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# Looking forward through the past. Identification of fifty priority research questions in palaeoecology

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**Running Title:** 50 Priority Research Questions in Palaeoecology

## Summary

1. Priority question exercises are becoming an increasingly common tool to frame future agendas in conservation and ecological science. They are used to identify research foci that advance the field and that also have high policy and conservation relevance.
2. To date there has been no coherent synthesis of key questions and priority research areas for palaeoecology, which combines biological, geological,

chemical and molecular techniques in order to reconstruct past ecological and environmental systems on timescales from decades to millions of years.

3. We adapted a well-established methodology to identify 50 priority research questions in palaeoecology. Using a set of criteria designed to identify realistic and achievable research goals, we selected questions from a pool submitted by the international palaeoecology research community and relevant policy practitioners.
4. The integration of online participation, both before and during the workshop, increased international engagement in question selection.
5. The questions selected are structured around six themes: human–environment interactions in the Anthropocene; biodiversity, conservation, and novel ecosystems; biodiversity over long timescales; ecosystem processes and biogeochemical cycling; comparing, combining and synthesizing information from multiple records; and new developments in palaeoecology.
6. Future opportunities in palaeoecology are related to improved incorporation of uncertainty into reconstructions, an enhanced understanding of ecological and evolutionary dynamics and processes, and the continued application of long-term data for better-informed landscape management.
7. **SYNTHESIS**: Palaeoecology is a vibrant and thriving discipline and these 50 priority questions highlight its potential for addressing both pure (e.g. theoretical) and applied (e.g. environmental) research questions related to ecological science and global change.

**Keywords:**

Anthropocene; Biodiversity; Conservation; Ecology, Evolution; Human-Environment Interactions; Land-use history; Paleoecology, Palaeoecology; Research Priorities.

## Introduction

Palaeoecology combines biological, geochemical and molecular information from natural archives to reconstruct ecological and evolutionary systems deep into the past. Because ecological monitoring records do not typically extend beyond the past few decades, palaeoecology is key to understanding how ecosystems have responded to past disturbance, evaluating their resilience to perturbations, and defining their pre-anthropogenic variability (Jackson 2007; Willis *et al.* 2010). High-resolution sediment sequences, for example, were pivotal in assessing the timing and extent of lake acidification across large areas of northern Europe and North America in the 1980s, and for attributing the cause to acidifying compounds derived from the combustion of fossil fuels since the Industrial Revolution (Battarbee *et al.* 2010). Today, European legislation such as the Water Framework Directive (WFD) requires assessment of ecological quality in relation to pre-anthropogenic baselines. Palaeoecology has been demonstrated to be the best approach to provide objective information about past conditions (Bennion *et al.* 2010).

Long-term insights are also crucial for identifying and understanding ecological and evolutionary processes. From around 50,000 years ago, a disproportionate amount of large-bodied mammals and birds (megafauna) began to go extinct in Eurasia, Australia and the Americas (Barnosky 2004). Accurately dated chronologies of the Pleistocene fossils have allowed the timing and potential causes of these megafaunal extinctions to be constrained (Burney & Flannery 2005). In addition, they have demonstrated that the loss of large herbivores led to the formation of novel ecosystems (Gill *et al.* 2009) and resulted in major changes in vegetation composition and fire regimes (Rule *et al.* 2012). In this case the integrated analysis of palaeoecological records revealed the unexpected legacies of extinction events on ecosystem functioning; this cannot be accomplished by studying modern systems alone.

But what are the future important questions that palaeoecological studies could and should be addressing? This paper describes the results from an exercise to identify 50 priority research questions in palaeoecology. This was inspired by previous studies, which have used specific criteria to identify priority research questions to advance the field of a given discipline (Sutherland *et al.* 2009; Pretty *et al.* 2010; Sutherland *et al.* 2011; Grierson *et al.* 2011; Petrokofsky, Brown & Hemery 2012; Sutherland *et al.* 2013; Walzer *et al.* 2013). Here we present the results of a two-day workshop held at the Biodiversity Institute, University of Oxford, in December 2012 and describe both the empirical (e.g. ecological and evolutionary, methodological) and applied research questions (e.g. environmental and conservation) on timescales covering decades to millions of years.

## Materials and methods

We adapted the methodology of Sutherland *et al.* (2011) to incorporate an open application process and online voting over the course of the workshop. We asked individuals to identify their top priority questions in various branches of palaeoecological science (see Supporting Information 1). Prior to the workshop, 905 questions were submitted online from 127 individuals, laboratories and organisations, which spanned 26 countries and five continents. Workshop coordinators [AWRS, AWM, AGB] pre-screened the submitted questions for duplication, which resulted in

804 questions organised into 55 topics. The questions were then selected and refined through an iterative process of voting and reworking using a simple scoring system (0, zero priority; 1, low priority; 2, high priority) (Fig. 1). All participants are listed as co-authors above. Questions are identified in the text by reference to their number [Q1] and are not ranked but are grouped thematically, both between and within working groups.

## Results

### Human-environment interactions in the Anthropocene

1. When did human activities first trigger global environmental change and can we define the start of the Anthropocene with reference to these activities?
2. How did changes in human livelihood, settlement strategies and land-use affect land cover, ecosystem structure, nutrient cycles, and climate over the late-Quaternary?
3. Why are some species and ecosystems more sensitive to environmental change than others, and therefore respond first or to the greatest degree?
4. Why do different species and ecosystems experience varying time-lags in their response to environmental change?
5. What effect has Holocene landscape fragmentation had on the ability of natural and semi-natural vegetation types to respond to environmental change?
6. How can the relationships between climate, herbivory, fire and humans be disentangled?
7. What are the impacts of pollutants on biota, including contaminants of emerging concern and their interactions with other stressors?

It has long been known that combustion of fossil fuels pollutes the Earth's atmosphere. The concept of the Anthropocene recognises that human activity has now transformed many of the Earth's ecosystems on a global scale (Crutzen & Stoermer 2000), yet formalizing the Anthropocene as a new geological epoch remains controversial (Zalasiewicz *et al.* 2011; Gibbard & Walker 2013). One debate surrounds whether it began at the onset of the Industrial Revolution, or thousands of years earlier following the expansion of agriculture and concomitant increases in atmospheric $CO_2$ and $CH_4$ (Ruddiman 2012). An important future challenge for palaeoecologists is to understand the timing of impact [Q1] and how ecosystems responded in these human mediated landscapes [Q2-6].

