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# Learning from the past: opportunities for advancing ecological research and practice using palaeoecological data

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**Abstract**: Palaeoecology involves analysis of fossil and sub-fossil evidence preserved within sediments to understand past species distributions, habitats and ecosystems. However, while palaeoecological research is sometimes made relevant to contemporary ecology, especially to advance understanding of biogeographical theory or inform habitat-based conservation at specific sites, most ecologists do not routinely incorporate palaeoecological evidence into their work. Thus most cross-discipline links are palaeoecology→ecology rather than ecology→palaeoecology. This is likely due to lack of awareness and/or the misnomer that palaeoecology invariably relates to the "distant past" (thousands of years) rather than being applicable to the "recent past" (last ~100-200 years). Here, we highlight opportunities for greater integration of palaeoecology within contemporary ecological research, policy, and practice. We identify situations where palaeoecology has been, or could be, used to: (1) quantify recent temporal change (e.g. population dynamics; predator-prey cycles); (2) "rewind" to a particular point in ecological time (e.g. setting restoration/rewilding targets; classifying cryptogenic species); (3) understand current ecological processes that are hard to study real-time (e.g. identifying keystone species; detecting tipping points); (4) complement primary data and historical records to bridge knowledge gaps (e.g. informing reintroductions and bioindicator frameworks); (5) disentangle natural and anthropogenic processes (e.g. climate change); and (6) draw palaeoecological analogues (e.g. impacts of pests). We conclude that the possibilities for better uniting ecology and palaeoecology to form an emerging cross-boundary paradigm are as extensive as they are exciting: we urge ecologists to learn from the past and seek opportunities to extend, improve, and strengthen their work using palaeoecological data.

**Keywords**: ecological monitoring, ecological management, conservation, spatiotemporal change

## Introduction

Palaeoecology is the study of ecological patterns and processes of the past. Palaeoecological studies (and research within the cognate fields of palaeobiology and palaeontology) involve examining fossil and sub-fossil evidence to understand past species distributions, habitats, ecological patterns and ecosystem processes. Such evidence can be preserved within rock, terrestrial sediments (e.g. bog and lacustrine deposits) and marine and estuarine sediments, and can involve many different types of preserved biological material. For plants this includes palynological remains (pollen grains and non-pollen palynomorphs such as spores of ferns) and plant macrofossils such as seeds or preserved vegetative material. For fauna in terrestrial or aquatic environments, evidence includes vertebrate bones, shells from Mollusca and Crustacea, and insect remains (especially of Coleoptera where elytra are often well-preserved). More specialist fossil and sub-fossil evidence includes unicellular testate amoebae and diatoms – both of which can occur within freshwater and marine contexts as well as terrestrial sediments – as well as coral, coralline algae, bryozoans, fungal hyphae/spores, and lichens. It is often possible to date evidence directly (e.g. radiocarbon dating of bones) or indirectly by dating the sediment associated with evidence (e.g. luminescence dating of quartz-rich sediment surrounding preserved pollen). Palaeoecological evidence can also be compared to biogeochemical data to enable inferences to be made about environmental conditions (Roberts 2013; Lowe and Walker 2014). When evidence from several consecutive time periods is pieced together, it can provide insights into temporal transformation of environments.

A classic study demonstrating the utility of palaeoecology to reconstruct past environments was that of Walker (1982), which quantified pollen preserved in terrestrial sediments to identify changing climate after the last ice age in Britain. The 5 m sediment core revealed pollen from pioneer vegetation shortly after the ice retreated 20,000 years ago and the subsequent change in vegetation over thousands of years to a climax community. Similar studies can be undertaken in the marine environment, for example Anderson and Vos (1992) demonstrated how diatoms could be used to study the evolution of the coastline of The Netherlands in relation to changes in sea level caused by natural and anthropogenic processes. More recently, palaeoecology has been employed to study more complex patterns and the use of multiple types of evidence within single studies is now commonplace. Such multi-proxy research can provide a comprehensive understanding of changing climate (e.g. Njagi et al. 2021; Roland et al. 2015), ecological interactions (e.g. Gałka et al. 2018), human occupation and activity (e.g. Kittel et al. 2018; Bishop et al. 2019), or extreme events (e.g. Yao et al. 2021). As the discipline has progressed and methods have advanced, there has been a drive to move away from traditional single-site palaeoecological reconstructions to synthesise data from multiple sites to further understand continental or global-scale ecological patterns (Barber et al. 2003; Barber et al. 2004; Blundell et al. 2008). A good example of this approach is a study by Roland et al. (2015), which documented a major climate event 5,200 years ago across multiple sites in Ireland. This study utilised testate amoebae and plant macrofossils, alongside humification analysis and stable isotope analysis, to identify the extent and timing of wetter conditions and revealed the cause to be persistent cyclonic weather patterns across northwest Europe. Such broadscale research can also reveal no-analogue communities. Examples of ecosystems that do not have a modern equivalent in terrestrial environments are reviewed by Jackson and Williams (2004) and Birks (2019), while the work of Novak et al (2013) on the Indonesian coast revealed high biodiversity reef systems in low energy mesophotic environments, which are no longer extant.

