 84–9
- Odgaard B V 1999 Fossil pollen as a record of past biodiversity *J. Biogeogr.* **26** 7–17
- Ostling A M 2012 Large-scale spatial synchrony and the stability of forest biodiversity revisited *J. Plant Ecol.* **5** 52–63
- Pereira H M *et al* 2013 Essential biodiversity variables *Science* **339** 277–8
- Perring M P, Standish R J, Price J N, Craig M D, Erickson T E, Ruthrof K X, Whiteley A S, Valentine L E and Hobbs R J 2015 Advances in restoration ecology: rising to the challenges of the coming decades *Ecosphere* **6** art131
- Perrotti A G and Van Asperen E 2019 Dung fungi as a proxy for megaherbivores: opportunities and limitations for archaeological applications *Veget. Hist. Archaeobot.* **28** 93–104
- Peters D P C, Loescher H W, SanClements M D and Havstad K M 2014 Taking the pulse of a continent: expanding site-based research infrastructure for regional- to continental-scale ecology *Ecosphere* **5** art29
- Pinot S, Ramstein G, Harrison S P, Prentice I C, Guiot J, Stute M and Joussaume S 1999 Tropical paleoclimates at the last glacial maximum: comparison of paleoclimate modeling intercomparison project (PMIP) simulations and paleodata *Clim. Dyn.* **15** 857–74

- Pisarcic M F J, Holt C, Szeicz J M, Karst T and Smol J P 2003 Holocene treeline dynamics in the mountains of northeastern British Columbia, Canada, inferred from fossil pollen and stomata *Holocene* **13** 161–73
- Pollen Database Administration 2007 *Pollens Database Manual* (available at: www.europeanpollendatabase.net/data/downloads/image/pollen-database-manual-20071011.doc)
- Power M J et al 2008 Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data *Clim. Dyn.* **30** 887–907
- Ratajczak Z, Carpenter S R, Ives A R, Kucharik C J, Ramiadantsoa T, Stegner M A, Williams J W, Zhang J and Turner M G 2018 Abrupt change in ecological systems: inference and diagnosis *Trends Ecol. Evol.* **33** 513–26
- Redelings B D and Holder M T 2017 A supertree pipeline for summarizing phylogenetic and taxonomic information for millions of species *Peer J.* **5** e3058
- Refsgaard J C et al 2014 A framework for testing the ability of models to project climate change and its impacts *Clim. Change* **122** 271–82
- Reitalu T, Kuneš P and Giesecke T 2014 Closing the gap between plant ecology and quaternary palaeoecology *J. Veget. Sci.* **25** 1188–94
- RISCAPE-project 2017 What is a research infrastructure? *RISCAPE* (available at: <https://blogs.helsinki.fi/riscap-project/what-is-a-research-infrastructure/>)
- Rittel H W J and Webber M M 1973 Dilemmas in a general theory of planning *Policy Sci.* **4** 155–69
- Roberts S, Jones V J, Allen J R M and Huntley B 2015 Diatom response to mid-Holocene climate in three small Arctic lakes in northernmost Finnmark *Holocene* **25** 911–20
- Rull V 2010 Ecology and palaeoecology: two approaches, one objective *Open Ecol. J.* **3** 1–5
- Rull V 2012 Palaeobiodiversity and taxonomic resolution: linking past trends with present patterns *J. Biogeogr.* **39** 1005–6
- Saarinén J and Lister A M 2016 Dental mesowear reflects local vegetation and niche separation in Pleistocene proboscideans from Britain *J. Quat. Sci.* **31** 799–808
- Sampérez P G et al 2013 Reconstrucción paleoambiental del último ciclo glacial-interglacial en la Iberia continental: la secuencia del Cañizar de Villarquemado (Teruel) *Cuadernos De Investigación geográfica/Geogr. Res. Lett.* **39** 49–76
- Schoonmaker P and Foster D 1991 Some implications of paleoecology for contemporary ecology *Botanical Rev.* **57** 204–45
- Seddon A W R, Festi D, Robson T M and Zimmermann B 2019 Fossil pollen and spores as a tool for reconstructing ancient solar-ultraviolet irradiance received by plants: an assessment of prospects and challenges using proxy-system modelling *Photochem. Photobiol. Sci.* **18** 275–94
- Steffen W et al 2005 *Global Change and the Earth System: A Planet under Pressure* (Berlin: Springer)
- Stewart K M and Rufolo S J 2020 Kanapoi revisited: paleoecological and biogeographical inferences from the fossil fish *J. Hum. Evol.* **140** 102452