The broad theme of human-environment interactions was identified as an area where a strong overlap exists between ecological and palaeoecological research (see, e.g., Sutherland *et al*. 2013). However, an additional challenge identified by palaeoecologists concerned the threats posed by new and emerging pollutants, especially when interactions with other stressors such as climate change were considered (Noyes *et al.* 2009; Murray, Thomas & Bodour 2010) [Q7]. For example, widespread application on boats of antifouling tributylin (TBT) in the Norfolk Broads resulted in the decline in grazing organisms and subsequent proliferation of phytoplankton, which led to the collapse in aquatic macrophyte communities (Sayer *et al.* 2006) (Fig. 2). Palaeoecological records were vital in identifying major changes in ecosystem structure and function representing regime shifts, and have much to offer in disentangling the drivers and impacts of these stressors.

## Biodiversity, conservation and novel ecosystems

8. In the context of global change and cultural landscapes, is the concept of natural variability more useful than baselines in informing management targets, and, if so, how can it be defined and measured in the palaeorecord?
9. How can palaeoecological data be used to inform ecosystem restoration, species recovery and reintroductions?
10. How can the palaeoecological record be applied to understand the interactions of native, alien and invasive species?
11. How can palaeoecology help define, characterize, and inform the management of novel ecosystems?
12. How can palaeocology be applied to characterize the dynamics of ecosystem services?
13. How should palaeoecological results be translated and communicated effectively to ensure they are adaptively integrated into environmental strategies for the present and future?
14. What are the legacies of past environmental changes on the current structure, resilience and dynamics of natural and socio-ecological systems?
15. Which factors make some systems more resilient to environmental change than others?
16. Can palaeoecological records provide improved insight into the theory, causes, consequences and modelling of critical transitions and alternative stable states?
17. What can palaeoecology reveal about early warning signals of abrupt change?

Successful conservation and management of ecosystems requires knowledge of long-term change and variability. Several biodiversity intactness indices, for example, require knowledge of a 'baseline' ecological state (Scholes & Biggs 2005; Nielsen *et al.* 2007), but this fundamental information is often cited as a 'key deficiency' or knowledge gap (The Royal Society 2003; Froyd & Willis 2008). Furthermore, in novel ecosystems or in those that have experienced very rapid change or species reshuffling, a return to baseline conditions may not be achievable or even appropriate (Hobbs *et al.* 2006). 'Conservation paleobiology' is emerging as a discipline to address the challenges of using long-term data to inform restoration and management (Dietl & Flessa 2011). Important questions to be answered in the future include assessing the degree of change from specified historical ecosystems (Fluin *et al.* 2007; Gillson & Duffin 2007); [Q8]; the viability and level of intervention required to restore such historic conditions where desirable (van Leeuwen *et al.* 2008) [Q9, 10]; the extent of human influence and the management of  cultural landscapes (Chambers *et al.* 2013; Shaw & White 2013) [Q8, 9, 11]; and identifying and guiding conservation of emerging novel ecosystems in order to maintain ecosystem services (Jackson & Hobbs 2009) [Q11, 12]. Promoting and communicating palaeoecological data in conservation planning could also play an important role in informing ecosystem management [Q13].

Resilience theory has also becoming an influential framework in landscape management due to its potential for understanding ecological change in complex systems. The theory highlights the importance of identifying slow variables (i.e. processes occurring over decadal- centennial timescales or longer) that can lead to transitions between alternative stable states (Holling 1973; Scheffer & Carpenter 2003). For example, the relationship between resilience, environmental change, and political dynasties was explored by Dearing (2008) in the Erhai lake-catchment in Yunnan Province, China (Fig. 3). Analysis of lake sediment and historical records showed that agricultural expansion ~1400 cal yr BP initiated widespread gullying that continued for ~600 years. These long-term records revealed the possibility of alternate steady states in the catchment, and suggested that the landscape was characterized by low resilience today. Identifying critical thresholds and predicting when they might be crossed has been highlighted as a priority research area in ecology (Scheffer & Carpenter 2003; Sutherland *et al.* 2013) and one where palaeoecology has the potential to provide many exciting insights [Q14-17].

### Biodiversity over long timescales

18. What is the role of sea-level change in community and diversity dynamics through time and across marine and terrestrial environments?
19. What drives the spatial expansion and contraction of a species over its duration?
20. At what rates have species ranges shifted during past intervals of climate change, and what geophysical factors, biological traits and their interactions have affected these rates?
21. How can the rate and spatial dynamics of extinctions in the fossil record, together with palaeoclimate modelling, help in predicting future ecological and biodiversity loss?
22. Why do the co-occurrences of some species persist through time? Is the stability of these associations caused by similar environmental niches, co-evolutionary relationships, or randomness?
23. What processes control the stability/variability of realized and fundamental niches through time?

24. How has varying atmospheric composition shaped biotic interactions (e.g., between C3 and C4 plants, trees and grasses, megaherbivores and forage, insects and plants)?
25. What are the appropriate null models in palaeoecology for testing hypotheses about ecological and evolutionary processes?

Biodiversity dynamics are primarily regulated through the interaction of speciation and extinction rates through time. Molecular phylogenies on extant taxa are limited in that they typically only provide insights into the speciation process. In contrast, palaeoecological records can be used to track the waxing and waning of a species, and in some cases (e.g. Cenozoic planktonic foraminifera) the record can interpreted as a single line of descent that begins with speciation and ends in extinction (Simpson 1962). One important consideration is the abiotic processes (including, but not limited to, temperature) influencing diversification rates. Sea-level variations throughout the Phanerozoic, for example, are likely to have had major influences on the evolutionary trajectories of different species through reproductive isolation and speciation. Sea-level changes may also influence evolutionary processes by increasing chances of dispersal and changing habitat type (Abe & Lieberman 2009). Similarly, environmental instability early on in a species' lifespan has been shown to influence species' persistence over time (Liow *et al.* 2010) but what is still poorly understood is the rate and driving mechanisms of this process [Q18,19]. On shorter timescales, changes in climate on glacial-interglacial cycles have also been demonstrated to influence migration rates, dispersal and range size changes (Bennett 1997). Understanding how these environmental variables influence geographic range and niche dynamics is essential as geographic range directly impacts on the extinction risk of species. This is an area of research where palaeoecology has much to offer [Q20, 21, 23].