Palaeoecology is inherently informed by theory used within contemporary ecology, including use of concepts such as competition, ecological succession patterns, and niche theory to understand and model past dynamics and temporal change (e.g. Birks 2019). It also has an important role in the study of biogeographical patterns and processes, especially linking ecological change to climate. For example, there are single-site studies spanning multiple glacial/interglacial cycles (e.g. temporal change in tree species in the French Massif Central over 430,000 years (de Beaulieu et al. 2006)), cross-continental spatial changes since the end of the last ice age (e.g. range shifts in European flora (Huntley and Birks 1983)) and detailed studies of rapid climate perturbations (e.g. Webb and Goodenough, 2021). Understanding of other biogeographical patterns is also informed by palaeoecological investigation, including the Latitudinal Diversity Gradient (e.g. Silvertown 1985; Mannion 2020; Meseguer and Condamine 2020; Song et al. 2020) and the Bergmann and Allen rules of thermal biology for vertebrates (Smith and Betancourt 2003; Boulbes and van Asperen 2019; Davis 2019) and marine protists (Mousing et al. 2017).

To extend reach into more applied ecological contexts, some palaeoecologists have sought to make data and inferences about the past relevant to current challenges, especially in relation to habitat conservation. Such research is often in relation to specific single sites. For example, at Llangorse Lake in South Wales, diatoms, Mollusca, and Crustacea from sediment cores were used alongside sedimentological evidence to demonstrate recent human-accelerated infilling of the lake is ecologically unsustainable (Chambers 1999); Chambers et al. (2007) were also able to utilise palaeoecology to document natural habitat change at upland heath sites in Wales to inform current conservation. However, while some palaeoecological researchers have made considerable effort to make their studies increasingly relevant to contemporary ecological contexts, there are fewer examples of contemporary ecologists routinely reaching back into the past to incorporate palaeoecological evidence in their work. This is despite repeated calls to unite palaeoecology and contemporary ecology (e.g. Kowalewski 2001; Willis and Birks 2006; Willis et al. 2007; Jackson 2007; Davies and Bunting

2010; Rull 2010; Waller et al. 2012, Birks 2019), including specifically for the study of ecosystem change and resilience (Buma et al. 2019), marine protection (Pandolfi 2011), and ecosystem restoration (Jackson and Hobbs 2009; Wingard et al. 2017; Reid et al. 2021). The need to better integrate ecology and palaeoecology is also being recognised in research networks, forums and working groups, such as the US-based Conservation Paleobiology Network and the UK-based Palaeoecology Group within the British Ecological Society.

We suggest that one reason for most links being palaeoecology→ecology rather than being balanced by an equal number of ecology→palaeoecology links might be lack of awareness within the ecological research community of the extensive possibilities for using palaeoecological approaches within current ecological research, as well as applied monitoring, management and conservation initiatives. Possibly more importantly, although ecologists might think that palaeoecological studies invariably relate to the "distant past" (thousands of years ago), actually palaeoecological research can explore change over timescales a short as the last 100-200 years. Examples include studies in terrestrial New Zealand (Wilmshurst et al. 2013), freshwater ecosystems in the UK (Bennion et al. 2018; Bishop et al. 2019) and marine environments off the west coast of the Iberian Peninsula (Ribeiro et al. 2012) and in the Mediterranean (Agiadi and Albano 2020). These "recent past" timeframes are often vital to understand current patterns and processes in terrestrial and marine environments (Finney et al. 2002; Rull 2010), and palaeoecological approaches are especially valuable where there are incomplete primary survey data or documentary evidence (Davidson et al. 2005; Salgado et al. 2010; Bishop et al. 2019; Seddon et al. 2019). A terrestrial example of this is afforded by Sherriff et al. (2014), who undertook spatially-explicit modelling of fire regimes in Colorado over 300 years using both primary survey and palaeoecological data to show that recent fires were larger than those experienced historically and to identify specific high-risk areas outside of historical norms. Pandolfi et al. (2003) took a similar approach in a marine study that combined paleontological, archaeological, historical, and primary ecological data to assess change in coral reefs in relation to human pressures. Where a direct combination of datasets is not possible, use of palaeoecological analogues can sometimes be employed to help understand current ecological changes in ways that have direct implications for ecological policy and practice. For example, Webb and Goodenough (2021) studied biodiversity metrics over a past rapid climate event and showcased how woodland vegetation might respond to contemporary rapid climate change, and related this to the need to focus contemporary monitoring on gamma rather than alpha richness.

In this *Concepts* paper, we review the value of using palaeoecological data in a wide range of contemporary ecological contexts. We are not seeking to provide a fully comprehensive review of any one topic, but rather to highlight – through discussion of themes, questions, and scenarios – the extensive opportunities for greater integration of palaeoecology within ecological disciplines as an emerging cross-boundary paradigm. We discuss examples where palaeoecological data or palaeoecological analogues have been, or could be, used to allow ecologists to better understand the utility of palaeoecology in current ecological research, as well as within in the applied contexts of monitoring, management and conservation. Inevitably there will be some overlap with some previous work – especially Willis and Birks (2006), Willis et al (2007), Davies and Bunting (2010), Rull (2010) and Birks (2019) – but our aim is to build on this important topic and develop new perspectives and insights. We do this in five interconnected ways: (1) writing from an ecological perspective that is accessible to both ecological researchers and practitioners to develop greater ecology→palaeoecology linkages to complement existing palaeoecology→ecology linkages; (2) focusing on applied ecology topics (rather than theoretical ecology or biogeography) that have clear implications for policy and practice; (3) taking a holistic perspective to ensure that studies on a wide range of environments are represented so that, while there may be a slight bias towards terrestrial ecosystems, research using freshwater aquatic and marine palaeoecology is fully embedded; (4) highlighting multiple types of palaeoecological evidence within a single review rather than focusing specifically on palynology; (5) largely, although not exclusively, concentrating on consideration of "recent past" to highlight how palaeoecology can be a useful tool over timespans as recent as the last couple of hundred years. We hope that, by highlighting these possibilities, ecologists will become more aware of opportunities for advancing ecological research and practice using palaeoecological approaches.

