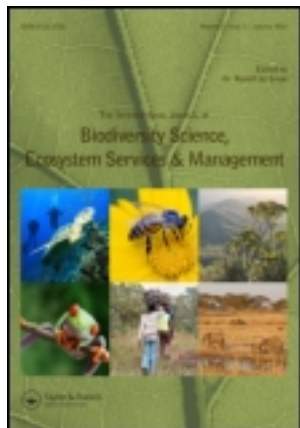


This article was downloaded by: [Universitetsbiblioteket I Trondheim NTNU]

On: 04 December 2012, At: 03:54

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## International Journal of Biodiversity Science, Ecosystem Services & Management

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tbsm21>

### Ecological palaeoecology and conservation biology: controversies, challenges, and compromises

H. John B. Birks<sup>a b c</sup>

<sup>a</sup> Department of Biology and Bjerknes Centre for Climate Research, University of Bergen, PO Box 7803, N-5020, Bergen, Norway

<sup>b</sup> Environmental Change Research Centre, University College London, Gower Street, London, WC1E 6BT, UK

<sup>c</sup> School of Geography, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK

Version of record first published: 05 Jul 2012.

To cite this article: H. John B. Birks (2012): Ecological palaeoecology and conservation biology: controversies, challenges, and compromises, International Journal of Biodiversity Science, Ecosystem Services & Management, 8:4, 292-304

To link to this article: <http://dx.doi.org/10.1080/21513732.2012.701667>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae, and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand, or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

## RESEARCH LETTER

### Ecological palaeoecology and conservation biology: controversies, challenges, and compromises

H. John B. Birks<sup>a,b,c\*</sup>

<sup>a</sup>Department of Biology and Bjerknes Centre for Climate Research, University of Bergen, PO Box 7803, N-5020 Bergen, Norway;

<sup>b</sup>Environmental Change Research Centre, University College London, Gower Street, London WC1E 6BT, UK; <sup>c</sup>School of Geography, University of Oxford, South Parks Road, Oxford OX1 3QY, UK

Until recently, ecological palaeoecology (a part of long-term ecology) and conservation biology were considered two separate subjects with little relevance to each other. With the shift from description and evaluation in conservation biology in the 1960s–1990s to the paradigm of ‘conservation in a rapidly changing world’ in the late 1990s, conservationists began to realise the importance of the temporal dimension in developing conservation strategies to allow for landscape and ecosystem change.

Despite this paradigm shift, ecological palaeoecology is still largely ignored by conservation biology. I explore why this may be and outline recent advances in the subject of direct relevance to conservation science. I present nine questions of critical importance to conservation that palaeoecology can answer.

Inevitably during this honeymoon phase of conservation biology and palaeoecology, there are controversies, challenges, and compromises. I outline these and suggest how some can be overcome by breakdown of the largely artificial boundaries between landscape history, cultural history, conservation, and palaeoecology, and by the appreciation that all can make important contributions to our understanding of people and nature and conservation in the face of changing land-use, environment, and landscapes.

**Keywords:** baseline conditions; diversity; ecological processes; land-use; landscapes; long-term ecology; novel ecosystems; pollen analysis; resilience; thresholds

#### Introduction

Ecological palaeoecology (hereafter called palaeoecology) is an important part of long-term ecology (Rull and Vegas-Vilarrúbia 2011). Palaeoecology and conservation biology have, until recently, been considered as two subjects with little or no relevance to each other, with their own research symposia, journals, and approaches. As conservation biology shifted from the primarily descriptive and evaluation phase in the 1960s–1990s to the problems of devising management policies for ‘conservation in a rapidly changing world’ in the 1990s and the publication of the *Millennium Ecosystem Assessment* in 2005, conservationists began to recognise the importance of the temporal dimension in developing conservation strategies and policies that incorporate ecological and evolutionary processes in response to the challenges of conservation in light of current and future biotic, landscape, and ecosystem changes (Gillson and Willis 2004; Willis et al. 2007a).

The structure of this article is as follows. First, I discuss briefly palaeoecology and conservation biology and their current links. I then outline nine critical questions in conservation management that palaeoecology can help answer. I conclude by discussing the controversies, challenges, and compromises in linking conservation biology and palaeoecology.

This article makes no attempt to be a comprehensive review of palaeoecology and conservation biology.

Birks (1996), Willis and Birks (2006), Willis et al. (2007a, 2007b, 2010), Froyd and Willis (2008), Davies (2009), Davies and Bunting (2010), Willis and Bhagwat (2010), and Vegas-Vilarrúbia et al. (2011) provide such reviews.

#### Ecological palaeoecology and conservation biology

Ecological palaeoecology uses palaeoecological techniques (Birks and Birks 1980; Delcourt and Delcourt 1991; Flessa and Jackson 2005) to resolve critical questions about long-term ecological changes. It is concerned primarily with the ecological impacts of environmental change (‘drivers’) on organisms, populations, communities, landscapes, and ecosystems. It uses the palaeoecological record of fossil pollen, leaves, seeds, animal remains, and so on, preserved in lake or bog sediments as a long-term ecological laboratory or observatory (Flessa and Jackson 2005). Long-term ecology is not primarily concerned with reconstructing past environments (e.g. climate) (as is geological palaeoecology – see Birks et al. (2010)) but with the response of organisms in the past to environmental change, including human activity (Rull 2010). Besides palaeoecology, long-term ecology includes vegetation re-sampling (Britton et al. 2009; Dengler et al. 2011; Kapfer 2011), repeat photography (Zier and Baker 2006), use of documentary material (Andersen and Baker 2005; Edmonds 2005), use of herbarium or museum collections (Hoffmann et al. 2007; Dolan et al. 2011;

\*Email: john.birks@bio.uib.no

Johnson et al. 2011), dendrochronology (Kipfmüller and Swetnam 2005), and related techniques that comprise historical ecology (Egan and Howell 2005; Balée 2006). My focus here is on ecological palaeoecology.

Besides the intellectual fascination with reconstructing and understanding the past, there are many important reasons for studying long-term ecology. Pigott and Walters (1977) wrote 'There is scarcely a feature in the countryside today that does not have its explanation in an evolution whose roots pass deep into the twilight of time. Human hands have played a leading role in this evolutionary process, and those who study vegetation cannot afford to neglect its history'. Aldo Leopold (1963), a key-mover in the early development of national parks in the United States, wrote 'The first step in management is historical research, to ascertain as accurately as possible what plants and animals and biotic associations existed originally in each locality'. Despite these views, landscape management and conservation biology rarely take history into account (Willis et al. 2005). The *Millennium Ecosystem Assessment* (2005), for example, concluded that there is little knowledge of how ecosystems respond to the interactive effects of different ecosystem drivers in particular regions and across different scales. The longest temporal data set used is 45 years (1960–2005) and the UK *National Ecosystem Assessment* of 2011 (<http://uknea.unep-wcmc.org>) considers, at most, the last 65 years, but generally the last 40 years. Such short time perspectives are clearly inadequate when biotic systems have substantial inertia and the impact of changes occurring today may not be seen for years or decades. Some important changes may have occurred in the past but we are only seeing their effects today, the so-called historical legacies (Willis and Birks 2006). Milar and Woolfendon (1999), for example, show by tree-ring analyses of forests in the eastern Sierra Nevada, California, that there are three age classes – old-growth red firs 300–550 years old, lodgepole pines 100–250 years old, and young red firs <100 years old. The old-growth red firs date from two warm dry periods during 900–1350 AD when there were more fire events leading to an increased abundance of red fir in high-elevation stands. During the 'Little Ice Age' (1400–1900 AD), there was a decrease in fire events and lodgepole pines became dominant. Following the 'Little Ice Age' (1900–present), red firs became established again. It is clear from these studies that today's forest is a reflection of three climatic shifts in the past 1000 years and there is thus a strong historical legacy in today's forest structure. It is not possible to understand or manage today's forest without this long-term historical perspective. There are many other examples of ecosystems with a strong historical legacy, including forests (Koerner et al. 1997; Dupouey et al. 2002; Dambrine et al. 2007) and grasslands (Gustavsson et al. 2007; Pärtel et al. 2007; Reitalu et al. 2010) in Europe.

Conservation biology is used here to mean the planned management of natural resources and the retention of structure, diversity, and evolutionary potential within a constantly changing environment (Klein et al. 2009). It involves the protection, management, and/or

maintenance of biodiversity in its many manifestations (richness, evenness, composition, etc.). The concept of biodiversity covers many scales in space, time, and biological organisation, ranging from biomes and landscapes to species and genes. Biodiversity hotspots occur at global, continental, national, county, and local scales. All are of conservation value and important at different spatial and temporal scales.

There have been major paradigm shifts in conservation biology in the last 20 years and these shifts are reflected, in part, by the links between palaeoecology and conservation biology. An essential first stage in conservation was the basic descriptive and evaluation phase, leading to the recognition of biodiversity hotspots, areas of special scientific interest, potential nature reserves, and so on (Ratcliffe 1977a, 1977b, 1986; Myers 1990). In the UK *Nature Conservation Review* (Ratcliffe 1977a), 11 criteria for conservation evaluation were applied, 6 of which could be assessed using palaeoecological studies (Oldfield 1969, 1970; Edwards 1986; Birks 1993). One of the main conclusions from such palaeoecological studies is that many modern plant associations have not been in existence for more than 1000–1500 years at the most (Birks 1996; Jackson 2006). Many appear to have arisen by the direct or indirect influence of humans and their animals. Such findings have important implications for nature conservation and management (Dolman and Sutherland 1991; Gillson 2009; Dudley 2011).