Biotic interactions can also shape evolutionary processes. Whilst the Quaternary record shows constant turnover of communities and development of novel ecosystems, particularly at times of rapid climate change, on deeper timescales the persistence of some species, especially plants, is remarkable (Willis and McElwain 2014). This leads to the question of which factors lead to long-term persistence [Q22] and the challenges of quantifying the interplay between abiotic change and biotic interactions (Ezard *et al.* 2011). A classic example of this is the relationship between C3 and C4 plants from the Oligocene (approx. 33 Ma); how this biotic interaction was influenced by changing atmospheric $CO_2$ concentrations and aridity is still poorly understood (Strömberg 2011) [Q24].

Interestingly, a question on 'null models' [Q25] emerged in the priority list. Null models use permutation procedures on ecological data in order to produce a distribution that would be expected in the absence of a particular ecological mechanism (Gotelli & Graves 1996). Although null models have played a particularly important role for explaining patterns of dispersal (Hubbell 2001), this approach is fundamental to all scientific disciplines and yet is rarely considered.

## Ecosystem processes and biogeochemical cycling

26. How have terrestrial carbon, nitrogen and silica cycles been linked in the past, specifically at times of abrupt climate change?

27. What was the effect of centennial-scale climate variability on the carbon balance of terrestrial and aquatic ecosystems at regional to global scales?
28. How can palaeoecological data from continental shelf areas help characterise anthropogenic impacts on geochemical fluxes (e.g. silica, C, N and P) from land to shallow marine ecosystems during the Holocene?
29. How does species turnover (e.g. immigrations, extinctions) and varying community composition affect ecosystem function, including carbon sequestration?
30. How can sedimentary records be used to address process-based questions and to test mechanistic ecological models so as to provide insights about the past functioning of ecological systems?
31. How can ecological interactions (e.g. competition, predation, mutualism, commensalism) and their possible evolutionary consequences be inferred from palaeoecological data?
32. How can disturbances such as insect outbreaks or pathogens be detected in palaeoecological data?
33. What are the taphonomic characteristics of ancient DNA, in particular under different climatic and sedimentary contexts?

Ecological systems are linked with the abiotic environment through fluxes of energy and matter. Therefore, quantifying the rate and magnitude of the biogeochemical cycling of different nutrients, and how these rates respond to different stressors, is fundamental to understanding how an ecosystem functions and something that palaeoecological science can help address [Q26-29]. The uptake of carbon by terrestrial ecosystems, for example, is limited by N availability (Mitchell and

Chandler in Sokolov et al. 2008). A key question for global change ecologists involves understanding how these two cycles will co-vary in the future, particularly in the context of increasing carbon dioxide concentrations and excess nitrogen deposition (Galloway & Cowling 2002) [Q27]. The utility of this approach has recently been demonstrated in an integrated palaeoecological study from 86 sites globally. This revealed the slow response of the global N cycle relative to major changes in $CO_2$ during the glacial-interglacial transition (McLauchlan *et al.* 2013). Overall, a decline in N availability was observed between 15,000 and 7,500 years ago (declining values of $\delta^{15}N$), with no net change in global sedimentary N availability observed in the past 500 years (Fig. 4). This result was surprising, since one might expect an increase in sedimentary $\delta^{15}N$ following the excess N input into systems at this time. Such studies highlight the important role that palaeoecology can play in understanding ecological functioning, particularly at times of abrupt climate change.

In ecological research, problems involving complex trophic interactions, biogeochemical cycling and population dynamics are often addressed using process-based models [Q30-31]. This represents an exciting area of palaeoecological research, particularly for understanding demographic effects and biotic interactions (Jeffers *et al.* 2011). Similar approaches might also be applied in, for example, research concerning pest-pathogen outbreaks, for which reliable detection methods are still required [Q32]. Finally, major ecological insights can be gained from understanding changes in genetic variability of populations through the recovery and study of ancient DNA (aDNA) from fossil remains. A remaining technical challenge in this research area concerns the understanding of taphonomic processes influencing aDNA preservation [33] (e.g. Haile *et al.* 2007).

## Comparing, combining and synthesizing information from multiple records

34. What methods can be used to develop more robust quantitative palaeoenvironmental reconstructions and ensure reliable estimates of the associated uncertainties?
35. How can palaeoecologists disentangle the separate and combined effects of multiple causal factors in palaeoecological records?
36. When using modern analogues, what measures can be taken to be sure that the training set is sufficient to reconstruct the full range of likely past conditions, and if not, what else should be used to supplement these methods?
37. What methods can be used to identify and quantify the effect of diagenetic and taphonomic processes on the palaeoecological record?
38. How does taxonomic and numerical resolution affect the recognition of community, metacommunity, and other ecological patterns?
39. How can common environmental signals be identified in multiple records at different spatial and temporal scales?
40. What methods can be used to better assess the leads, lags, and synchronicities in palaeorecords at different spatial scales?
41. Given that palaeoecology relies on accurately dated chronologies, how can the often incompatible dates derived from different dating techniques (e.g. $^{210}$Pb &$^{14}$C, $^{14}$C & OSL) be reconciled to improve the dating of key time periods (e.g. the Industrial period; MIS 3)?

Modern research in palaeoecology focuses both on understanding the ecology and environment of single geographical locations (via, for example, analysis of lake, peat, ocean and ice core records) and on reconstructing past environments and ecosystems at regional, continental and global scales. While tools for single-site analysis have been evolving since the earliest work in palaeoecology (e.g. Fægri & Iversen 1950), tools for inter-site comparison and regional synthesis are relatively undeveloped and face two main challenges. The first is to disentangle the effects of multiple causal factors on palaeoecological records at single sites and across multi-site networks (Cunningham *et al.* 2013; Juggins 2013). The second is to quantify the sources of uncertainty that accumulate as one moves through the causal chain that links climate or other environmental drivers to the palaeoecological observations (Fig. 5).