## Invasion Ecology

As noted by Willis and Birks (2006), palaeoecology is inherently concerned with the distribution of past species and thus has obvious relevance to the study of invasion ecology. Although the concept of nativeness – whether a species occurs naturally within a given community – is an intuitive ecological principle, in practice there is often a lack of consensus about the demarcation between "native" and "non-native" (Carlton 1996). The classification of a species depends not only on geographical history, but also how that history fits with a specific date. For example, within Europe, the start of mass trade around the year 1500CE is often used to classify species as either archæophytic (old; native) or neophytic (new; non-native). However, there are many examples of where the history of a species in a particular area is unknown or contentious and these are termed cryptogenic ("secret origin") species. The number of cryptogenic species is, by definition, hard to quantify but a systematic study by Carlton (1996) suggested there were ~100 marine cryptogenic species in San Francisco Bay alone.

It is often vital for ecologists to know whether a species is native or non-native: this is not simply an academic debate as there are real implications for legal status and subsequent management (Goodenough 2016). For example, the northern pool frog (*Pelophylax* (formerly *Rana*) *lessonae*) has a cosmopolitan distribution in freshwater aquatic ecosystems across Europe but, until recently, was considered to be an introduced non-native species in the UK. As a result, the species was a candidate for listing under Schedule 9 of the UK's Wildlife and Countryside Act as legally permissible to cull. However, additional research was prompted by historical documents suggesting that *Pelophylax* was already present before the earliest known introductions, and this revealed that the species was, in fact, native (Beebee et al. 2005). Following reclassification, the species moved from being listed as a pest to being considered to be conservation priority: reintroduction and supplementation has now taken place to create self-supporting populations (Buckley and Foster 2005).

In the pool frog example, nativeness was suggested by historical documents, which prompted analysis of museum specimens and genetic profiling, as well as consideration of amphibian bones from radiocarbon dated palaeoecological sites (Gleed-Owen 2000). In many cases though, historical documentation and museum specimens are absent and this is where palaeoecological approaches might be especially helpful. For example, the "non-native" aquatic species water lettuce (*Pistia stratiotes)* in Florida, USA, was shown to be native when palaeoecological records were evaluated (Evans 2013), 800-year-old fossilised pollen in the Galápagos was used to identify which contemporary species are native to the oceanic archipelago (van Leeuwen et al. 2008), and in Ireland palaeoecology was used to resolve a long debate on the nativeness of Scots pine *(Pinus sylvestris)* (Roche 2019). Detailed studies can even reveal complex invasion pathways. This is exemplified by work on the toxic marine phytoplankton species *Gymnodinium catenatum* in the Atlantic Ocean to show spatiotemporal spread along the Iberian Peninsula (Ribeiro et al. 2012) and research on the European eagle owl (*Bubo bubo*), which showed that although the small extant population in the UK is founded upon captive escapees, the palaeoecological record indicates that the species itself is native (Stewart 2007).

It is not just identifying the origins of cryptogenic species where palaeoecology can be useful within invasion ecology research. From an applied perspective, understanding interactions between non-native and native species, and thus wider ecological impacts, is paramount (Goodenough 2010). In some situations, the actual introduction event is known and impacts can be monitored directly from that point. In most cases, however, non-native species become established before any monitoring commences. In such cases, analysing the recent palaeoecological record can be helpful to "rewind" to the initial introduction event and thus study impacts in retrospect. This approach was used on Skomer Island, Wales, to infer the vegetation of the island from pollen records before the introduction of non-native rabbits (*Oryctolagus cuniculus*) (Webb et al. 2017), and in the marine environment to better understand the impacts of the biotic homogenisation in the Mediterranean that occurred after the construction of the Suez Canal in 1869 linked it to the Red Sea (Agiadi and Albano 2020).