In the 1990s with the increasing realisation of global change involving climate warming, land-use changes, habitat loss, invasive species, and so on, a new paradigm developed in conservation biology concerning conservation in a rapidly changing world. The seminal publication of Mace et al. (1998) presented three major conclusions. First, much progress has been made in the descriptive and evaluation phases worldwide in identifying priority areas for biodiversity conservation. Second, it is essential now to build an understanding of ecological and evolutionary processes into management and planning (Klein et al. 2009; Perrings et al. 2011). Third, conservationists must consider the dynamic processes of species and their interactions with the rapidly changing environment and to assess resilience in a landscape setting. Mace et al. (1998) set a new agenda for conservation and management that is applicable at all spatial scales. The *Millennium Ecosystem Assessment* (2005) similarly concluded that there is limited understanding of the characteristics of ecosystems that lead to resilience, thresholds, and irreversible change. There have been major shifts in the research approach of conservation biologists in response, in part at least, to the new paradigm of conservation in a rapidly changing world (Sutherland 1998, 2006; Sutherland et al. 2004, 2006, 2009, 2010; Carpenter et al. 2006; Carwardine et al. 2009; Sutherland and Woodroof 2009; Dawson et al. 2011; Hole et al. 2011).

Some palaeoecologists have responded to this shift away from the 'balance of nature' paradigm (Pimm 1991; Kricher 2009) toward the 'dynamic flux of nature' paradigm (Mace et al. 1998) by broadening their research

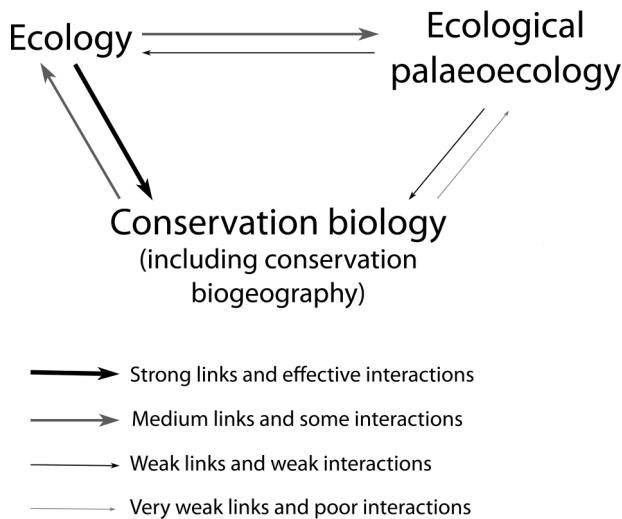


Figure 1. The current situation of existing links and interactions between ecology, ecological palaeoecology, and conservation biology (including conservation biogeography).

agendas, focusing on specific ecological and environmental threats, and developing a clear question-oriented research with a strong hypothesis-testing component (Brncic et al. 2007; Virah-Sawmy, Bonsall et al. 2009; Virah-Sawmy, Gillson et al. 2009; Virah-Sawmy, Willis et al. 2009; Willis et al. 2010; Seddon et al. 2011). But progress is slow and much palaeoecological research remains descriptive, without any clear research questions or underlying testable hypotheses. There are thus only weak links and poor interactions between palaeoecology and conservation biology (Figure 1).

Why, therefore, are there such weak links and poor interactions between palaeoecology and conservation biology? There are several possible explanations. First, to many conservation biologists, palaeoecological data seem too descriptive and too imprecise in terms of spatial, temporal, and taxonomic resolution. Such data are thus considered to be of little or no relevance to real-life conservation management. Second, palaeoecological studies are published in unfamiliar literature and employ unfamiliar concepts, methods, and terminology. Third, with increasing specialisation within universities today, palaeoecologists are often located in geology or geography departments, whereas conservation biologists are situated in biology or environmental science departments. This spatial separation can contribute to poor communication between palaeoecologists and conservation biologists. Fourth, palaeoecological data are often presented in a complex, reader-unfriendly way, such as the dreaded unreadable long pollen-stratigraphical diagram! To many palaeoecologists, conservation biology is not viewed as an important user of palaeoecological data and they do not see the relevance of their own data to questions of thresholds, resilience, or baseline conditions. The vast majority of palaeoecologists are interested in timescales of the Holocene (post-glacial), late-glacial, or detectable human impact. Many do not concentrate on the last

500 years, the period that is often most relevant to conservation. Many, rather surprisingly, appear not to be interested in present-day ecology, community or landscape conservation, management, or the many developing models and theories of ecosystem response to environmental change.

There are thus two sub-cultures, conservationists and palaeoecologists, seemingly interested in biodiversity and landscape and ecosystem dynamics, past, present, and future but not interested in each other's sub-cultures. There are, of course, some exceptions (Oldfield 1969, 1970; Birks 1993, 1996; Gillson and Willis 2004; Willis et al. 2004, 2007a, 2007b, 2010; Willis and Birks 2006; Froyd and Willis 2008; Hanley et al. 2008; Hanley, Tinch et al. 2009; Jackson et al. 2009; Davies and Bunting 2010; Willis and Bhagwat 2010; Davies 2011; Dietl and Flessa 2011), but, in general, palaeoecology and conservation biology have fewer links than they could have.

In some ways the apparent gap between palaeoecology and conservation biology may be the fault of palaeoecologists. They present their data in a poor and complex way. The data often lack spatial, temporal, or taxonomic precision. Many palaeoecologists are slow to take advantage of the many advances made in Quaternary palaeoecology in the last 25 years. Many tend to rely too heavily on pollen analysis. Many other environmental 'proxies' are preserved in sedimentary sequences, such as fruits, leaves, conifer stomata, fungal spores, animal remains, sediment inorganic and organic geochemistry, stable isotopes (C, H, N), and, in lakes, diatoms, chironomids, cladocerans, and so on. (Flessa and Jackson 2005). Palaeoecologists rarely state explicitly the assumptions of their methods (cf. Birks, Line et al. 1990; Birks et al. 2010). Such assumptions are generally known and accepted within the palaeoecological community, but because they are not clearly stated, this lack of explicit assumptions discourages researchers from other disciplines accepting palaeoecological results. On the other hand, there is no excuse for conservationists to ignore much of the relevant findings from palaeoecology (Birks 2005; Mitchell 2005) as in the special issue of *British Wildlife* (Branson 2009) on 'Naturalistic grazing and re-wilding in Britain: Perspectives from the past and future directions'.

There have been many key advances in palaeoecological methodology that can greatly improve the quality and relevance of palaeoecological data to conservation biology. These include:

- (1) Major advances in detailed pollen morphology and hence in the taxonomic precision of pollen-analytical data. With ever-increasing pollen reference collections, detailed pollen-morphological monographs, improved microscopy, and new identification aids, it is now possible to identify over 250 pollen and spore taxa in Holocene lake sediments from East Anglia (Peglar 1993) and over 120 taxa in south Norwegian Holocene lake sediments (Peglar and Birks, unpublished data).

- (2) Major advances in fine-scale sampling with improved coring equipment and field and laboratory techniques. It is now possible to sample at 1–2 mm resolution if required (typically about every 5–10 years) (Smol 2008, 2009).
- (3) Major advances in understanding the likely pollen-source area from which the bulk of the pollen preserved in a bog or lake is derived from (Davis 2000). Relevant source areas of pollen range from 50–100 m (local scale) for a small hollow of 5–10 m radius to 600–800 m (landscape scale) for a lake with a 250 m radius. Major advances in inferring past forest composition from pollen data are also occurring (Sugita 1994, 2007a, 2007b; Paciorek and McLachlan 2009).
- (4) Major advances in the use of lake sediments as a long-term record of many environmental proxies from the atmosphere, catchment, and groundwater and from the lake itself (Smol 2008).
- (5) Major advances in developing multi-proxy studies where many different palaeoecological proxies are studied together in the same sediment core in an integrated way (Birks and Birks 2006).
- (6) Major advances in numerical methods as tools for the summarisation and analysis of complex multivariate long-term ecological data and for the testing of specific hypotheses (Birks et al. 2012).
- (7) Increasing thought and care about site selection, problem formulation, and hypotheses to be tested by palaeoecological data (Birks, Berge et al. 1990).
- (8) Increasing realisation of the importance of spatial and temporal scales in the interpretation and integration of palaeoecological data (Jackson et al. 2009; Dearing et al. 2011).

All these advances are very relevant to the full and effective use of palaeoecological data in conservation and management. Palaeoecological studies can address questions about biological vulnerability and resilience that relate directly to societal concerns such as the design of biological reserves, the effects of biological and environmental change on ecosystem services and goods, the stability of biogeochemical cycles, and the direct and indirect impacts of invasive species and extinction of species (Flessa and Jackson 2005; Willis and Birks 2006; Dietl and Flessa 2009, 2011; Jackson and Hobbs 2009; Willis et al. 2010).

#### **Questions of importance in conservation biology and management**

In this section, I consider briefly nine questions of direct relevance to conservation and management that palaeoecology has uniquely provided answers to. The underlying philosophy common to these studies are (Willis and Bhagwat 2010):

- (1) What do we need to know about the ecology, including the history, of the system of interest in

order to conserve, maintain, or restore biodiversity in a changing environment at the scale of concern for management?

- (2) What ecological processes, theories, and concepts are most relevant and at what spatial and temporal scales?
- (3) How do we incorporate evolutionary and ecological knowledge into practical and meaningful conservation policy and management so as to ensure continuity of evolutionary and ecological processes (Froyd and Willis 2008; Willis and Bhagwat 2010; Willis et al. 2010)?