There are many sources of uncertainty in palaeoecology. Some relate simply to the stochasticity of the natural world, but others arise because of the often indirect link between the palaeoenvironment and the observations obtained. For example, palaeoecological records typically comprise multi-species assemblages from multiple biological groups (Birks & Birks 2006) that are preserved in long environmental archives that experience complex post-depositional processes (Birks & Birks 1980). The transfer function methods used to quantify the relationship between ecological assemblage and climate are already used to formalise some of the links in the causal chain from palaeoenvironment to field and lab observations (e.g. Haslett *et al.* 2006). However, such explicitly causal models are rare and many such links are simply described qualitatively and not formally modelled. Five questions draw attention to these issues in general or as they relate to specific links in the causal chain [Q34-38].

An additional challenge involves the synthesis of information from multiple sites [Q39-41]. For such projects issues of chronology often become a primary focus since, unless the records to be combined are on a comparable time scale (with reliable estimates of uncertainties), robust synthesis is impossible (Blaauw & Heegaard 2012). There is a need to improve existing and develop new chronological techniques, and to understand and reconcile the differences observed between the chronologies derived from different techniques (e.g. Piotrowska *et al.* 2010; Blockley *et al.* 2012). The need to develop new methods for dating 19th century sediments is seen as a particular priority (e.g. see Rose & Appleby 2005). This time period is increasingly beyond the range of $^{210}$Pb dating and as the gap between conventional $^{14}$C and $^{210}$Pb dating becomes progressively greater, novel dating techniques such as $^{32}$Si hold great potential (Morgenstern *et al.* 2013) [Q41].

## Developments in palaeoecology

42. Do ecological principles, formulated to account for present day (10-100 years) patterns, hold when applied to palaeoecological patterns (>100-1000 years), or are there palaeoecologically important ecological processes that are impossible to study with modern observational data?
43. What common questions can be addressed by ecologists and palaeoecologists to bridge the contrasting spatial and temporal scales between the two disciplines effectively?
44. How can palaeoecological records contribute to and advance key concepts that are currently central to ecological thinking, including model comparison and stochastic process modeling?

45. How can forest inventory data, modern pollen databases, and pollen loading equations be integrated effectively to facilitate the generation of robust estimates of tree and land cover?
46. How best can palaeoecologists create an accessible, consistent, usable and future-proof record of historical and archaeological sources integrated with contemporary ecological observations?
47. What new opportunities and research agendas, arising from the availability of higher spatial, temporal and taxonomic resolution data, will be created with the adoption of automated counting systems for microfossils?
48. What are the developmental and genetic controls on morphology, and how can the fossil record be used to study phenotypic plasticity and the evolution of developmental systems?
49. How do palaeoecologists encourage hypothesis testing rather than data-dredging approaches when exploring relationships between proxies and records?
50. How can closer collaboration between palaeoecologists and statisticians be fostered in order to ensure development and dissemination of appropriate statistical techniques?

In the last three decades, palaeoecology has been transformed from a discipline dominated by studies on the composition and structure of fossil assemblages preserved in sediments (e.g. Birks & Birks 1980) into a sophisticated multi-disciplinary science involving not only palaeobotany, palaeozoology and archaeology, but also inorganic and organic geochemistry, stable-isotope assays, geochronology, dendrochronology, aDNA studies, modelling and applied statistics (Flessa & Jackson

2005; Birks 2008). Here, two outstanding developments were identified. New identification and counting systems (Holt *et al.* 2011; Punyasena *et al.* 2012) and multivariate morphometric techniques (Claude 2008) [47] have the potential to investigate morphological variability observed in the fossil record in detail. For example, when combined with aDNA techniques [Q33], these new tools could be used to investigate whether genotypic changes can be disentangled from phenotypic shifts [48]. The second involves the fast emerging discipline of palaeoecoinformatics (Brewer, Jackson & Williams 2012), which is encouraging open-access databases of palaeoecological data (e.g. Neotoma 2013). Rigorous data standardization of both fossil and modern pollen is essential in data-synthesis. Data-mining exercises could be used to provide more reliable reconstructions of species dynamics, vegetation composition and landscape structure in space and time [Q45, 46].

But despite these new developments, some fundamental principles remain to be answered. Thus, the importance of the essential links between palaeoecology and ecology was emphasised, with a focus on integrating data across spatial, taxonomic and temporal scales (e.g. Gray 2004; Helama *et al.* 2010) [Q42-44]. Finally, three questions were targeted at challenging the research approaches of palaeoecologists themselves. There is an increasing need to exploit the full potential of dynamic modelling, quantitative model comparison and statistical hypothesis-testing in palaeoecological analyses (Jeffers *et al.* 2011; 2012) [Q44, 49] so as to provide a rigorous basis for further quantitative analytical approaches in palaeoecology (Birks 1985; Birks 2012) [see also Q25]. This requires close collaboration between palaeoecologists, ecological modellers, and applied statisticians [Q50].

## Discussion

### Evaluation

Our study follows other priority research exercises in, for example, ecology, applied ecology and conservation science (Sutherland *et al.* 2006; Sutherland *et al.* 2009; 2013). All of these exercises are dependent on the individual skills, interests and expertise of the participants and our questions do not, therefore, represent a definitive list. We also noted that whilst the 804 screened questions were a mixture of both general and specific, questions became increasingly general through subsequent iterations. More than 100 questions involving pollen analysis were submitted, for example, but these were translated into more general questions that could be applied to multiple proxy groups or habitat types. The end result is a list of questions that can be tailored to a variety of research problems.

As an example, a widespread decline of *Tsuga canadensis* (Eastern hemlock) is observed in fossil pollen records ca. 5,500 cal yr BP across its entire range in eastern North America. Its drivers have been ascribed to climate (Shuman, Newby & Donnelly 2009), a pest-pathogen outbreak (Davis 1981), or a combination of the two (e.g. Booth *et al.* 2012). Whilst there is some evidence for fossil head capsules of insect pests found in limited sites around the time of the decline (Bhiry & Filion 1996), evidence for a range-wide outbreak remains inconclusive. Thus, one obvious important development is to find new ways of detecting pest-pathogen outbreaks in the palaeoecological record [Q32]. Additional information could be inferred using process-based models to infer population dynamics [Q31, 44]. If the hemlock decline was driven by climate, then an additional question would be why this species responded more sensitively than others [Q3], or whether it was the result of cross-scale interactions between climate and the pathogen, or the interactions of multiple stressors [Q35, 39]. Thorough testing of the problem also requires integrating multiple palaeoecological sites [Q39]. Even the timing and synchrony of the hemlock decline is now being debated so resolving age uncertainties between pollen and other climate records is vital [Q40].