## Disease Ecology

The ability to investigate patterns over many years is useful in the study of ecological pests and diseases where learning lessons from previous disease outbreaks, including vector identification and/or quantifying impacts, can also be helpful. This is especially important as the consequences of pests and diseases are not always immediately apparent (there is a lag time between emergence and impact), but the optimal time to act to prevent damage is at the start of an outbreak, where the chances of eradication or effective suppression are highest (Goodenough and Hart 2017). For example, a widely-recorded decline in elm (*Ulmus*) around 5,500 years ago in northwest Europe and evident in palaeoecological data (review by Parker et al. 2002), was used to inform understanding of the ecological consequences of the more recent Dutch Elm Disease (Flynn and Mitchell 2019). These findings might be useful insights into diseases that are still emerging and increasing in prevalence, such as ash dieback (*Hymenoscyphus fraxineus*). In other situations, the immediate impacts of disease are clear from primary monitoring but the historical context is lacking. For example, starting in the late 1980s, white-band disease nearly eliminated the staghorn coral (*Acropora cervicornis*) from reefs in the coastal waters of Belize, which caused mass species turnover. While this was dramatic, it was not clear whether or not it was atypical until palaeoecological research by Aronson et al. (2002) revealed that staghorn coral had been dominant continuously for the previous 3,000 years and no mass turnover had occurred within that timeframe in these uncemented lagoonal reefs. This research highlighted the urgent need for disease alert monitoring in other areas of the Caribbean and reduction of the anthropogenic stressors that facilitate outbreaks of white-band disease.

## Community Ecology

Ecological communities are intricate networks of co-occurring species that interact with one another and their abiotic environment. Many aspects of community ecology are best studied through direct observational fieldwork or manipulation in the field or laboratory. For example, the effect of herbivores on woodland regeneration can be studied using exclosures (Dauwalter et al. 2018; Bradfield et al. 2021), while lab-based microcosm experiments can be useful for examining species’ coexistence (e.g. Luckinbill 1973), competition (e.g. Bonsall and Hassell 1997), and predation (e.g. Morin 1999). However, some aspects of community ecology involve changes over long time periods, or patterns that fluctuate temporally, and it is in these cases that palaeoecology can offer real insights and circumvent the problems inherent in research that uses space-for-time substitution.

Space-for-time (SFT) substitution is an approach to studying longitudinal change, for example in plant succession after glaciation, whereby change is not studied at one fixed location over time but over a spatial gradient, or chronosequence, based on time since deglaciation (Walker et al. 2010). However, SFT has recently been subject to increasing criticism because assumptions are too simplistic for dynamic environments and can lead to inconsistent results (Johnson and Miyanishi 2008; Damgaard 2019). Palaeoecological approaches can be very valuable here, since they allow past changes to be studied directly without SFT assumptions. The approach is currently underutilized (Louys et al. 2021) but examples of where it has been used to good effect can be found in the palaeoecological literature. For example, a detailed study by Payette (1988) demonstrated the complexities in northern Canadian peatland succession, where self-perpetuating vegetation cycles illustrate the dynamic and rapid shifts between autogenic and allogenic succession, while a study in the coastal mangroves of Mexico used palaeoecology to understand the role of natural disturbance (hurricanes) on successional processes and understand modern community ecology patterns (Torrescano-Valle and Islebe 2012).

Palaeoecology can also be helpful when studying aspects of community ecology that, unlike succession, might not be inherently temporal but where examining patterns over many years is advantageous (Rull 2010). Examples of where this approach has been used to good effect include examining species turnover in woodland flora in relation to climate change across Europe (Webb and Goodenough 2021), quantifying variation in predator-prey cycles in Italian mammals (Raia et al. 2007), analyzing the long-term effects of herbivory in the UK (Whitehouse and Smith 2010) and considering long-term synchronous population changes in sockeye salmon (*Oncorhyncus nerka*) in the north Pacific in relation to changes in different freshwater nursery lakes on Kodiak Island, Alaska (Finney et al. 2002).

One area of community ecology that has gained increasing traction as we enter the Anthropocene is the consideration of ecological tipping points. Tipping points occur when an ecological threshold is breached and the system “tips over” into disequilibrium, quickly leading to long-lasting change or ecosystem collapse (Gladwell 2000). As tipping points cannot be studied until they occur, and are notoriously hard to simulate experimentally (Cairns 2004), they are challenging to predict with any accuracy. However, evidence of past tipping points can sometimes be available in the palaeoecological record, which might predict contemporary tipping points and inform appropriate avoidance, mitigation, or buffering strategies. The power of this approach is shown by Sander et al. (2021), who use palaeoecological tools to investigate the collapse of a (fossil) bed of European flat oysters (*Ostrea edulis*) in the North Sea. They conclude that influx of sediment from continental rivers was a stressor but that the tipping point for population collapse was the sudden increase in boring sponge (*Cliona* sp.) c. 700 years ago. This North Sea oyster bed research involved identification of a biotic tipping point but Hájková et al. (2012) demonstrated the approach works for abiotic tipping points too. Hájková studied pollen, plant macrofossils and testate amoeba to reveal that change in moisture levels was the tipping point for abrupt change as calcareous fen replaced original sphagnum bogs in Slovakia c. 10,700 years ago as bog vegetation could no longer be supported. This highlights the importance of contemporary management to reduce the risk of desiccation, for example, by the addition of bunds in drainage channels to change the hydrological regime in similar habitats today.

In rare cases, it might be possible to actually avoid tipping points by studying the fossil record. For example, suppression of the natural fire regime was mandated in several of the early US National Parks, including Yosemite and Sequoia from 1890, because fire was seen as being destructive and thus non-desirable and in 1935 the US Forest Service fire suppression policy was formally adopted by the National Park Service. Although the wisdom of this was questioned – notably by George Wright in the early 1930s (Kilgore 2007) – the Leopold report (Leopold et al. 1963) was the catalyst for slow change towards the current Wildland Fire Use policy. This report highlighted the ecological importance of fire, which was reinforced by later studies showing that giant sequoia (*Sequoiadendron giganteum*) rely on fire to release seeds from cones, expose bare soil for seedlings to root, and to open canopy gaps and reduce competition from shade-loving species (Kilgore 1973; Meyer and Safford 2011). Although this complex series of interactions could probably not have been inferred from pollen data, the presence of charcoal and subsequent high levels of *Sequoiadendron* pollen in the palaeoecological record (potentially after a short lag) would at least have suggested that fire would not be detrimental to this species.