#### ***What determines the development of the mosaic structure of a landscape rich in flora and fauna?***

In many areas in the American Rocky Mountains, there are mosaics of forest patches and treeless grassland areas, the so-called ‘parks’. By careful selection of small ponds with a local-scale pollen-source area in forest and in park patches, and detailed pollen and numerical analyses, Lynch (1998) was able to falsify the permanent site hypothesis (parks had always been parks and forest patches had always been forest) and the remnant hypotheses that all patches had once been parks and some had become forest patches. Her data indicate that the replacement hypothesis by, for example, disturbance could not be rejected and that all patches had once been forested but that present-day park areas have developed as a result of disturbance, possibly associated with changes in fire frequency and/or climate change. As this mosaic structure in areas like the Wind River Mountains provides major habitats for mammals, birds, insects, and plants in these landscapes, management plans need to understand how the mosaic came about in order to be able to manage it in the future.

#### ***What determines landscape and habitat diversity over time?***

Ecologists increasingly recognise the importance of habitat diversity (eco-diversity or eco-complexity) of a landscape in influencing species richness within and between landscapes and biotic responses to environmental change (Burnett et al. 1998; Nichols et al. 1998; Hotchkiss et al. 2007). Whittaker (1977) recognised several types of diversity – community ( $\alpha$ -diversity), between-community ( $\beta$ -diversity), landscape ( $\gamma$ -diversity), between-landscape ( $\delta$ -diversity), and regional ( $\epsilon$ -diversity). Palaeoecological data are potentially relevant to all these scales (Odgaard 2007).

It is possible to reconstruct landscape-scale diversity from palaeoecological data if many local-scale sites are available from a small area (Odgaard 2007). Smith and Cloutman (1988), for example, prepared 13 pollen diagrams with over 100 radiocarbon dates from a 15 ha upland bog area in the south Welsh uplands. Six dryland and five wetland vegetation types could be recognised from

the pollen stratigraphies (Odgaard 2007) and their occurrences mapped in space and time. This remarkable data set shows a decrease in landscape ( $\gamma$ ) diversity with the expansion of blanket mire in the last 4000 years, leading to progressive landscape homogenisation. These results have important implications for management and habitat restoration in oceanic, upland landscapes.

### ***Have landscapes (including their soils) changed over time?***

Here, palaeolimnology (Smol 2008, 2009), especially the study of diatoms preserved in lake sediments, can contribute much to our understanding of landscape dynamics including the lake's catchment and its soils, as the catchment and its soils are an important driver of the lake environment (Birks et al. 2000; Lotter and Birks 2003). Freshwater diatoms are excellent indicators of lake-water chemistry, especially pH. Numerical calibration functions based on the modern relationships between contemporary lake-water pH and diatom assemblages (Birks, Line et al. 1990) have been developed to provide quantitative reconstructions of lake-water pH through time (Birks, Line et al. 1990; Smol 2008, 2009). Such reconstructions played a major part in the so-called 'acid-rain' research of the 1980s and early 1990s. This palaeoecological research led to major changes in the emission policies from the power industry in the United Kingdom (The Management Group 1990; Birks 1996).

As a side result from examining many modern short sediment cores collected for acid-rain studies, a large amount of evidence became available to show the considerable loss of upland heath in the last 200 years in the United Kingdom (Stevenson and Thompson 1993). There are several possible drivers of change, including increasing sheep grazing pressure, extensive upland afforestation from the 1920s, acid deposition leading to a weakening of heather's physiological health, atmospheric nitrogen deposition favouring grasses, especially *Molinia caerulea*, over-weakened heather, insect infestations, and interactions between these drivers. There are also considerable palaeoecological data concerning erosion of upland blanket mires that started about AD 1500–1700. There are several likely drivers, including grazing and burning, loss of *Sphagnum* species by excessive acidification by nitrogen and sulphur compounds, climate change at the time of the 'Little Ice Age', and interactions between these drivers (Tallis 1964a, 1964b, 1965; Birks 1988; Stevenson et al. 1990).

### ***What are the major drivers of ecosystem change at different timescales?***

There are, of course, a multitude of drivers or factors that can change one or more aspects of an ecosystem. These include direct drivers such as climate change, air and water pollution, succession, disease, human impacts, and land-use change. Indirect drivers include demographic, economic, socio-political, cultural, and religious changes.

Such indirect drivers are frequently ignored (cf. Davies 2007, 2009; Bhagwat et al. 2011).

A palaeoecological perspective can identify many potentially important direct drivers such as Dutch elm disease, chestnut blight, and hemlock defoliation (Davis 1981; Allison et al. 1986; Peglar and Birks 1993). Land-use changes and resulting secondary succession are also important direct drivers. Fuller et al. (1998), for example, studied 11 sites in the Harvard Forest area of Massachusetts. Historical records indicate that the region was totally cleared for agricultural land in the eighteenth century and abandoned in the nineteenth century. Fuller et al. (1998) used local-scale pollen analysis to compare present-day forest composition with that prior to widespread clearance. Their results showed that at all 11 sites, the composition of the forest following secondary succession was similar, but at all sites the composition of the resulting secondary forest was markedly different to its preceding pre-settlement primary forest. These results have important implications for restoration ecology and long-term management of woodlands. The results also indicate the role of intermediate disturbance (Connell 1978) and of patch dynamics in creating the mosaic of vegetation types we see today.

Palaeoecological studies can help to identify potentially important indirect drivers such as economic factors in upland landscapes. For example, Hanley et al. (2008) combined local-scale pollen stratigraphical data from small bogs in livestock farms, documentary and estate records, and econometric statistical modelling at 11 sites in different biogeographical zones in the Scottish uplands. They asked what are the principal drivers of pollen richness in the last 400 years and showed that the 'best' predictor (in a statistical sense) for pollen-richness changes is livestock prices, a proxy for grazing pressure. Increased grazing led to decreased pollen diversity, as did land abandonment. As in the other questions considered above, intermediate disturbance gives the highest pollen diversity. Hanley et al. (2008) (see also Hanley, Tinch et al. 2009) is a unique study that combines natural and social sciences to show that long-term management of Scottish upland areas should focus on grazing pressure as a key driver of ecosystem change. It also highlights the problems of establishing 'baselines' or 'natural' target levels for biodiversity.

### ***Can palaeoecological studies establish baseline conditions?***

Considerable interest has recently been focused on the concept of baseline conditions, namely ecosystem conditions before human influence became pronounced in the landscape (Froyd and Willis 2008; Dudley 2011). Attempts to define baseline conditions are widespread in palaeolimnology using diatom assemblages at a particular time period, for example the European Union Water Framework Directive has selected AD 1850 as the reference time (Bennion et al. 2004, 2011; Bennion and Simpson 2011).

### ***Can palaeoecological studies establish the natural variability of ecosystems?***

Ecological systems are not static entities, as is often implicitly assumed in baseline studies (Jackson 2001, 2006; Dudley 2011), but can be highly dynamic systems. There is thus a need to define an envelope of temporal variability characterised in terms of, for example, rates, magnitude, and frequency of change (Palmer et al. 2006; Froyd and Willis 2008). Such envelopes of temporal variability can be constructed using fine-resolution pollen (vegetation variability), charcoal data (fire variability) (Cyr et al. 2009), and stable isotope and geochemical studies (climate variability). Such envelopes have not, as far as I know, been constructed in northwest Europe but their construction is, in theory, possible. Given such an envelope in two or more dimensions, it would be possible to identify what ecological state lies within an acceptable limit of variability. Such constructs would be highly relevant in restoration and management studies (Froyd and Willis 2008; Jackson and Hobbs 2009; Bullock et al. 2011; Dudley 2011).

### ***Can palaeoecological studies establish 'thresholds of potential concern' as benchmarks for management?***

Working in the savannah-dominated landscape of the Kruger National Park, Gillson and Duffin (2007) used fine-scale pollen stratigraphies and modern pollen–vegetation relationships to address if woody cover had decreased below 80% of its 'highest ever value', a threshold set by ecosystem managers to define the upper and lower levels of acceptable variation in the ecosystem. The results of Gillson and Duffin (2007) indicate that during the past 5000 years, estimated woody vegetation cover has remained at or above 20% of its 'highest ever value'. Thus, management intervention in this part of the Kruger Park is not needed at present. However, the differences in the estimates of the maximum 'highest ever value' between sites highlight the importance of site-specific thresholds of potential concern (Froyd and Willis 2008).

### ***Can palaeoecological studies identify critical thresholds and resilience in ecosystems?***

An ecological threshold (Groffman et al. 2006; Walker and Salt 2006) is the point at which there is an abrupt change in an ecosystem quality, property, or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem. Ecological resilience (Gunderson and Holling 2001; Walker and Salt 2006; Gunderson et al. 2010) is the ability of systems to absorb disturbances and still maintain the same relationships between populations or state variables or the degree to which an entity can be changed without altering its minimal structure. Resilience is thus a property of an ecosystem, whereas persistence is the outcome of resilience.

Virah-Sawmy, Gillson et al. (2009) and Virah-Sawmy, Willis et al. (2009) examined long-term resilience and

recovery of littoral forests on eastern Madagascar in relation to marine surges using a range of palaeoecological techniques (pollen, diatom, and geochemical analyses). They showed that open upland *Uapaca* heath forest has low resilience to threshold events of marine storm surges and subsequent drought and that a switch from one stable state to another had occurred in open littoral forest (Willis et al. 2010). Closed littoral forest showed much greater resilience to repeated storm surges than open upland forest. Identifying resilience in such systems (Willis et al. 2010) is a first step in developing management policies to try to combat future impacts associated with climate change and sea-level rise or changes in land-use practices (Gunderson and Pritchard 2002; Dearing 2008).