## Looking forward

This exercise also provided an opportunity to reflect on the status of the discipline today. How do our questions compare to those identified in fundamental ecology and what can we infer about the future directions? Von Post's seminal work in the early 20th century was heavily focused on describing patterns of vegetation change as a relative dating tool over the past 11,000 years. There was little consideration of the underlying ecological mechanisms responsible for the observed changes. In contrast, from the 1980s onwards, many fossil pollen data-sets were developed specifically to reconstruct past climate change with little attention given to the patterns of vegetation change. In these studies quantification and reconstructions of single sites was a key focus, whilst there were a growing number of studies that were being applied to test ecological hypotheses.

The questions identified in this study highlight a different situation for modern palaeoecological science. Only 8% of the initial questions submitted to the website were specifically targeted at filling data gaps, or represented a specific regional study. None of these were selected in the final question list. Instead, topics covered included community, species and diversity dynamics (18%); ecosystem functioning (12%);

global change ecology and human impacts (18%); and ecosystem management (12%). Therefore, primarily through its ability understand ecological responses to environmental change, the perceived disconnect between neo-ecology and palaeoecology that has been reported in the past is being eroded (see, e.g. Froyd & Willis 2008). As a result, common themes between these questions and those in the recent fundamental ecology exercise (Sutherland *et al.* 2013) can be identified. Examples include factors that control species range shifts; biogeochemical cycling under rapid climate change; and measuring and quantifying ecological resilience. This suggests that there is great potential for further integration between the two sub-disciplines.

One other striking feature of the 50 questions is the heavy dependence on methods. 40% of the questions were related to methodology, either directly by focusing upon improved precision and accuracy, or by finding new ways to apply and interpret palaeoecological data to address broader questions of, for example, landscape management. In palaeoecological research this is not surprising. Proxy data are indirect measures of a targeted environmental variable, whilst robust palaeoecological inferences are also heavily dependent on indirect dating techniques. This is in contrast to, for example, neo-ecology, in which the ecological units of analysis can often be directly observed. This result does not undermine the capability of palaeoecology to provide long-term insights. It does, however, highlight the continued rigour in the discipline and widespread acknowledgement of the importance of understanding what proxy data can and cannot tell us. A major focus for the future then, will remain in characterizing the uncertainties between target variable and proxy source to make robust ecological and evolutionary inferences (e.g. Jackson 2012) (Fig. 5).

The questions selected also hint at cross cutting themes that have the potential to influence palaeoecological research in the future. The move from site-specific descriptions towards addressing global scale issues, for example, is reliant on upscaling and comparing multiple records. This will require efficient data management techniques that are able to compare and correlate multiple proxies. A second cross-cutting theme involves disentangling the synergistic effects of multiple variables (e.g. fire, human impact, faunal composition). We now realise that ecosystems represent complex systems, experiencing chaotic fluctuations and alternative stable states, and these dynamics partially explain the unpredictable ecosystem responses following an extrinsic forcing. Finally, there are a number of questions that highlight the importance of biotic interactions. Better characterization of these in palaeoecological records may also improve our understanding of community dynamics in complex systems.

In summary, the 50 questions identified and discussed in this paper highlight the potential for palaeoecology to address both empirical and applied research questions related to ecological science and global change. These questions demonstrate the critical importance of historical context in understanding the Earth system and, whilst we do not claim that they are definitive, they outline key areas in the future palaeoecological research agenda.

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## References

Abe, F.R. & Lieberman, B.S. (2009) The Nature of Evolutionary Radiations: A Case Study Involving Devonian Trilobites. *Evolutionary Biology*, **36**, 225–234.

Barnosky, A.D. (2004) Assessing the Causes of Late Pleistocene Extinctions on the Continents. *Science*, **306**, 70–75.

Battarbee, R.W., Charles, D.F., Bigler, C., Cumming, B.F. & Renberg, I. (2010) Diatoms as indicators of surface-water acidity. *The Diatoms: Applications for the Environmental and Earth Sciences* (eds J.P. Smol & E.F. Stoermer pp. 98–121. Cambridge University Press.

Bennett, K.D. (1997) *Evolution and Ecology: the Pace of Life*. Cambridge, UK.

Bennion, H., Battarbee, R.W., Sayer, C.D., Simpson, G.L. & Davidson, T.A. (2010) Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology: a synthesis. *Journal of Paleolimnology*, **45**, 533–544.

Bhiry, N. & Filion, L. (1996) Mid-Holocene Hemlock Decline in Eastern North America Linked with Phytophagous Insect Activity. *Quaternary Research*, **45**, 312–320.

Birks, H.H. & Birks, H.J.B. (2006) Multi-proxy studies in palaeolimnology. *Vegetation History and Archaeobotany*, **15**, 235–251.

Birks, H.J.B. (1985) Recent and possible future mathematical developments in quantitative palaeoecology. *Palaeogeography Palaeoclimatology Palaeoecology*, **50**, 107–147.

Birks, H.J.B. (2008) Palaeoecology. *Encyclopedia of Ecology* (ed S.E. Jørgensen pp.

2623–2634. Elsevier Ltd, Oxford.

Birks, H.J.B. (2012) Conclusions and Future Challenges. *Tracking Environmental Change Using Lake Sediments. Volume 5: Data Handling and Numerical Techniques.* (eds H.J.B. Birks, A.F. Lotter, S. Juggins & J.P. Smol pp. 643–673. Dordrecht: Springer.

Birks, H.J.B. & Birks, H.H. (1980) *Quaternary Palaeoecology*. Edward Arnold, London (Reprinted 2004 by the Blackburn Press, New Jersey).

Blaauw, M. & Heegaard, E. (2012) Estimation of age-depth relationships. *Tracking Environmental Change Using Lake Sediments, Volume 5: Data Handling and Numerical Techniques* (eds H.J.B. Birks, A.F. Lotter, S. Juggins & J.P. Smol pp. 379–413. Dordrecht: Springer.