**Functional Ecology**

Keystone species have an especially important role within their ecosystem and, by their very definition, variation in the population of keystone species has a greater impact than variation in the population of non-keystone species. When the identity of a keystone species is known, palaeoecological studies might complement historical or contemporary evidence to enable longer-term study than would otherwise be possible. For example, Slade et al. (2021) studied Mollusca remains over the last 6,000 years to indirectly monitor temporal change in the population size of sea otters (*Enhydra lutris*): a keystone predator in British Columbia, Canada. However, it is not always possible to identify a particular species as being keystone until that species declines to a low level or becomes extirpated: in other words, evidence of keystone status often comes from ecosystem consequences of keystone species loss. Indeed, the removal experiment of Paine (1966) – whereby predatory sea stars (*Pisaster ochraceus*) were removed leading to predator release for mussels (*Mytilus californianus*) that then outcompeted other species and ultimately led to the term “keystone species” being coined (Paine 1969) – has become one of most-cited experimental ecological studies (Lafferty and Suchanek 2016). It is, however, not always possible or ethical to undertake removal experiments to identify keystone species, or determine impacts of decline or extirpation, and this is where looking to the palaeoecological record could again be informative. For example, Gilson

(2004) undertook research on 1,400 years of vegetation change in Tsavo National Park, Kenya, which demonstrated the ecosystem effects of variation in the population size of African elephant (*Loxodonta africana*). Thus, the currently observable impacts of this species on vegetation through trophic interactions (herbivory) that have caused it to become belatedly classified by many ecologists as a keystone species (Western 1989) were already evident in the palaeoecological record.

One specific type of keystone species is an ecosystem engineer: species that modify (literally “engineer”) the environment physically through their activities. Although the impacts of ecosystem engineers can often be studied real-time in field research, being able to establish impacts of ecosystem engineers in the past can be useful, since the role of the ecosystem engineer, and indeed the response of the ecosystem, might not be temporally consistent. For example, American beaver (*Castor canadensis*) fell trees and use these to dam water courses, creating complex riverine ecosystems and transition across terrestrial and freshwater environments. Persico and Meyer (2009) studied sediments in historic beaver ponds and found that beaver presence/absence  were associated with different riparian vegetation assemblages, especially in relation to aspen (*Populus tremuloides*) which is preferentially used in beaver dams. This highlights the potential for palaeoecological work to explore causes of the cascade effects of population change in ecosystem engineers at ecosystem level.

Other species that can have a very important role in habitat functioning are dominant species, especially where these are long-lived. Once again, because there is a time dimension here, quantifying the impacts of abundance change in dominant species is not without challenge. Palaeoecological analogues can be helpful, however. For example, in North America the palaeoecological record indicates a sharp decline in hemlock (*Tsuga canadensis*) around 4,000-5,000 years ago (Bhiry and Filion 1996), which caused long-lasting change to the understory species assemblage, and, in turn, affected local hydrological processes.

## Restoration Ecology

Rewilding has become one of the most-commonly used (and most-commonly misused) terms in conservation ecology over the last decade. It is often seen as a “magic bullet” in reversing biodiversity decline in the Anthropocene but it remains a controversial concept in conservation (e.g. Rubenstein and Rubenstein 2016; Pettorelli et al. 2019). This is partly because there is no accepted universal definition and the term is thus used for a diverse range of initiatives, and partly because the aims of rewilding are often unclear or unspecified (Nogués-Bravo et al. 2016; Hayward et al. 2019; Pettorelli and Hoffmann 2021). One of the key challenges in rewilding, and indeed in ecosystem restoration more generally, is that defining specific ecological targets is often problematic. This is because restoration and rewilding are inherently about recreating previous ecological conditions. Detailed understanding of past habitats, species dynamics and ecological interactions is essential both to allow restoration aims to be clearly articulated and to inform optimal methods to realise those aims (Seddon et al. 2019). For example, it was always assumed that, during the climax communities found in Europe after the last ice age ~4,000-9,000 years ago, land was covered by continuous and relatively-closed wildwood. However, modelling of palaeoecological vegetation and Coleoptera data (Vera 2000; Whitehouse and Smith 2004; Birks 2005; Whitehouse and Smith 2010) revealed that actually there was a relatively open mosaic wood-pasture landscape. In an analysis of the more recent past, Hanley et al. (2008; 2009) analysed plant diversity in upland Scotland over the last 400 years using an approach that combined palynological and historical datasets. The authors showed that diversity levels have varied considerably since 1600CE, indicating that static baselines and 'naturalness' are problematic concepts in rewilding (and indeed in conservation and ecology more widely) (Davies and Bunting 2010). Thus, any rewilding schemes should use a palaeoecologically-derived baseline to set appropriate habitat targets, or alternatively use the trajectory of natural change derived from the palaeoecological record to determine forward looking goals for restoration (e.g. Jackson and Hobbs 2009; Wingard et al. 2017). In particular, care must be taken when attempting to create an environment that mirrors the palaeoecologically-informed past, as the modern species assemblage will inevitably be different (especially in regard to non-native species), which may have important implications.