### ***Can palaeoecological studies establish if particular species of management concern are native?***

The distinction between what is native and what is not is often unclear. A species is usually classified as either native or exotic according to whether it is located in its presumed areas of evolutionary origin and/or whether human agency is responsible for its current distribution (Willis and Birks 2006). In the absence of a palaeoecological record, the distinction between native and exotic easily becomes blurred.

Oceanic islands such as the Azores or the Galápagos are particularly liable to invasions and it is often difficult to assess if a particular species is native or introduced (Willis and Birks 2006). Palaeoecological studies are essential to answer such a question (Jackson 1997; Willis and Birks 2006; van Leeuwen et al. 2008; Coffey et al. 2011). For example, the Galápagos Islands retain 95% of their native biodiversity and have had a short period of human presence with European contact beginning in AD 1535. Despite their high biodiversity and high species retention, the islands have some of the highest extinction rates on Earth. As a result, there are management plans to eradicate non-native species. But what species are native, non-native, and 'doubtful native'?

Pollen and plant macrofossil analyses (van Leeuwen et al. 2008; Coffey et al. 2011) show that several 'doubtful native' species and one assumed non-native species have actually been present on the Galápagos Islands for the last 2000 years, and are thus part of the native Galápagos flora. The risk of applying inappropriate management to what are in fact native species is minimised by having a palaeoecological perspective on the history of particular species. This type of study highlights the need for detailed palaeoecological studies to help develop evidence-based management plans for oceanic islands.

### ***Other questions of importance in conservation biology and management***

There are many other critical questions in conservation and management that require a palaeoecological perspective, including several raised by Sutherland et al. (2006,

2009). Davies and Bunting (2010) discuss the potential for palaeoecological data to contribute to answering some of the 100 key questions in UK conservation policy identified by Sutherland et al. (2006). They concluded that palaeoecological studies have a major potential contribution to 25 of these questions, minor contribution to 31 questions, and minimal contribution to 48 questions.

Such critical questions of obvious relevance to palaeoecologists and conservation biologists include (Sutherland et al. 2006, 2009):

- (1) How is the resilience of ecosystems to climate change affected by human activities and interventions?
- (2) How will climate change affect the distribution and impacts of climate-dependent disturbance regimes such as fires and storms?
- (3) Which aquatic species and communities are most vulnerable to human impacts, and how would their degradation affect the provision of ecosystem services?
- (4) What are the likely risks, costs, and benefits of re-introducing and translocating species as a response to climate change?
- (5) What time lags can be expected between climate change and ecological change?
- (6) What was the condition of ecosystems before significant human disruption, and how can this knowledge be used to improve current and future management?
- (7) What is the likely relationship between the extent of climate change and the patterns of species extinctions?

These questions and others identified by Sutherland et al. (2006, 2009) provide the basis for rich, challenging, and exciting future research agendas. They are a challenge to palaeoecologists to develop new research approaches to try to answer these questions and others that require a temporal perspective of 100–1000 years.

Palaeoecology has, with care, already contributed to critical management questions by

- (1) contributing to the current debates about ‘re-wilding’ in wilderness areas;
- (2) providing a factual basis for management within the presumed natural variability of ecosystems;
- (3) establishing the role of large infrequent disturbances in landscape dynamics;
- (4) providing a basis for establishing if present-day landscape changes are a result of recent climate change or land-use changes and cultural impact; and
- (5) demonstrating very clearly that humans are an important part of ecosystems over long time periods.

Oldfield (1969, 1970), Birks (1993, 1996), Willis et al. (2004, 2007a, 2007b, 2010), Froyd and Willis (2008), and Willis and Bhagwat (2010) provide details of these and related palaeoecological studies in relation to these questions.

## Discussion

This discussion falls into three parts – controversies, challenges, and compromises in utilising palaeoecological data in conservation and management.

### Controversies

Conservation biology has embraced the importance of different spatial scales in its approaches but largely ignores the importance of temporal scales. The *Millennium Ecosystem Assessment* (2005) considers the last 45–50 years, whereas the *Intergovernmental Panel on Climate Change* (Jansen et al. 2007) discusses climate change over the last 1–5 million years. Why is ecosystem history so ignored in contrast to climate history?

The new paradigm of conservation in a rapidly changing world invokes many new concepts and theories in ecology and hence in palaeoecology (Gunderson and Holling 2001; Gunderson and Pritchard 2002; Walker and Salt 2006; Gunderson et al. 2010). Palaeoecology seems reluctant to consider new concepts and theories about landscapes and ecosystem dynamics and about the importance of different spatial scales. As a result many conservationists tend to ignore the findings of palaeoecologists, to the detriment of understanding the historical legacies in many ecosystems.

Many palaeoecologists do not appear to recognise the relevance of their findings to key questions like natural variability, baselines, thresholds, resilience, ‘regime’ shifts, and ‘assisted migration’ in conservation biology. A brief perusal of my reprint collection in January 2010 revealed over 300 palaeoecological articles with data and results directly relevant to conservation in the twenty-first century but with no mention of conservation in the title, abstract, keywords, or text. No electronic search would ever find these articles, all of which represent months or years of hard work at the microscope, because their keywords are pollen, late-glacial, Holocene, vegetation history, charcoal, and so on, and not resilience, stability, baselines, and so on. There is thus a largely hidden literature in palaeoecology that is of great relevance to conservation biology.

There are surprisingly few links between conservation biology, palaeoecology, and global-change research, even though they all have common concerns – biodiversity changes, environmental and climate changes, and habitat changes – at different spatial and temporal scales (Anonymous 2009). The links between conservation and palaeoecology are weak for many reasons (see above) – the failure to appreciate each other’s research; a confusion of spatial and temporal scales, the difficulties of publishing

conservation-based palaeoecological articles in the mainstream conservation biology literature, and the difficulties of obtaining research funding for 'applied' research (e.g. palaeoecology, ecological economics, landscape ecology).

### Challenges

Despite these controversies, there are many challenges in trying to link palaeoecology and conservation biology.

In order to interact closely with conservation biology and management, palaeoecologists must speak the same scientific language, address the same research problems, and be appreciative and respectful of each other's data and research approaches. Palaeoecologists need to take full advantage of the many advances in the theory and practice of palaeoecology – different levels of spatial, temporal, and taxonomic precision; multi-proxy studies; the use of lakes and appropriate numerical techniques; project design and site selection; coring methods; and so on. Detailed palaeoecology is very time-consuming. It is therefore essential to study the best available site for a specific conservation problem. Pilot studies and datings are essential but are rarely done in palaeoecology because they are often regarded as a 'waste of time and money', although they are not a waste of time or resources if they result in finding the most suitable site to resolve a particular research question. Automated pollen counting using the newly developed Classifynder (=Autostage) (Holt et al. 2011) has the potential to revolutionise pollen analysis and to make essential pilot studies fast and simple.

Additional challenges are the linking of palaeoecological studies with the active fields of restoration ecology (Hobbs 2009; Jackson and Hobbs 2009; Dudley 2011), of land-use economics and social and cultural dynamics (Hanley et al. 2008; Cooke et al. 2009; Hanley, Ready et al. 2009; Hanley, Tinch et al. 2009; Dearing et al. 2010, 2011, Collins et al. 2011), and biodiversity changes and species turnover (Jackson and Sax 2009). An important challenge is to draw up a comprehensive list of relevant questions of high policy relevance in the uplands of the United Kingdom and Norway that palaeoecology can contribute to (cf. Sutherland et al. 2006) and also a list of relevant questions of importance in the conservation of global mountain biological diversity (cf. Sutherland et al. 2009). An additional challenge for palaeoecologists is to improve our communication skills (Lovejoy 2009) by using plain language and to become more engaged in highlighting the policy implications and applicability of our science and its relevance to conservation biology, earth-system science, and biodiversity management. Communication to fellow palaeoecologists is not enough: palaeoecologists need to communicate with a much wider audience.

### Compromises

Despite extensive fieldwork and careful pilot studies, there might not be the 'perfect' site in the landscape of interest

that is relevant to the management question of concern. Palaeoecologists should acknowledge this limitation and avoid the temptation to 'over-interpret' their hard-earned data.

For an effective interaction between conservation biology and palaeoecology, conservationists need to try to formulate their research questions, if at all possible, at the spatial, temporal, and taxonomic scales that can be attained in palaeoecology. Inevitably, some compromises will be needed here as no data are ever 'perfect'.

Testing alternative explanatory hypotheses about, for example, the current or long-term status of tree-lines and forest-limits, may require the use of dynamic vegetation models. Such models (Heiri et al. 2006), although mathematically and analytically sophisticated, often, by necessity, have to simplify the ecological situation and make compromises between ecological simplicity and tractable numerical solutions and ecological complexity and intractable numerical solutions. Some compromise is essential.

Palaeoecologists and conservation biologists should be prepared for 'ecological surprises' in the future or as Ellison (2007) has proposed 'here be dragons'. Our rapidly changing climate may present us with completely new climatic and hence ecological scenarios (Williams and Jackson 2007; Williams et al. 2007). These will almost certainly lead to reshuffling of species and novel or 'no-analogue' assemblages and communities (Jackson and Williams 2004; Ellison 2007; Fox 2007; Jackson 2007; Lovejoy 2007; Keith et al. 2009). There may be unpredictable interactions between new climatic patterns and existing species and vegetation types, potentially resulting in many 'ecological surprises' (Williams and Jackson 2007; Willis and Bhagwat 2010).