Blockley, S.P.E., Lane, C.S., Hardiman, M., Rasmussen, S.O., Seierstad, I.K., Steffensen, J.P., Svensson, A., Lotter, A.F., Turney, C.S.M., Ramsey, C.B. & members, I. (2012) Synchronisation of palaeoenvironmental records over the last 60,000 years, and an extended INTIMATE[1] event stratigraphy to 48,000 b2k. *Quaternary Science Reviews*, **36**, 2–10.

Booth, R.K., Brewer, S., Blaauw, M., Minckley, T.A. & Jackson, S.T. (2012) Decomposing the mid-Holocene Tsugadecline in eastern North America. *Ecology*, **93**, 1841–1852.

Brewer, S., Jackson, S.T. & Williams, J.W. (2012) Paleoecoinformatics: applying geohistorical data to ecological questions. *Trends in Ecology & Evolution*, **27**, 104–112.

Burney, D. & Flannery, T. (2005) Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology & Evolution*, **20**, 395–401.

Chambers, F.M., Cloutman, E.W., Daniell, J.R.G., Mauquoy, D. & Jones, P.S. (2013) Long-term ecological study (palaeoecology) to chronicle habitat degradation and inform conservation ecology: an exemplar from the Brecon Beacons, South Wales. Biodiversity and Conservation, 22, 719–736.

Claude, J. (2008) *Morphometrics with R*. Springer, New York.

Crutzen, P.J. & Stoermer, E.F. (2000) The Anthropocene. *Global Change Newsletter*, **41**, 17–18.

Cunningham, L.K., Austin, W.E.N., Knudsen, K.L., Eiriksson, J., Scourse, J.D., Wanamaker, A.D., Butler, P.G., Cage, A.G., Richter, T., Husum, K., Hald, M., Andersson, C., Zorita, E., Linderholm, H.W., Gunnarson, B.E., Sicre, M.-A., Sejrup, H.P., Jiang, H. & Wilson, R.J.S. (2013) Reconstructions of surface ocean conditions from the northeast Atlantic and Nordic seas during the last millennium. *The Holocene.*

Davis, M.B. (1981) Outbreaks of forest pathogens in Quaternary history. *IV International Palynology Conference, Lucknow (1976-1977)*, **3**, 216–228.

Dearing, J.A. (2008) Landscape change and resilience theory: a palaeoenvironmental assessment from Yunnan, SW China. *The Holocene*, **18**, 117–127.

Dietl, G.P. & Flessa, K.W. (2011) Conservation paleobiology: putting the dead to work. *Trends in Ecology & Evolution*, **26**, 30–37.

Ezard, T.H.G., Aze, T., Pearson, P.N. & Purvis, A. (2011) Interplay between changing climate and species' ecology drives macroevolutionary dynamics. *Science*, **332**, 349–351.

Flessa, K.W. & Jackson, S.T. (2005) *The Geological Record of Ecological Dynamics. Understanding the Biotic Effects of Future Environmental Change.* National Research Council of the National Academies, Washington, DC.

Fluin, J., Gell, P., Haynes, D., Tibby, J. & Hancock, G. (2007) Palaeolimnological evidence for the independent evolution of neighbouring terminal lakes, the Murray Darling Basin, Australia - Springer. *Hydrobiologia*, **591**, 117–134.

Froyd, C.A. & Willis, K.J. (2008) Emerging issues in biodiversity & conservation management: The need for a palaeoecological perspective. *Quaternary Science Reviews*, **27**, 1723–1732.

Fægri, K. & Iversen, J. (1950) *Text Book of Modern Pollen Analysis*. John Wiley and Sons.

Galloway, J.N. & Cowling, E.B. (2002) Reactive Nitrogen and The World: 200 Years of Change. *AMBIO: A Journal of the Human Environment*, **31**, 64–71.

Gibbard, P.L. & Walker, M.J.C. (2013) The term “Anthropocene” in the context of formal geological classification. *A Stratigraphic Basis for the Anthropocene* (eds C. Waters, J. Zalasiewicz, M. Williams, M. Ellis & A. Snelling Geological Society Special Publication.

Gill, J.L., Williams, J.W., Jackson, S.T., Lininger, K.B. & Robinson, G.S. (2009) Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, **326**, 1100–1103.

Gillson, L. & Duffin, K.I. (2007) Thresholds of potential concern as benchmarks in the management of African savannahs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **362**, 309–319.

Gotelli, N.J. & Graves, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press.

Gray, A. (2004) Ecology and government policies: the GM crop debate. *Journal of Applied Ecology*, **41**, 1–10.

Grierson, C.S., Barnes, S.R., Chase, M.W., Clarke, M., Grierson, D., Edwards, K.J., Jellis, G.J., Jones, J.D., Knapp, S., Oldroyd, G., Poppy, G., Temple, P., Williams, R. & Bastow, R. (2011) One hundred important questions facing plant science research. *New Phytologist*, **192**, 6–12.

Haile, J., Holdaway, R., Oliver, K., Bunce, M., Gilbert, M.T.P., Nielsen, R., Munch, K., Ho, S.Y.W., Shapiro, B. & Willerslev, E. (2007) Ancient DNA Chronology within Sediment Deposits: Are Paleobiological Reconstructions Possible and Is DNA Leaching a Factor? *Molecular Biology and Evolution*, **24**, 982–989.

Haslett, J., Whiley, M., Bhattacharya, S., Salter-Townshend, M., Wilson, S.P., Allen, J.R.M., Huntley, B. & Mitchell, F.J.G. (2006) Bayesian palaeoclimate reconstruction. *Journal of the Royal Statistical Society: Series A (Statistics in Society)*, **169**, 395–438.

Helama, S., Seppa, H., Birks, H.J.B. & Bjune, A.E. (2010) Reconciling pollen-stratigraphical and tree-ring evidence for high- and low-frequency temperature variability in the past millennium. *Quaternary Science Reviews*, **29**, 3905–3918.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R. & Zobel, M. (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Holling, C.S. (1973) Resilience and stability of ecological systems. *Annual review of ecology and systematics*, **4**, 1–23.