Within "Pandora's box" of rewilding concepts (Nogués-Bravo et al. 2016) are two specific types of rewilding. Pleistocene rewilding aims to restore ecosystems shaped by populations of megafauna extirpated since the Late Pleistocene where populations of these species are still extant elsewhere and thus could be reintroduced (e.g. European bison (*Bison bonasus*) and musk ox (*Ovibos moschatus*)). Trophic rewilding has a similar aim but uses the mechanism of surrogate species that have a similar ecological role to that of the megaherbivores (e.g. using Heck cattle as a substitute for the extinct aurochs (*Bos primigenius*) (Svenning et al. 2016; Perino et al. 2019)). For such initiatives to work, a detailed understanding of megaherbivore distributions, densities, and ecological impacts is vital. This can sometimes be undertaken using direct palaeoecological study of the species concerned but, in other cases, palaeoecological proxies can be valuable: for example, a recent study (van Asperen et al. 2021) used coprophilous fungal spores that are associated with the dung of megaherbivores as a proxy for spatiotemporal abundance in these species.

Although rewilding is – or at least should be – a large-scale approach, smaller-scale restoration ecology still requires detailed knowledge of past conditions. An excellent example of where palaeoecology has informed contemporary restoration ecology is van de Velde et al. (2019) who used the assemblage of 28 Mollusc species from 2,000–2,500 years ago found in shelly deposits from Great Turali Lake, Russia, to reveal a baseline for ecological restoration planning that pre-dates the current threats in the region. A similar approach has been used in fen restoration in minerotrophic peatlands in southeastern Canada, where a "reference ecosystem" has been classified based on the complementary analysis of multiple peat cores and characterisation of contemporary natural sites (Bérubé, et al. 2017). Palaeoecological reconstructions using species tolerance ranges have also been used to guide restoration targets for abiotic environments at ecosystem level, including those enshrined within environmental policy. For example, in relation to salinity levels in the Everglades in Florida (reviewed by Wingard et al 2017), nitrogen levels in coastal fjords in Norway in relation to the EU Water Framework Directive (Anderson et al. 2004) and modelling natural freshwater flow through the Colorado River to address critical information gaps caused by the lack of direct surveying prior to alteration of natural conditions and to facilitate appropriate restoration (Kowalewski et al. 2000; Rodriquez et al. 2001).

Species reintroduction is undertaken for many different reasons. In some cases, reintroduction is a part of a broader restoration or rewilding project, when the ecological role of a species is the fundamental driver for the reintroduction (Hale and Koprowski 2018). In other cases, reintroduction can be motivated by desire to repair fragmented guilds by reinstating extirpated species, especially where charismatic species are involved or where people feel a moral obligation to replace species lost through direct human activity (Seddon et al. 2005; Hawkins et al. 2020; Lee et al. 2021). There might also be economic arguments, either relating to ecosystem services or ecotourism potential (Stringer and Gaywood 2016; Auster et al. 2020). Reintroduction can also be undertaken as part of species conservation: 43% of the reintroductions analysed by Seddon et al. (2005) involved species listed as threatened by the IUCN, with 21% being endangered or critically endangered. Alternatively, reintroductions might aim to create wild populations for species otherwise only existing in captive collections, to broaden a species' current range to reduce extinction risk, or to facilitate overall growth in global population if carrying capacity has been reached at current locations (Maunder 1992; Walzer et al. 2012).

Regardless of the motivation for species reintroduction, IUCN (2013) guidelines state that, within the initial feasibility study, it is vital to check: (1) the species was previously present in the target release area (i.e. it is a ***re***introduction); and (2) that, where possible, the target release area is near the core of the historic range or in an area where extirpation was relatively recent. In many cases, these questions can be answered by examining past documentary evidence, considering capture locations of museum specimens (Winker 2004), using instances of where settlement or road names can be used to infer presence of species historically (Williams et al. 2020), and, in some recent cases, through direct ecological records and human memory (e.g. Californian condor (*Gymnogyps californianus*), Przewalski's horse (*Equus ferus przewalskii*) and common crane (*Grus grus*) (Toone and Wallace 1994; Walzer et al. 2012; Redondo 2017)). However, in some cases, these lines of evidence are missing or ambiguous and this is when palaeoecological investigation can be especially helpful. For example, palaeoecological studies have been helpful in refining historical documentary records of "pelicans" inhabiting aquatic ecosystems in the UK and Denmark to a specific species: the Dalmatian pelican (*Pelecanus crispus*) (Stewart 2004), paving the way for a potential reintroduction to UK wetlands (MacDonald 2020). Reintroductions of extirpated plants are also possible using information from palaeoecological records. Researchers in New Zealand were surprised to find that woodland in Twahiti Rahi now dominated by pohutukawa (*Metrosideros excelsa*) consisted of numerous native trees just 100 years ago and, based on this palaeoecological evidence, programmes have begun to reintroduce native species that were present before inter-tribal disputes caused forest disturbance (Wilmshurst et al. 2013). Similarly, *Pritchardia aylmerrobinsonii* palms were reintroduced on the Hawaiian island of Kaua'i from the adjacent island of Niihau after investigations revealed the species had previously existed on both islands (Burney and Burney 2007).