Most ecosystems today are sufficiently altered in their composition, structure, and function that can be regarded, in a long-term temporal perspective, as novel ecosystems (Fox 2007). The management of novel ecosystems may require novel approaches (Hobbs et al. 2006, 2009; Seastedt et al. 2008; Bridgewater et al. 2011). Compromises are likely between existing, familiar management approaches and novel, unfamiliar approaches. The palaeoecological record provides many examples of 'no-analogue' assemblages (Jackson and Williams 2004; Gill et al. 2009) that appear to have developed under unique conditions of climate, fire, megaherbivory, and other disturbance regimes. Elucidating the underlying ecological processes behind such novel ecosystems in the past is an important research area where insights from palaeoecology can directly contribute to future management plans (Willis et al. 2010).

### Conclusions

Overall, there are promising signs that palaeoecologists are beginning to make important contributions to conservation biology and landscape management *and* that conservationists and managers are recognising the importance of a

palaeoecological perspective in understanding and managing ecosystems. Recent books (e.g. Bonn et al. 2009; Dietl and Flessa 2009; Hall 2010) reflect closer links between palaeoecology and conservation science than existed when I wrote a review of the contributions of Quaternary palaeoecology to conservation biology and coined the term 'applied palaeoecology' (Birks 1996). Several articles in these volumes are particularly relevant to the theme of this article (Anderson et al. 2009; Evans 2009; Jackson et al. 2009; Yallop et al. 2009; Davies 2010; Vera 2010; Whitehouse 2010).

It is becoming increasingly clear that to understand long-term dynamics in the past as a tool for predicting and managing biodiversity in the future, there are important needs for a strong and effective interaction and collaboration between palaeoecology and conservation. There is much to learn from 'lessons from the past' and to understand the many 'legacies from the past' in designing effective management plans. We should not view modern ecology and palaeoecology as separate entities, but we should view palaeoecology as part of the temporal continuum in ecology and evolution (Rull 2010).

Clearly, the timescales needed to address a particular research question depend on the ecological processes and the organisms of interest (e.g. trees, long-lived dwarfshrubs, annual herbs). There is within conservation biology today an increasing emphasis on ecological and evolutionary processes (Klein et al. 2009) and on ecosystem services and goods in management (Bullock et al. 2011). Palaeoecology can provide a temporal dimension to these processes, services, and goods.

Conservation biology has embraced the importance of spatial scales but it has yet to do so with regard to temporal scales. In contrast, palaeoecology embraces different temporal scales but has hardly addressed the problems posed by different spatial scales.

Palaeoecology has clearly shown that landscapes and biota are not static entities. They are constantly changing in space and time. The broad-scale EU ALARM project (Spangenberg 2007; Settle et al. 2010) involving 35 countries presented an impressive synthesis and predictions involving major drivers and pressures on biodiversity, including socio-economic changes, species invasions, climate change, and atmospheric nitrogen deposition. The starting points in ALARM's predictions were 'stable' or 'static' communities and the predictions considered changes from one 'stable' state to another 'stable' state. There appears to be no consideration of systems that today already have a strong historical legacy and are highly dynamic (Emanuelsson 2009). All ecosystems are dynamic and have a history (Jackson 2001, 2006, 2007; Willis and Birks 2006; Kricher 2009).

### Acknowledgements

I am very grateful to many colleagues for helpful discussions and for freely exchanging ideas, particularly Gunnar Austrheim, Shonil Bhagwat, Hilary Birks, Althea Davies, Cynthia Froyd,

Lindsey Gillson, Steve Jackson, the late Derek Ratcliffe, James Speed, Des Thompson, Malika Virah-Sawmy, and Jack Williams. I am particularly indebted to Kathy Willis who has contributed much to this article through generously sharing many important ideas. Comments from three anonymous reviewers have helped clarify the text. I am very grateful to Cathy Jenks for her invaluable help.

I dedicate this article to the memory of the late Derek Ratcliffe. Derek was a life-long friend and field companion who stimulated my interest not only in adventure botany but also in the relevance of palaeoecology to nature conservation.

### References

- Allison TD, Moeller RE, Davis MB. 1986. Pollen in laminated sediments provides evidence for a mid-Holocene forest pathogen outbreak. *Ecology*. 67(4): 1101–1105.
- Andersen MD, Baker WL. 2005. Reconstructing landscape-scale tree invasion using survey notes in the Medicine Bow Mountains, Wyoming, USA. *Landscape Ecol.* 21(2): 243–258. doi:10.1007/s10980-005-1938-3.
- Anderson P, Buckler M, Walker J. 2009. Moorland restoration: potential and progress. In: Bonn A, Allott T, Hubacek K, Stewart JR, editors. *Drivers of environmental change in uplands*. Abingdon (UK): Routledge. p. 432–448.
- Anonymous. 2009. Bridging the biodiversity gap. *Nat Geosci.* 2:733. doi:10.1038/ngeo688.
- Balée W. 2006. The research program of historical ecology. *Annu Rev Anthropol.* 35:75–98. doi:10.1146/annurev.anthro.35.081705.123231.
- Bennion H, Fluin J, Simpson GL. 2004. Assessing eutrophication and reference conditions for Scottish freshwater lochs using subfossil diatoms. *J Appl Ecol.* 41(1):124–138. doi:10.1111/j.1365-2664.2004.00874.x.
- Bennion H, Simpson GL. 2011. The use of diatom records to establish reference conditions for UK lakes subject to eutrophication. *J Paleolimnol.* 45(4):469–488. doi:10.1007/s10933-010-9422-8.
- Bennion H, Simpson GL, Anderson NJ, Clarke G, Dong X, Hobæk A, Guilizzoni P, Marchetto A, Sayer CD, Thies H, et al. 2011. Defining ecological and chemical reference conditions and restoration targets for nine European lakes. *J Paleolimnol.* 45(4):415–431. doi:10.1007/s10933-010-9418-4.
- Bhagwat SA, Dudley N, Harrop SR. 2011. Religious following in biodiversity hotspots: challenges and opportunities for conservation and development. *Conserv Lett.* 4(3):234–240. doi:10.1111/j.1755-263X.2011.00169.x.
- Birks HH, Battarbee RW, Birks HJB. 2000. The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the late glacial and early Holocene: a synthesis. *J Paleolimnol.* 23(1):91–114.
- Birks HH, Birks HJB. 2006. Multi-proxy studies in palaeolimnology. *Veg Hist Archaeobot.* 15(4):235–251.
- Birks HJB. 1988. Long-term ecological change in the British Uplands. In: Usher MB and Thompson DBA, editors. *Ecological change in the uplands*. Oxford (UK): Blackwell. p. 37–56.
- Birks HJB. 1993. Quaternary paleoecology and vegetation science: current contributions and possible future developments. *Rev Palaeobot Palynol.* 79(1–2):153–177.
- Birks HJB. 1996. Contributions of Quaternary palaeoecology to nature conservation. *J Veg Sci.* 7(1):89–98.
- Birks HJB. 2005. Mind the gap: how open were European primeval forests? *Trends Ecol Evol.* 20(4):154–156.
- Birks HJB, Berge F, Boyle JF, Cumming BF. 1990a. A palaeoecological test of the land use hypothesis for recent lake acidification in south west Norway using hill top lakes. *J Paleolimnol.* 4:69–85.