Holt, K., Allen, G., Hodgson, R., Marsland, S. & Flenley, J. (2011) Progress towards an automated trainable pollen location and classifier system for use in the palynology laboratory. *Review of Palaeobotany and Palynology*, **167**, 175–183.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton.

Jackson, S.T. (2007) Looking forward from the past: history, ecology, and conservation. *Frontiers in Ecology and the Environment*, **5**, 455–455.

Jackson, S.T. (2012) Representation of flora and vegetation in Quaternary fossil assemblages: known and unknown knowns and unknowns. *Quaternary Science Reviews*, **49**, 1–15.

Jackson, S.T. & Hobbs, R.J. (2009) Ecological restoration in the light of ecological history. *Science*, **325**, 567–569.

Jeffers, E.S., Bonsall, M.B. & Willis, K.J. (2011) Stability in ecosystem functioning across a climatic threshold and contrasting forest regimes. *PloS one*, **6**.

Jeffers, E.S., Bonsall, M.B., Watson, J.E. & Willis, K.J. (2012) Climate change impacts on ecosystem functioning: evidence from an Empetrum heathland. *New Phytologist*, **193**, 150–164.

Juggins, S. (2013) Quantitative reconstructions in palaeolimnology: new paradigm or sick science? *Quaternary Science Reviews*, **64**, 20–32.

Liow, L.H., Skaug, H.J., Ergon, T. & Schweder, T. (2010) Global occurrence trajectories of microfossils: environmental volatility and the rise and fall of individual species. *Paleobiology*, **36**, 224–252.

McLauchlan, K.K., Williams, J.J., Craine, J.M. & Jeffers, E.S. (2013) Changes in global nitrogen cycling during the Holocene epoch. *Nature*, **495**, 352–355.

Morgenstern, U., Ditchburn, R.G., Vologina, E.G. & Sturm, M. (2013) 32Si dating of sediments from Lake Baikal. *Journal of Paleolimnology*, **50**, 345–352.

Murray, K.E., Thomas, S.M. & Bodour, A.A. (2010) Prioritizing research for trace pollutants and emerging contaminants in the freshwater environment. *Environmental Pollution*, **158**, 3462–3471.

Nielsen, S.E., Bayne, E.M., Schieck, J., Herbers, J. & Boutin, S. (2007) A new method to estimate species and biodiversity intactness using empirically derived reference conditions. *Biological Conservation*, **137**, 403–414.

Noyes, P.D., McElwee, M.K., Miller, H.D., Clark, B.W., Van Tiem, L.A., Walcott, K.C., Erwin, K.N. & Levin, E.D. (2009) The toxicology of climate change: Environmental contaminants in a warming world. *Environment International*, **35**, 971–986.

Petrokofsky, G., Brown, N.D. & Hemery, G.E. (2012) Matching a scientific knowledge base with stakeholders' needs. *Forest Policy and Economics*. doi:10.1016/j.forpol.2012.05.005

Piotrowska, N., De Vleeschouwer, F., Sikorski, J., Pawlyta, J., Fagel, N., Le Roux, G. & Pazdur, A. (2010) Intercomparison of radiocarbon bomb pulse and Pb-210 age models. A study in a peat bog core from North Poland. *Nuclear Instruments & Methods in Physics Research Section B-Beam Interactions with Materials and Atoms*, **268**, 1163–1166.

Pretty, J., Sutherland, W.J., Ashby, J. & Auburn, J *et al.* (2010) The top 100 questions of importance to the future of global agriculture. *International Journal of Agricultural Sustainability,* **8**, 219–236.

Punyasena, S.W., Tcheng, D.K., Wesseln, C. & Mueller, P.G. (2012) Classifying black and white spruce pollen using layered machine learning. *New Phytologist*, **196**, 937–944.

Rose, N.L. & Appleby, P.G. (2005) Regional applications of lake sediment dating by spheroidal carbonaceous particle analysis I: United Kingdom. *Journal of Paleolimnology*, **34**, 349–361.

Ruddiman, W.F. (2012) The Anthropocene. *Annual Review of Earth and Planetary Sciences*, **41**, 4.1–4.24.

Rule, S., Brook, B.W., Haberle, S.G., Turney, C.S.M., Kershaw, A.P. & Johnson, C.N. (2012) The Aftermath of Megafaunal Extinction: Ecosystem Transformation in Pleistocene Australia. *Science*, **335**, 1483–1486.

Sayer, C.D., Hoare, D.J., Simpson, G.L., Henderson, A.C.G., Liptrot, E.R., Jackson, M.J., Appleby, P.G., Boyle, J.F., Jones, J.I. & Waldock, M.J. (2006) TBT Causes

Regime Shift in Shallow Lakes. *Environmental Science & Technology*, **40**, 5269–5275.

Scheffer, M. & Carpenter, S.R. (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution*, **18**, 648–656.

Scholes, R.J. & Biggs, R. (2005) A biodiversity intactness index. *Nature*, **434**, 45–49.

Shaw, H. & White, I. (2013) Land management and biodiversity through time in upper Ribblesdale, North Yorkshire, UK: understanding the impact of traditional management. Cultural Severance and the Environment. *The Ending of Traditional and Customary Practice on Commons and Landscapes Managed in Common* (eds. M. Agnoletti & I.D. Rotherham) Springer.

Shuman, B.N., Newby, P. & Donnelly, J.P. (2009) Abrupt climate change as an important agent of ecological change in the Northeast U.S. throughout the past 15,000 years. *Quaternary Science Reviews*, **28**, 1693–1709.

Simpson, G.G. (1962) *Principles of Animal Taxonomy*. Columbia University Press, New York, USA.

The Royal Society, 2003. *Measuring Biodiversity for Conservation. Royal Society Working Party*. URL http://www.royalsociety.org.

Strömberg, C.A. (2011) Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences*, **39**, 517–544.