Another key aspect of a species reintroduction feasibility study is to consider whether or not the habitat conditions currently in existence at a site are similar to the habitat that would have supported the species in that location historically, and thus whether a reintroduction is likely to be successful. A cautionary tale is that of failed attempts to reintroduce a rare aquatic plant, *Najas flexilis*, to the English Lake District. The species was last recorded in the 1980s and was thought to have declined quite rapidly before this time, mainly due to deteriorating water quality. With water quality returning to pre-1980 levels, attempts have been made to reintroduce *N. flexilis* (JNCC 2012) but these ultimately failed. Palaeoecological study incorporating abiotic measurements by Bishop et al. (2019) found that the species actually declined much earlier and that reintroduction attempts had been premature.

### Monitoring Ecology

The presence/absence and abundance of species can be used by ecologists to infer abiotic conditions (environmental indicators), ecosystem dynamics (biological indictors), or biodiversity patterns (biodiversity indicators). Use of indicator species, and numerical biotic indices such as the Ellenberg system for inferring soil conditions from plants (Ellenberg 1974; Ellenberg et al. 1992) and macroinvertebrate indices for inferring dissolved oxygen in freshwater ecosystems (López-López and Sedeño-Díaz 2015), are common tools within ecology. However, in some cases, additional insights can be gained from considering palaeoecological evidence. For example, Webb and Goodenough (2018) examined UK woodland sites with detailed contemporary vegetation records and palaeoecological data to critique whether “Ancient” Woodland Indicator (AWI) plant species are appropriate for determining whether a wooded site is ancient (>400 years old) or not. They found that although there are disturbance-sensitive species associated with stable (old) woodland habitats (Peterken and Game 1984; Rackham 2003; Glaves et al. 2009), AWIs can be surprisingly resilient to woodland interruptions or even tree clearance, with rich AWI communities found at sites unwooded for at least 2,800 years. They concluded that the use of floristic AWIs alone in defining ancient woodland should be reviewed, and recommended that a weighted AWI index or multi-taxa indicator system should be developed.

While Webb and Goodenough’s study involved using palaeoecological data to test the appropriateness of an indictor system widely-used in modern ecological contexts, the work of Seddon et al. (2019) provides a nice example of how the same indicator system can be used to enable temporal comparisons when applied to palaeoecological, historical and contemporary data, this time within the aquatic environment. The authors compared data on Gastropoda, Trichoptera and Coleoptera using Biological Monitoring Working Party (BMWP) and Average Score Per Taxon (ASPT) biotic indices (Furse et al. 1981; Armitage et al. 1983) to consider likely oxygen levels, and thus water quality, in a UK chalk river from the ~1840s to 2011. This is much longer than would have been possible without incorporation of palaeoecological data. A similar approach was taken using protists to monitor current marine ecological quality along the Norwegian Skagerrak coast in relation to pristine conditions as a way of implementing and auditing pollution legislation compliance (Bouchet et al. 2012). There is also the potential to use the palaeoecological record to highlight how changes within a species community can be used as a form of alert monitoring or Early-Warning Signal of more dramatic change being likely. A good example of this approach is using diatom flickering in Lake Erhai in China as an indicator of a major ecological regime shift being imminent (Wang et al. 2012) – although as Carstensen et al. (2013) highlight, careful statistical processing is vital to ensure observed patterns are not analytical artefacts.

## Conclusion and Recommendations

Throughout this paper, we have considered the value of using palaeoecological data in contemporary ecological study thematically. We have discussed ecological topics, and provided specific examples, of situations where palaeoecological information can be useful within contemporary ecological research (e.g. quantifying biogeographical patterns, understanding species interactions) or in applied ecological contexts (e.g. informing management of non-native species, creating appropriate restoration or rewilding targets, devising suitable reintroduction schemes). An alternative way to conceptualise this is via consideration of the six main types of opportunity where palaeoecological data can be used within ecological contexts; these are summarised in Figure 1.

In terms of tangible recommendations for bridging the gap between palaeoecology and ecology, and promoting ways in which some of the opportunities presented in this paper can be acted upon, we suggest that:

1. There needs to be a greater awareness by both research and applied ecologists that palaeoecology is not solely concerned with the "distant past". The opportunities for using palaeoecology to quantify the "recent past" make palaeoecological approaches extremely valuable in many contemporary ecological contexts in terrestrial environments (e.g. Rull 2010; Wilmshurst et al. 2013), freshwater aquatic environments (e.g. Bennion et al. 2018; Bishop et al. 2019) and marine environments (Finney et al. 2002; Agiadi and Albano 2020).