- Birks HJB, Birks HH. 1980. Quaternary palaeoecology. (Reprinted 2004 by the Blackburn Press, New Jersey.) London (UK): Edward Arnold.
- Birks HJB, Heiri O, Seppä H, Bjune AE. 2010. Strengths and weaknesses of quantitative climate reconstructions based on late-quaternary biological proxies. *Open Ecol J*. 3 (Special issue 1):68–110. doi:10.2174/1874213001003020068.
- Birks HJB, Line JM, Juggins S, Stevenson AC, ter Braak CJF. 1990b. Diatoms and pH reconstruction. *Philos Trans R Soc Lond B*. 327(1240):263–278.
- Birks HJB, Lotter AF, Juggins S, Smol JP, editors. 2012. Tracking environmental change using lake sediments volume 5: data handling and numerical techniques. Dordrecht (The Netherlands): Springer.
- Bonn A, Allott T, Hubacek K, Stewart JR, editors. 2009. Drivers of environmental change in uplands. Abingdon (UK): Routledge.
- Branson R. 2009. Naturalistic grazing and re-wilding in Britain: perspectives from the past and future directions. *Br Wildl*. 20(5 Special Supplement):1–63.
- Bridgewater P, Higgs ES, Hobbs RJ, Jackson ST. 2011. Engaging with novel ecosystems. *Front Ecol Environ*. 9(8):423. doi:10.1890/1540-9295-9.8.
- Britton AJ, Beale CM, Towers W, Hewison RJ. 2009. Biodiversity gains and losses: evidence for homogenisation of Scottish alpine vegetation. *Biol Conserv*. 142(8):1728–1739. doi:10.1016/j.biocon.2009.03.010.
- Bronic TM, Willis KJ, Harris DJ, Washington R. 2007. Culture or climate? The relative influences of past processes on the composition of the lowland Congo rainforest. *Philos Trans R Soc B*. 362(1478):243–251. doi:10.1098/rstb.2006.1984.
- Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM. 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol Evol*. 26(10):541–549. doi:10.1016/j.tree.2011.06.011.
- Burnett MR, August PV, Brown JH, Killingbeck KT. 1998. The influence of geomorphological heterogeneity on biodiversity I. A patch-scale perspective. *Conserv Biol*. 12(2):363–370.
- Carpenter SR, DeFries R, Dietz T, Mooney HA, Polasky S, Reid WV, Scholes RJ. 2006. Millennium ecosystem assessment: research needs. *Science*. 314(5797):257–258. doi: 10.1126/science.1131946.
- Carwardine J, Klein CJ, Wilson KA, Pressey RL, Possingham HP. 2009. Hitting the target and missing the point: target-based conservation planning in context. *Conserv Lett*. 2(1):3–10. doi:10.1111/j.1755-263X.2008.00042.x.
- Coffey EED, Froyd CA, Willis KJ. 2011. When is an invasive not an invasive? Macrofossil evidence of doubtful native plant species in the Galápagos Islands. *Ecology*. 92(4):805–812.
- Collins SL, Carpenter SR, Swinton SM, Orenstein DE, Childers DL, Gragson TL, Grimm NB, Grove JM, Harlan SL, Kaye JP, et al. 2011. An integrated conceptual framework for long-term social-ecological research. *Front Ecol Environ*. 9(6):351–357. doi:10.1890/100068.
- Connell JH. 1978. Diversity in tropical rain forests and coral reefs. *Science*. 199(4335):1301–1310.
- Cooke IR, Queenborough SA, Mattison EHA, Bailey AP, Sandars DL, Graves AR, Morris J, Atkinson PW, Trawcik P, Freckleton RP, et al. 2009. Integrating socio-economics and ecology: a taxonomy of quantitative methods and a review of their use in agro-ecology. *J Appl Ecol*. 46(2):269–277. doi:10.1111/j.1365-2664.2009.01615.x.
- Cyr D, Gauthier S, Bergeron Y, Carcaillet C. 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Front Ecol Environ*. 7(10):519–524. doi:10.1890/080088.
- Dambrine E, Dupouey JL, Laüt L, Humbert L. 2007. Present biodiversity patterns in France related to former Roman agriculture. *Ecology*. 88(6):1430–1438.
- Davies A. 2007. Upland agriculture and environmental risk: a new model of upland land-use based on high spatial-resolution palynological data from West Affric, NW Scotland. *J Archaeol Sci*. 34(12):2053–5063. doi:10.1016/j.jas.2007.02.003.
- Davies A. 2009. Review of the historical environmental changes in the UK uplands relevant to management and policy. Stirling (UK): University of Stirling.
- Davies A. 2010. Palaeoecology, management, and restoration in the Scottish Highlands. In: Hall M, editor. Restoration and history: the search for a usable environmental past. Abingdon (UK): Routledge. p. 74–85.
- Davies A. 2011. Long-term approaches to native woodland restoration: palaeoecological and stakeholder perspectives on Atlantic forests of Northern Europe. *For Ecol Manage*. 261(3):751–763. doi:10.1016/j.foreco.2010.12.006.
- Davies A, Bunting MJ. 2010. Applications of palaeoecology in conservation. *Open Ecol J*. 3(Special issue 1):54–67. doi:10.2174/1874213001003020054.
- Davis MB. 1981. Outbreaks of forest pathogens in quaternary history. In: Bharadwaj DC, Mittre V, Maheshwari HK, editors. Proceedings of the Fourth International Palynological Conference, 1976–1977. Lucknow (India): Birbal Sahni Institute of Palaeobotany. p. 216–228.
- Davis MB. 2000. Palynology after Y2K: understanding the source area of pollen in sediments. *Annu Rev Earth Planet Sci*. 28:1–18.
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM. 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science*. 332(6025):53–58. doi:10.1126/science.1200303.
- Dearing J. 2008. Landscape change and resilience theory: a palaeoenvironmental assessment from Yunnan, SW China. *Holocene*. 18(1):117–127. doi:10.1177/0959683607085601.
- Dearing JA, Braimoh AK, Reenberg A, Turner BL, van der Leeuw S. 2010. Complex land systems: the need for long time perspectives to assess their future. *Ecol Society*. 15(4):21.
- Dearing J, Dotterweich M, Foster T, Newman L, von Gunten L, editors. 2011. Integrative paleoscience for sustainable management. *Pages News* 19(2):41–92.
- Delcourt HR, Delcourt PA. 1991. Quaternary ecology. A paleoecological perspective. London (UK): Chapman & Hall.
- Dengler J, Jansen F, Glöcker F, Peet RK, De Cáceres M, Chytrý M, Ewald J, Oldeland J, Lopez-Gonzalez G, Finckh M, et al. 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *J Veg Sci*. 22(4):582–597. doi:10.1111/j.1654-1103.2011.01265.x.
- Dietl GP, Flessa KW, editors. 2009. Conservation paleobiology: using the past to manage for the future. Boulder (CO): The Paleontological Society Papers.
- Dietl GP, Flessa KW. 2011. Conservation paleobiology: putting the dead to work. *Trends Ecol Evol*. 26(1):30–37. doi:10.1016/j.tree.2010.09.010.
- Dolan RW, Moore ME, Stephens JD. 2011. Documenting effects of urbanization on flora using herbarium records. *J Ecol*. 99(4):1055–1062. doi:10.1111/j.1365-2745.2011.01820.x.
- Dolman P, Sutherland W. 1991. Historical clues to conservation. *New Scientist*. 129(1751):40–43.
- Dudley N. 2011. Authenticity in nature: making choices about the naturalness of ecosystems. London (UK): Earthscan.
- Dupouey JL, Dambrine E, Lafite JD, Moares C. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology*. 83(11):2978–2984.
- Edmonds M. 2005. The pleasures and pitfalls of written records. In: Egan D and Howell EA, editors. The historical ecology handbook. Washington (DC): Island Press. p. 73–99.

- Edwards ME. 1986. Disturbance histories of four Snowdonian woodlands and their relation to Atlantic bryophyte distributions. *Biol Conserv.* 37(4):301–320. doi:10.1016/0006-3207(86)90075-3.
- Egan D, Howell EA, editors. 2005. *The historical ecology handbook*. Washington (DC): Island Press.
- Ellison K. 2007. Here there be dragons. *Front Ecol Environ.* 5(9):512.
- Emanuelsson U. 2009. *The rural landscapes of Europe: how man has shaped European nature*. Stockholm (Sweden): The Swedish Research Council Formas.
- Evans M. 2009. Natural changes in upland landscapes. In: Bonn A, Allott T, Hubacek K, Stewart JR, editors. *Drivers of environmental change in uplands*. Abingdon (UK): Routledge. p. 13–33.
- Flessa KW, Jackson ST. 2005. *The geological record of ecological dynamics: understanding the biotic effects of future environmental change*. Washington (DC): National Research Council of the National Academies.
- Fox D. 2007. Back to the no-analog future? *Science.* 316(5826):823–825. doi:10.1126/science.316.5826.823.
- Froyd CA, Willis KJ. 2008. Emerging issues in biodiversity and conservation management: the need for a palaeoecological perspective. *Quat Sci Rev.* 27(17–18):1723–1732. doi:10.1016/j.quascirev.2008.06.006.
- Fuller JL, Foster DR, McLachlan JS, Drake N. 1998. Impact of human activity on regional forest composition and dynamics in central New England. *Ecosystems.* 1(1):76–95. doi:10.1007/s100219900007.
- Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS. 2009. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science.* 326(5956):1100–1103. doi:10.1126/science.1179504.
- Gillson L. 2009. Landscapes in time and space. *Landscape Ecol.* 24(2):149–155. doi:10.1007/s10980-008-9315-7.
- Gillson L, Duffin KI. 2007. Thresholds of potential concern as benchmarks in the management of African savannahs. *Philos Trans R Soc B.* 362(1478):309–319. doi:10.1098/rstb.2006.1988.
- Gillson L, Willis KJ. 2004. 'As Earth's testimonies tell': wilderness conservation in a changing world. *Ecol Lett.* 7(10):990–998.
- Groffman PM, Baron JS, Blett T, Gold AJ, Goodman I, Gunderson LH, Levinson BM, Palmer MA, Paerl HW, Peterson GD, et al. 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems.* 9(1):1–13. doi:10.1007/s10021-003-0142-z.
- Gunderson LH, Allen CR, Holling CS, editors. 2010. *Foundations of ecological resilience*. Washington (DC): Island Press.
- Gunderson LH, Holling CS, editors. 2001. *Panarchy: understanding transformation in human and natural systems*. Washington (DC): Island Press.
- Gunderson LH, Pritchard L. 2002. *Resilience and the behaviour of large-scale systems*. Washington (DC): Island Press.
- Gustavsson E, Lennatsson T, Emanuelsson M. 2007. Land use more than 200 years ago explains current grassland plant diversity in a Swedish agricultural landscape. *Biol Conserv.* 138(1–2):47–59. doi:10.1016/j.biocon.2007.04.004.
- Hall M, editor. 2010. *Restoration and history: the search for a usable environmental past*. Abingdon (UK): Routledge.
- Hanley N, Davies A, Angelopoulos K, Hamilton A, Ross A, Tinch D, Watson F. 2008. Economic determinants of biodiversity change over a 400-year period in the Scottish uplands. *J Appl Ecol.* 45(6):1557–1565. doi:10.1111/j.1365-2664.2008.01570.x.
- Hanley N, Ready R, Colombo S, Watson F, Stewart M, Bergmann EA. 2009a. The impacts of knowledge of the past on preferences for future landscape change. *J Environ Manage.* 90(3):1404–1412. doi:10.1016/j.jenvman.2008.08.008.
- Hanley N, Tinch D, Angelopoulos K, Davies A, Barbier EB, Watson F. 2009b. What drives long-run biodiversity change? New insights from combining economics, palaeoecology and environmental history. *J Environ Economics Manage.* 57(1):5–20. doi:10.1016/j.jeem.2008.03.005.
- Heiri C, Bugmann H, Tinner W, Heiri O, Lischke H. 2006. A model-based reconstruction of Holocene treeline dynamics in the Central Swiss Alps. *J Ecol.* 94(1):206–216. doi:10.1111/j.1365-2745.2005.01072.x.
- Hobbs RJ. 2009. Woodland restoration in Scotland: ecology, history, culture, economics, politics and change. *J Environ Manage.* 90(9):2857–2865. doi:10.1016/j.jenvman.2007.10.014.
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob Ecol Biogeogr.* 15(1):1–7. doi:10.1111/j.1466-822x.2006.00212.x.
- Hobbs RJ, Higgs ES, Harris JA. 2009. Novel ecosystems: implications for conservation and restoration. *Trends Ecol Evol.* 24(11):599–605. doi:10.1016/j.tree.2009.05.012.
- Hoffmann H, Ulmi E, Bisang I, Müller N, Küchler M, Schnyder N, Schubiger C. 2007. Retrospective assessment of frequency changes in Swiss bryophytes over the last two centuries. *Lindbergia.* 32(1):18–32.
- Hole DG, Huntley B, Arinaitwe J, Stuart HMB, Collingham YC, Fishpool LDC, Pain DJ, Willis SG. 2011. Toward a management framework for networks of protected areas in the face of climate change. *Conserv Biol.* 25(2):305–315. doi:10.1111/j.1523-1739.2010.01633.x.
- 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. *Rev Palaeobot Palynol.* 167(3–4):175–183. doi:10.1016/j.revpalbo.2011.08.006.
- Hotchkiss SC, Calcote R, Lynch EA. 2007. Response of vegetation and fire to Little Ice Age climate change: regional continuity and landscape heterogeneity. *Landscape Ecol.* 22(Supplement 1):25–41. doi:10.1007/s10980-007-9133-3.
- Jackson ST. 1997. Documenting natural and human-caused plant invasions using paleoecological methods. In: Luken JO, Thieret JW, editors. *Assessment and management of plant invasions*. Berlin (Germany): Springer-Verlag. p. 37–55.
- Jackson ST. 2001. Finding your way back home, or at least learning how it looked. *Divers Distrib.* 7(6):301–305.
- Jackson ST. 2006. Vegetation, environment, and time: the origination and termination of ecosystems. *J Veg Sci.* 17(5):549–557. doi:10.1111/j.1654-1103.2006.tb02478.x.
- Jackson ST. 2007. Looking forward from the past: history, ecology, and conservation. *Front Ecol Environ.* 5(9):455.
- Jackson ST, Gray ST, Shuman B. 2009. Paleoeecology and resource management in a dynamic landscape: case studies from the rocky mountain headwaters. In: Dietl GP, Flessa KW, editors. *Conservation paleobiology using the past to manage for the future*. Boulder (CO): The Paleontological Society Papers. p. 61–80.
- Jackson ST, Hobbs RJ. 2009. Ecological restoration in the light of ecological history. *Science.* 325(5940):567–569. doi:10.1126/science.1172977.
- Jackson ST, Sax DF. 2009. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends Ecol Evol.* 25(3):153–160. doi:10.1016/j.tree.2009.10.001.
- Jackson ST, Williams JW. 2004. Modern analogs in quaternary paleoecology: here today, gone yesterday, gone tomorrow? *Annu Rev Earth Planet Sci.* 32:495–537. doi:10.1146/annurev.earth.32.101802.120435.
- Jansen E, Overpeck J, Briffa KR, Duplessy J-C, Joos F, Masson-Delmotte V, Olago D, Otto-Bliesner B, Peltier WR, Rahmstorf S, et al. 2007. Palaeoclimate. In: Solomon S, Qin