- Suding K N, Gross K L and Houseman G R 2004 Alternative states and positive feedbacks in restoration ecology *Trends Ecol. Evol.* **19** 46–53
- Sugita S 2007a Theory of quantitative reconstruction of vegetation I: pollen from large sites REVEALS regional vegetation composition *Holocene* **17** 229–41
- Sugita S 2007b Theory of quantitative reconstruction of vegetation II: all you need is LOVE *Holocene* **17** 243–57
- Turner M G, Dale V H and Gardner R H 1989 Predicting across scales: theory development and testing *Landscape Ecol.* **3** 245–52
- Tylmann W, Bonk A, Goslar T, Wulf S and Grosjean M 2016 Calibrating 210Pb dating results with varve chronology and independent chronostratigraphic markers: problems and implications *Quat. Geochronol.* **32** 1–10
- Uhen M D, Goring S, Jenkins J and Williams J 2018 EarthLife Consortium: supporting digital paleobiology *Past. Glob. Change Mag.* **26** 78–9
- Uthicke S, Patel F and Ditchburn R 2012 Elevated land runoff after European settlement perturbs persistent foraminiferal assemblages on the Great Barrier Reef *Ecology* **93** 111–21
- Valsecchi V, Chase B M, Slingsby J A, Carr A S, Quick L J, Meadows M E, Cheddadi R and Reimer P J 2013 A high resolution 15,600-year pollen and microcharcoal record from the Cederberg Mountains, South Africa *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **387** 6–16
- Varela S, Lobo J M and Hortal J 2011 Using species distribution models in paleobiogeography: a matter of data, predictors and concepts *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **310** 451–63
- Veloz S D, Williams J W, Blois J L, He F, Otto-Bliesner B and Liu Z 2012 No-analog climates and shifting realized niches during the late quaternary: implications for 21st-century predictions by species distribution models *Glob. Change Biol.* **18** 1698–713
- Vitousek P M 1994 Beyond global warming: ecology and global change *Ecology* **75** 1861–76
- Von Bargaen D, Lehmann J and Unverfaerth J 2016 Ostracod response to habitat change in an early Aptian shelf sea *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **459** 518–36
- Von Humboldt A and Bonpland A 2009 *Essay on the Geography of Plants* (Chicago: The University of Chicago Press)
- Whyte K P and Thompson P B 2012 Ideas for how to take wicked problems seriously *J. Agric. Environ. Ethics* **25** 441–5
- Williams J W et al 2017 Cyberinfrastructure in the paleosciences: mobilizing long-tail data, building distributed community infrastructure, empowering individual geoscientists *Authorea* (available at: www.authorea.com/users/152134/articles/165940-cyberinfrastructure-in-the-paleosciences-mobilizing-long-tail-data-building-distributed-community-infrastructure-empowering-individual-geoscientists)
- Williams J W and Jackson S T 2007 Novel climates, no-analog communities, and ecological surprises *Front. Ecol. Environ.* **5** 475–82
- Williams J W, Kharouba H M, Veloz S, Vellend M, McLachlan J, Liu Z, Otto-Bliesner B and He F 2013 The ice age ecologist: testing methods for reserve prioritization during the last global warming *Glob. Ecol. Biogeogr.* **22** 289–301
- Willis K J, Araújo M B, Bennett K D, Figueroa-Rangel B, Froyd C A and Myers N 2007 How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies *Phil. Trans. R. Soc. B* **362** 175–87
- Willis K J, Bennett K D, Bhagwat S A and Birks H J B 2010 4 °C and beyond: what did this mean for biodiversity in the past? *Systemat. Biodiver.* **8** 3–9
- Willis K J and Birks H J B 2006 What is natural? The need for a long-term perspective in biodiversity conservation *Science* **314** 1261–5
- Willis K J and MacDonald G M 2011 Long-term ecological records and their relevance to climate change predictions for a warmer world *Annu. Rev. Ecol. Evol. Syst.* **42** 267–87
- Wingard G L, Bernhardt C E and Wächnicka A H 2017 The role of paleoecology in restoration and resource management—the past as a guide to future decision-making: review and example from the greater everglades ecosystem, U.S.A. *Front. Ecol. Evol.* **5** 11