2. There needs to be better appreciation that primary ecological data, historical records, and palaeoecological evidence can be used in complementary ways to form a powerful integrated approach to better understand current ecology and solve future ecological challenges. Linking palaeoecological and contemporary ecological approaches also mitigates their inherent disadvantages. Palaeoecology is, by its very nature, observational and correlative and, because it is based on the preservation of material, there can be gaps in the evidence especially where preservation conditions are sub-optimal; there is also the potential for ecological inference to be confounded by taphonomic variables (Lowe and Walker 2014). Palaeoecological studies also have a fundamental limit to the level of detail that is possible, especially as regards temporal resolution (Jackson and Blois 2015), and there can be challenges in disentangling the local pollen signal (and thus local change) from the reginal pollen signal especially for pollen grains with wide dispersal properties (Davis 2000; Hellman et al. 2009). By contrast, contemporary ecology studies can, resources permitting, be much more detailed and there is often greater potential to study causality, including directly via manipulation. However, primary studies – even those that are long-term by the standards of ecological research – actually have comparatively short temporal reach, which might not align with ecologically-relevant timespans, and this can make it hard to distinguish natural change from human-induced change (Buma et al. 2019). Combining approaches can be a win-win situation, allowing ecologists to employ detailed, high-resolution, causally-based approaches but setting these within a longer temporal context.

3. Despite increases in inter-, multi- and trans-disciplinary working within the natural sciences, many academics and practitioners still work, to a greater or lesser extent, in intellectual silos. Examples of ecological projects that

reach into the palaeoecological past are still comparatively limited, especially when compared with the wealth of palaeoecological and ecological research that is undertaken in (relative) isolation. Increasing incorporation of palaeoecological concepts into University ecology modules and mainstream ecological textbooks would, in time, allow basic understanding of palaeoecology to become a routine part of the ecologists' toolkit. In many academic institutions, palaeoecology sits within geographical or earth sciences faculties whereas ecology typically falls within biosciences: greater promotion of cross-faculty working is paramount (Birks 2019).

4. Knowledge of the number and value of data repositories needs to be enhanced. For palaeoecology, key repositories include the European Pollen Database (Fyfe et al. 2009), the North American Pollen Database (accessible via Neotoma) (Williams et al. 2018), and the international Paleobiology Database PBDB (Peters and McClennen 2016) – many other databases are referenced on PAGES http://pastglobalchanges.org. For ecology, key repositories are the Global Biodiversity Information Facility, National Biodiversity Network, and PanTHERIA. Development of data repositories that seamlessly integrate ecological and palaeoecological data would greatly enhance the ability of researchers and practitioners to routinely access both types of data when searching for information on specific taxa, habitats or locations. Users also need better understanding of how to mine resources and better guidance on the constraints, caveats and limitations of the data therein. Such guidance needs to be widely accessible rather than assuming subject-specific prior knowledge. For example, ecologists need to understand that palynological data are usually presented at Family level not Genus/Species level because of limitations in the identification of pollen grains, appreciate the impact of different preservation conditions on fossil and sub-fossil evidence, and recognise the importance of dispersal and erosion on drawing inferences from palaeoecological evidence.

Overall, we conclude that the possibilities for using palaeoecology in contemporary ecological contexts are as extensive as they are exciting. We urge ecologists to learn from the past and seek out opportunities to extend, improve, and strengthen ecological research and practice using palaeoecological data.

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## Figures

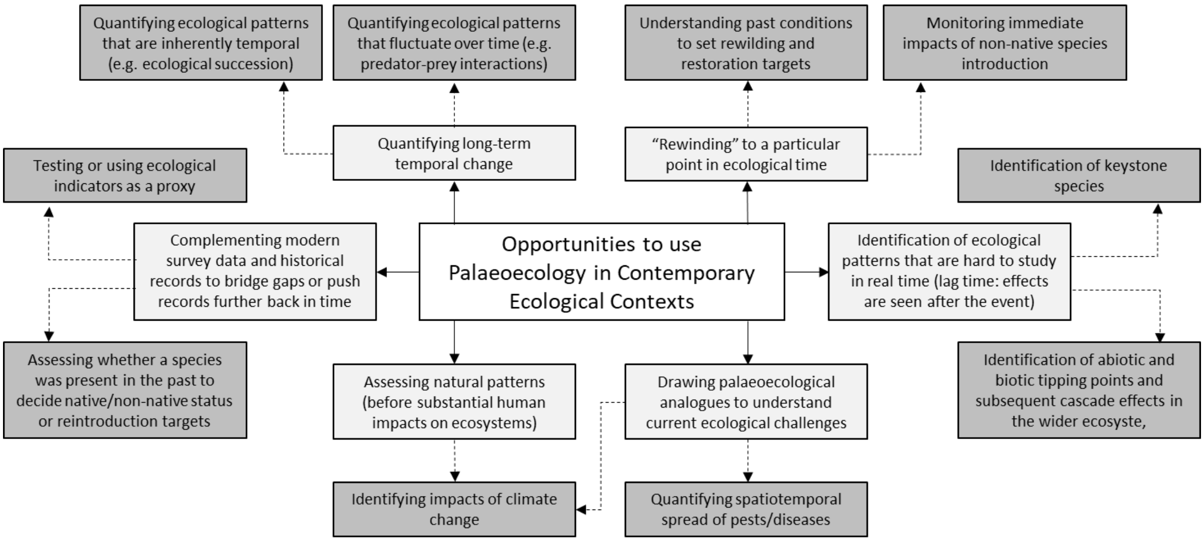

*Figure 1: Overview of the opportunities to use palaeoecology in contemporary ecological contexts*