- D, Manning M, Chen Z, Marquis M, Averyt KB, Tingnor M, Miller HL, editors. Climate change 2007: the physical science basis contribution to working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge (UK): Cambridge University Press. p. 433–497.
- Johnson KG, Brooks SJ, Fenberg PB, Glover AG, James KE, Lister AM, Michel E, Spencer M, Todd JA, Valsami-Jones E, et al. 2011. Climate change and biosphere response: unlocking the collections vault. *BioScience*. 61(2):147–153. doi:10.1525/bio.2011.61.2.10.
- Kapfer J. 2011. Last-century vegetational changes in northern Europe Bergen. Bergen (Norway): University of Bergen.
- Keith SA, Newton AC, Herbert RJH, Morecroft MD, Bealey CE. 2009. Non-analogous community formation in response to climate change. *J Nat Conserv*. 17(4):228–235. doi:10.1016/j.jnc.2009.04.003.
- Kipfmüller KF, Swetnam TW. 2005. Using dendrochronology to reconstruct the history of forest and woodland ecosystems. In: Egan D, Howell EA, editors. The historical ecology handbook. Washington (DC): Island Press. p. 199–228.
- Klein C, Wilson KA, Watts ME, Stein J, Berry S, Carwardine J, Smith MS, Mackey B, Possingham HP. 2009. Incorporating ecological and evolutionary processes into continental-scale conservation planning. *Ecol Appl*. 19(1):206–217. doi:10.1890/07-1684.1.
- Koerner W, Dupouey JL, Dambrine E, Benoit M. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges Mountains, France. *J Ecol*. 85(3): 351–358.
- Kricher J. 2009. The balance of nature: ecology's enduring myth. Princeton (NJ): Princeton University Press.
- Leopold AS. [cited 1963]. Wildlife management of the national parks: the Leopold report [Internet]. The National Park Service, US Department of the Interior. [cited 2012 Mar 1]. Available from: [http://www.nps.gov/history/history/online\\_books/leopold/leopold.htm](http://www.nps.gov/history/history/online_books/leopold/leopold.htm).
- Lotter AF, Birks HJB. 2003. The Holocene palaeolimnology of Sägistalsee and its environmental history: a synthesis. *J Paleolimnol*. 30(3):333–342.
- Lovejoy TE. 2007. Paleoecology and the path ahead. *Front Ecol Environ*. 5(9):456.
- Lovejoy TE. 2009. Managing for the future: the role of scientists. In: Dietl GP, Flessa KW, editors. Conservation paleobiology: using the past to manage for the future. Boulder (CO): The Paleontological Society Papers. p. 283–285.
- Lynch EA. 1998. Origin of a park-forest vegetation mosaic in the Wind River Range, Wyoming. *Ecology*. 79(4):1320–1338.
- Mace GM, Balmford A, Ginsberg JR, editors. 1998. Conservation in a changing world. Cambridge (UK): Cambridge University Press.
- Millar CI, Woolfenden W. 1999. The role of climate change in interpreting historic variability. *Ecol Appl*. 9(4):1207–1216. doi:10.1890/1051-0761(1999)009[1207:TROCCI]2.0.CO;2.
- Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Washington (DC): Island Press.
- Mitchell FJG. 2005. How open were European primeval forests? Hypothesis testing using palaeoecological data. *J Ecol*. 93(1):168–177.
- Myers N. 1990. The biodiversity challenge: expanded hotspots analysis. *Environmentalist*. 10(4):243–256. doi:10.1007/BF02239720.
- Nichols WF, Killingbeck KT, August PV. 1998. The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. *Conserv Biol*. 12(2):371–379.
- Odgaard BV. 2007. Reconstructing past biodiversity development. In: Elias SA, editor. Encyclopedia of quaternary science. Philadelphia (PA): Elsevier. p. 2508–2514.
- Oldfield F. 1969. Pollen analysis and history of land use. *Advancement Sci*. 25:298–311.
- Oldfield F. 1970. The ecological history of Blelham Bog National Nature Reserve. In: Walker D, West RG, editors. Studies in the vegetational history of the British Isles. Cambridge: Cambridge University Press. p. 141–157.
- Paciorek CJ, McLachlan JS. 2009. Mapping ancient forests: Bayesian inference for spatio-temporal trends in forest composition using the fossil pollen proxy record. *J Am Stat Assoc*. 104(486):608–622. doi:10.1198/jasa.2009.0026.
- Palmer MA, Falk DA, Zedler JB. 2006. Ecological theory and restoration ecology. In: Falk DA, Palmer MA, Zedler JB, editors. Foundations of restoration ecology. Washington (DC): Island Press. p. 1–10.
- Pärtel M, Helm A, Reitalu T, Liira J, Zobel M. 2007. Grassland diversity related to Late Iron Age human population density. *J Ecol*. 95(3):574–582. doi:10.1111/j.1365-2745.2007.01230.x.
- Peglar SM. 1993. The development of the cultural landscape around Diss Mere, Norfolk, UK, during the past 7000 years. *Rev Palaeobot Palynol*. 76(1):1–47.
- Peglar SM, Birks HJB. 1993. The mid-Holocene *Ulmus* fall at Diss Mere, South-east England: disease and human impact? *Veg Hist Archaeobot*. 2(2):61–68. doi:10.1007/BF00202183.
- Perrings C, Naem S, Ahrestani FS, Bunker DE, Burkill P, Canziani G, Elmqvist T, Fuhrman JA, Laksic FM, Kawabata Z, et al. 2011. Ecosystem services, targets, and indicators for the conservation and sustainable use of biodiversity. *Front Ecol Environ*. 9(9):512–520. doi:10.1890/100212.
- Pigott CD, Walters SM. 1977. The scientific basis of practical conservation: aims and methods of conservation. *Proc R Soc Lond B*. 197(1126):59–68. doi:10.1098/rspb.1977.0056.
- Pimm SL. 1991. The balance of nature? Ecological issues in the conservation of species and communities. Chicago (IL): University of Chicago Press.
- Ratcliffe DA, editor. 1977a. A nature conservation review, Volumes 1 and 2. Cambridge (UK): Cambridge University Press.
- Ratcliffe DA. 1977b. Nature conservation: aims, methods and achievements. *Proc R Soc Lond Ser B*. 197(1126):11–29. doi:10.1098/rspb.1977.0054.
- Ratcliffe DA. 1986. Selection of important areas for wildlife conservation in Great Britain: the Nature Conservancy Council's approach. In: Usher MB, editor. Wildlife conservation evaluation. London (UK): Chapman & Hall. p. 135–159.
- Reitalu T, Johansson LJ, Sykes MT, Hall K, Prentice HC. 2010. History matters: village distances, grazing and grassland species diversity. *J Appl Ecol*. 47(6):1216–1224. doi:10.1111/j.1365-2664.2010.01875.x.
- Rull V. 2010. Ecology and palaeoecology: two approaches, one objective. *Open Ecol J*. 3(Special issue 1):1–5.
- Rull V, Vegas-Vilarrúbia T. 2011. What is long-term ecology? *Trends Ecol Evol*. 26(1):3–4. doi:10.1016/j.tree.2010.10.002.
- Seastedt TR, Hobbs RJ, Suding KN. 2008. Management of novel ecosystems: are novel approaches required? *Front Ecol Environ*. 6(10):547–553. doi:10.1890/070046.
- Seddon AWR, Froyd CA, Leng MJ, Milne GA, Willis KJ. 2011. Ecosystem resilience and threshold response in the Galápagos coastal zone. *PLoS One*. 6(7):e22376. doi:10.1371/journal.pone.0022376.
- Settle J, Penev L, Georgiev T, Grabaum R, Grobelsnik V, Hammen V, Klotz S, Kotarac M, Kühn I. 2010. Atlas of biodiversity risk. Sofia – Moscow (Russia): Pensoft.
- Smith AG, Cloutman EW. 1988. Reconstruction of Holocene vegetation history in three dimensions at Waun-Fignen-Felen, an upland site in South Wales. *Philos Trans R Soc B*. 322(1209):159–219. doi:10.1098/rstb.1988.0124.
- Smol JP. 2008. Pollution of lakes and rivers: a paleoenvironmental perspective. 2nd ed. Oxford (UK): Blackwell.