Sutherland, W.J., Adams, W.M., Aronson, R.B., Aveling, R., Blackburn, T.M., Broad, S., Ceballos, G., Cote, I.M., Cowling, R.M., Da Fonseca, G.A.B., Dinerstein, E., Ferraro, P.J., Fleishman, E., Gascon, C., Hunter, M.J., Hutton, J., Kareiva, P., Kuria, A., Macdonald, D.W., Mackinnon, K., Madgwick, F.J., Mascia, M.B., Mcneely, J., Milner-Gulland, E.J., Moon, S., Morley, C.G., Nelson, S., Osborn, D., Pai, M., Parsons, E.C.M., Peck, L.S., Possingham, H.P., Prior, S.V., Pullin, A.S., Rands, M.R.W., Ranganathan, J., Redford, K.H., Rodriguez, J.P., Seymour, F., Sobel, J., Sodhi, N.S., Stott, A., Vance-Borland, K. & Watkinson, A.R. (2009) One Hundred Questions of Importance to the Conservation of Global Biological Diversity. *Conservation Biology*, **23**, 557–567.

Sutherland, W.J., Armstrong-Brown, S., Armsworth, P., Brereton, T., Brickland, J., Campbell, C., Chamberlain, D., Cooke, A., Dulvy, N., Dusic, N., Fitton, M., Freckleton, R., Godfray, H., Grout, N., Harvey, H., Hedley, C., Hopkins, J., Kift, N., Kirby, J., Kunin, W., Macdonald, D., Marker, B., Naura, M., Neale, A., Oliver, T., Osborn, D., Pullin, A., Shardlow, M., Showler, D., Smith, P., Smithers, R., Solandt, J., Spencer, J., Spray, C., Thomas, C., Thompson, J., Webb, S., Yalden, D. & Watkinson, A.R. (2006) The identification of 100 ecological questions of high policy relevance in the UK. *Journal of Applied Ecology*, **43**, 617–627.

Sutherland, W.J., Fleishman, E., Mascia, M.B., Pretty, J. & Rudd, M.A. (2011) Methods for collaboratively identifying research priorities and emerging issues in science and policy. *Methods in Ecology and Evolution*, **2**, 238–247.

Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D., Carmel, Y., Coomes, D.A., Coulson, T., Emmerson, M.C., Hails, R.S., Hays, G.C., Hodgson, D.J., Hutchings, M.J., Johnson, D., Jones, J.P.G., Keeling, M.J., Kokko, H., Kunin, W.E., Lambin, X., Lewis, O.T., Malhi, Y., Mieszkowska, N., Milner-Gulland, E.J., Norris, K., Phillimore, A.B., Purves, D.W., Reid, J.M., Reuman, D.C., Thompson, K., Travis, J.M.J., Turnbull, L.A., Wardle, D.A. & Wiegand, T. (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**, 58–67.

van Leeuwen, J.F.N., Froyd, C.A., van der Knaap, W.O., Coffey, E.E., Tye, A. & Willis, K.J. (2008) Fossil pollen as a guide to conservation in the Galapagos. *Science*, **322**, 1206–1206.

Walzer, C., Kowalczyk, C., Alexander, J.M., Baur, B., Bogliani, G., Brun, J.-J., Fuereder, L., Guth, M.-O., Haller, R., Holderegger, R., Kohler, Y., Kueffer, C., Righetti, A., Spaar, R., Sutherland, W.J., Ullrich-Schneider, A., Vanpeene-Bruhier, S.N. & Scheurer, T. (2013) The 50 most important questions relating to the maintenance and restoration of an ecological continuum in the European Alps. *PloS one*, **8**.

Willis, K.J., Bailey, R.M., Bhagwat, S.A. & Birks, H.J.B. (2010) Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends in Ecology & Evolution*, **25**, 583–591.

Zalasiewicz, J., Williams, M., Haywood, A. & Ellis, M. (2011) The Anthropocene: a new epoch of geological time? INTRODUCTION. *Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences*, **369**, 835–841.

## FIGURES

**Figure 1.** Schematic showing the pre-screening process followed by workshop structure used to reduce 905 submitted questions to the final 50 priority questions.

**Figure 2.** (from Sayer *et al.* 2006). Summary butyltin (μ g-1) profiles and biostratigraphy for a sediment core from Hickling Broad. Macrofossil data are expressed as a flux (no. cm2 yr-1) to account for differential rates of sediment accumulation over the core profile. Palaeoecological data was used to identify a regime shift in aquatic communities following exposure to pollutant stressors.

**Figure 3.** (from Dearing 2008). Landscape stability in alternative steady states from the Lake Erhai basin, China. Two 'steady' states can be identified from assessing the relationship between soil erosion rates and the % of non-arboreal pollen. A non-degraded state between 2960- 1430 cal yr BP, 600 yr transition period, and a degraded state between 800 cal yr BP and the present. This example demonstrates the value of palaeoecological data for testing attributes of resilience theory and for better understanding complex system dynamics.

**Figure 4.** (from MacLaughlan *et al.* 2013). Changes in lacustrine sedimentary d$^{15}$N during the late Pleistocene and Holocene. The d$^{15}$N record is a proxy for nitrogen availability, with higher $^{15}$N values occurring when N supply is high relative to biotic

demand. Palaeoecological evidence revealed both the slow response of the nitrogen cycle to major changes in $CO_2$ and temperature over the glacial-interglacial transition; and no net change in N demand over the past 500 years. This is surprising since there has been doubling of the pre-industrial supply of nitrogen in the past 200 years, and reveals the important long-term of net terrestrial C balance in maintaining global biogeochemical cycles. A) A smoothing spline curve (0.05 smoothing parameter) fitted to the means of sites in 100-yr bins is shown (red) with 95% bootstrapped confidence intervals (grey). Declines in sedimentary $d^{15}N$ from 15,000 cal. yr BP to the breakpoint at 7,056 6 597 cal. yr BP correspond with periods of global net terrestrial carbon gain (shaded green). Dotted black line is the breakpoint regression. B) A different set of high-resolution sedimentary $d^{15}N$ records shows no net change over the past 500 yr.

**Figure 5. (**from Jackson 2012) A general conceptual model for representation of vegetational, biogeographic, or other entities in paleoecological records. The target is the primary entity of interest, and the inference is the end point in the chain. Each oval represents a series of processes by which information is transferred and transformed, and each process is accompanied by distinct uncertainties, distortions, and loss of information. The aim is to ensure that properties of the final inference will correspond to those of the original target (i.e., reality). However, the inference is usually accompanied by substantial uncertainty accumulated along the chain.