- Smol JP. 2009. Conservation biology and environmental change: a paleolimnological perspective. In: Dietl GP, Flessa KW, editors. Conservation paleobiology: using the past to manage for the future Boulder (CO): The Paleontological Society Papers. p. 25–37.
- Spangenberg JH. 2007. Integrated scenarios for assessing biodiversity risks. *Sustain Dev.* 15(6):343–356. doi:10.1002/sd.320.
- Stevenson AC, Jones VJ, Battarbee RW. 1990. The cause of peat erosion: a palaeolimnological approach. *New Phytol.* 114(4):727–735.
- Stevenson AC, Thompson DBA. 1993. Long-term changes in the extent of heather moorland in upland Britain and Ireland: palaeoecological evidence for the importance of grazing. *Holocene.* 3(1):70–76. doi:10.1177/095968369300300108.
- Sugita S. 1994. Pollen representation of vegetation in quaternary sediments: theory and method in patchy vegetation. *J Ecol.* 82:881–897.
- Sugita S. 2007a. Theory of quantitative reconstruction of vegetation I: pollen from large sites reveals regional vegetation composition. *Holocene.* 17(2):229–241. doi:10.1177/0959683607075837.
- Sugita S. 2007b. Theory of quantitative reconstruction of vegetation II: all you need is love. *Holocene.* 17(2):243–257. doi:10.1177/0959683607075838.
- Sutherland WJ, editor. 1998. Conservation science and action. Oxford (UK): Blackwell Science.
- Sutherland WJ. 2006. Predicting the ecological consequences of environmental change: a review of the methods. *J Appl Ecol.* 43(4):599–616. doi:10.1111/j.1365-2664.2006.01182.x.
- Sutherland WJ, Adams WM, Aronson RB, Aveling R, Blackburn TM, Broad S, Ceballos G, Côté IM, Cowling RM, Da Fonseca GAB, et al. 2009. One hundred questions of importance to the conservation of global biological diversity. *Conserv Biol.* 23(3):557–567. doi:10.1111/j.1523-1739.2009.01212.x.
- Sutherland WJ, Albon SD, Allison H, Armstrong-Brown A, Bailey MJ, Brereton T, Boyd IL, Carey P, Edwards J, Gill M, et al. 2010. The identification of priority policy options for UK nature conservation. *J Appl Ecol.* 47(5):955–965. doi:10.1111/j.1365-2664.2010.01863.x.
- Sutherland WJ, Armstrong-Brown A, Armsworth PR, Brereton T, Brickland J, Campbell CD, Chamberlain DE, Cooke AI, Dulvy NK, Dusic NR, et al. 2006. The identification of 100 ecological questions of high policy relevance in the UK. *J Appl Ecol.* 43(4):614–627. doi:10.1111/j.1365-2664.2006.01188.x.
- Sutherland WJ, Pullin AS, Dolman PM, Knight TM. 2004. The need for evidence-based conservation. *Trends Ecol Evol.* 19(6):305–308. doi:10.1016/j.tree.2004.03.018.
- Sutherland WJ, Woodroof HJ. 2009. The need for environmental horizon scanning. *Trends Ecol Evol.* 24(10):523–527. doi:10.1016/j.tree.2009.04.008.
- Tallis JH. 1964a. Studies on Southern Pennine peats II: the pattern of erosion. *J Ecol.* 52(2):333–344.
- Tallis JH. 1964b. Studies on Southern Pennine peats III: the behaviour of *Sphagnum*. *J Ecol.* 52(2):345–353.
- Tallis JH. 1965. Studies on Southern Pennine peats IV: evidence of recent erosion. *J Ecol.* 53(2):509–520.
- The Management Group. 1990. Main conclusions of SWAP research programme. In: Mason BJ, editor. The surface waters acidification programme. Cambridge: Cambridge University Press. p. 509–515.
- van Leeuwen JFN, Froyd CA, van der Knaap WO, Coffey EED, Tye A, Willis KJ. 2008. Fossil pollen as a guide to conservation in the Galápagos. *Science.* 322(5905):1306. doi:10.1126/science.1163454.
- Vegas-Vilarrúbia T, Rull V, Montoya E, Safont E. 2011. Quaternary palaeoecology and nature conservation: a general review with examples from the neotropics. *Quat Sci Rev.* 30(9–10):2361–2388. doi:10.1016/j.quascirev.2011.02.006.
- Vera F. 2010. The shifting baseline syndrome in restoration ecology. In: Hall M, editor. Restoration and history: the search for a usable environmental past. Abingdon (UK): Routledge. p. 98–110.
- Virah-Sawmy M, Bonsall MB, Willis KJ. 2009a. ‘Tales of Symphonia’: extinction dynamics in response to past climate change in Madagascar rainforests. *Biol Lett.* 5(6):821–825. doi:10.1098/rsbl.2009.0428.
- Virah-Sawmy M, Gillson L, Willis KJ. 2009b. How does spatial heterogeneity influence resilience to climatic change? Ecological dynamics in southeast Madagascar. *Ecol Monog.* 79(4):557–574.
- Virah-Sawmy M, Willis KJ, Gillson L. 2009c. Threshold response of Madagascar’s littoral forest to sea-level rise. *Glob Ecol Biogeogr.* 18(1):98–110. doi:10.1111/j.1466-8238.2008.00429.x.
- Walker B, Salt D. 2006. Resilience thinking. Washington (DC): Island Press.
- Whitehouse NJ. 2010. Conservation lessons from the Holocene record in “natural” and “cultural” landscapes. In: Hall M, editor. Restoration and history: the search for a usable environmental past. Abingdon (UK): Routledge. p. 87–97.
- Whittaker RH. 1977. Evolutions of species diversity in land communities. *Evol Biol.* 10:1–67.
- Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Front Ecol Environ.* 5(9):475–482. doi:10.1890/070037.
- Williams JW, Jackson ST, Kutzbach JE. 2007. Projected distributions of novel and disappearing climates by 2100 AD. *Proc Natl Acad Sci USA.* 104(14):2735–2742. doi:10.1073/pnas.0606292104.
- Willis KJ, Bailey RM, Bhagwat SA, Birks HJB. 2010. Biodiversity baselines, thresholds, and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol Evol.* 25(10):583–591. doi:10.1016/j.tree.2010.07.006.
- Willis KJ, Bhagwat SA. 2010. Questions of importance to the conservation of global biological diversity: answers from the past. *Clim Past.* 6:759–769. doi:10.5194/cp-6-759-2010.
- Willis KJ, Birks HJB. 2006. What is natural? The need for a long-term perspective in biodiversity conservation. *Science.* 314(5803):1261–1265.
- Willis KJ, Gillson L, Brncic TM. 2004. How “virgin” is virgin rainforest? *Science.* 304(5669):402–403.
- Willis KJ, Gillson L, Brncic TM, Figueroa-Rangel BL. 2005. Providing baselines for biodiversity measurement. *Trends Ecol Evol.* 20(3):107–108. doi:10.1016/j.tree.2004.12.00.
- Willis KJ, Gillson L, Knapp S, editors. 2007a. Biodiversity hotspots through time: using the past to manage the future. *Philos Trans R Soc B.* 362(1478):167–333.
- Willis KJ, Gillson L, Knapp S. 2007b. Biodiversity hotspots through time: an introduction. *Philos Trans R Soc B.* 362(1478):169–174. doi:10.1098/rstb.2006.1976.
- Yallop AR, Clutterbuck B, Thacker JL. 2009. Burning issues: the history and ecology of managed fires in the uplands. In: Bonn A, Allott T, Hubacek K, Stewart JR, editors. Drivers of environmental change in uplands. Abingdon: Routledge. p. 171–185.
- Zier JL, Baker WL. 2006. A century of vegetation change in the San Juan Mountains, Colorado: an analysis using repeat photography. *For Ecol Manage.* 228(1–3):251–262. doi:10.1016/j.foreco.2006.02.049.