Ecology Letters, (2004) **7**: 990–998 doi: 10.1111/j.1461-0248.2004.00658.x

REVIEW

'As Earth's testimonies tell': wilderness conservation in a changing world

Lindsey Gillson[1]* **and**
Katherine J. Willis[2]
[1]*Long-Term Ecology Laboratory, Biodiversity Research Group, Environmental Change Institute, University of Oxford, 1A Mansfield Rd, OX1 3TB, UK*
[2]*Long-Term Ecology Laboratory, Biodiversity Research Group, School of Geography and the Environment, University of Oxford, Mansfield Rd, Oxford OX1 3TB, UK*
**Correspondence: E-mail: lindsey.gillson@eci.ox.ac.uk*

Abstract

Too often, wilderness conservation ignores a temporal perspective greater than the past 50 years, yet a long-term perspective (centuries to millennia) reveals the dynamic nature of many ecosystems. Analysis of fossil pollen, charcoal and stable isotopes, combined with historical analyses and archaeology can reveal how ongoing interactions between climatic change, human activities and other disturbances have shaped today's landscapes over thousands of years. This interdisciplinary approach can inform wilderness conservation and also contribute to interpreting current trends and predicting how ecosystems might respond to future climate change. In this paper, we review literature that reveals how increasing collaboration among palaeoecologists, archaeologists, historians, anthropologists and ecologists is improving understanding of ecological complexity. Drawing on case studies from forested and non-forested ecosystems in Europe, the Americas, Africa and Australia, we discuss how this integrated approach can inform wilderness conservation and ecosystem management.

Keywords

Anthropogenic, climate change, complexity, dynamic ecosystems, fire, forests, nonlinearity, restoration ecology, thresholds.

Ecology Letters (2004) 7: 990–998

INTRODUCTION

Current ecological understanding has recognised that most ecosystems are dynamic; all are subject to ongoing processes of changing climate and other environmental disturbances, and many landscapes have been shaped by humans for millennia (e.g. Botkin 1990; Pahl-Wostl 1995; Pickett & Ostfeld 1995; Wu & Loucks 1995; Russell 1997; Knapp 2003). According to these contemporary ecological ideas, the processes that shaped today's landscapes are ongoing and change is inevitable (e.g. Botkin 1990; Pahl-Wostl 1995; Pickett & Ostfeld 1995; Wu & Loucks 1995; Russell 1997; Knapp 2003). The implication for conservation and ecosystem management is that preventing change in many ecosystems is neither realistic nor desirable (Motzkin & Foster 2004).

Nevertheless, National Parks and other protected areas still largely follow the Yellowstone model, which emphasises the importance of 'wilderness' or the freedom from human influence (Chatty 2003). Furthermore, many large conservation organisations rely on terms like 'fragile', 'delicate', 'sensitive' and 'pristine wilderness' to generate support for conservation projects (e.g. WWF 2004; Conservation International 2004; WCS 2004). Ideas of pristine nature continue to persist in conservation discourse, with the result that disturbance or change – particularly if initiated by humans – is often assumed to be detrimental (Sprugel 1991; Peterken 1996; Fiedler *et al.* 1997; Trudgill 2001; Chatty 2003). Thus, a tension has emerged between ecological knowledge and conservation philosophy.

Linking history, ecology and conservation requires long-term data, but relatively few ecological studies last more than 5 years (May 1999), and even 'long-term ecology' tends to focus on the past few decades. So how is the gap between ecological theory, ecological data and conservation practice to be bridged?

Fossil pollen, stable isotopes, macro-fossils and charcoal, as well as historical records, photographs and archaeological data can provide records of past vegetation over thousands of years (e.g. Hunter *et al.* 1988; Birks 1996; Landres *et al.* 1999; Swetnam *et al.* 1999; Foster 2000). Such information can be used to interpret current trends and predict how

---

Title quote from T. Hardy's (1928) poem '*Before life and after*'.

ecosystems will respond to changing climate and land-use in the future (e.g. Delcourt & Delcourt 1991; Hannah *et al.* 2002a; Balmford *et al.* 2003).

In this paper, we review examples where long-term ecological data are being used to re-interpret today's landscapes and inform wilderness conservation, ecosystem management and conservation planning. First, we describe examples of how humans have influenced forested and non-forested ecosystems. Many 'ancient' and 'virgin' forests have been extensively modified by humans; how does this affect their conservation value and management? Are more open habitats like woodland mosaics, heathlands, savannas and grasslands of less conservation value than closed-canopy forests? Second, we describe examples of how climatic change affects ecosystem processes and biodiversity distribution. Can old-growth forests survive a warming climate? Third, we consider ecological complexity, and describe how a long-term perspective can help in understanding the interactions between human activities, climatic variability and disturbance. Finally, we explore the implications of long-term ecosystem dynamics for conservation planning and practice, and illustrate the application of long-term data in restoration ecology.

HUMAN–VEGETATION INTERACTIONS ON BIODIVERSE LANDSCAPES

Human influence on forest extent and biodiversity

Landscapes that are regarded as 'ancient' and 'pristine' are generally ascribed a higher conservation value than those that originated more recently, or that have been influenced by human activities (for a discussion, see e.g. Cronon 1996; Proctor 1996; Weddell 2002, pp. 291–294; Chatty 2003, pp. 94–97; Redford *et al.* 2003; Sanderson *et al.* 2003). This is particularly true of forested landscapes (e.g. Leach & Fairhead 2000; Bayliss-Smith *et al.* 2003; Heckenberger *et al.* 2003; Willis *et al.* 2004). In both temperate and tropical biomes, however, there is increasing evidence to suggest that many forests were extensively modified by humans in the past (Foster 1992; Day 1993; Foster & Zebryk 1993; Willis 1993; Russell 1997; Foster 2000; Bayliss-Smith *et al.* 2003; Rackham 2003; Willis *et al.* 2004). Moreover, far from reducing conservation value, in some cases human influences have increased forest extent and biodiversity (Fairhead & Leach 1996a; Tipping *et al.* 1999). In Kissidougou, West Africa, for example, the prevailing wisdom was that anthropogenic degradation was turning forest into savanna, but anthropological research revealed that forest fragments had actually been planted by local people. Furthermore, analysis of aerial photographs suggested that the extent of forest cover was increasing over time (Fairhead & Leach 1996b).

The full extent of anthropogenic impact in tropical forests is still emerging, but it is increasingly clear that human activities have affected large tracts of rainforest in some regions, and in these areas current rainforest structure is the legacy of disturbance several centuries ago (Willis *et al.* 2004). Species composition in some regions of the central African rainforest, for example, still reflects clearance for agriculture from 3 or 4 centuries ago (van Gemerden *et al.* 2003). Similarly, archaeological research in the upper Xingu region of Brazil has revealed extensive human settlements and a complex built environment as recently as 500 years ago (Heckenberger *et al.* 2003). This region is now dense rainforest. But perhaps the most dramatic example is from the Solomon Islands where archaeological studies revealed that apparently pristine rainforests in New Georgia have regenerated in less than 150 years (Bayliss-Smith *et al.* 2003). The fact that the current forest is enriched in secondary tree species raises an important question: is this regenerated rainforest more or less valuable in conservation terms?

In North America, studies have indicated that some forests that were originally assumed to be 'ancient' underwent extensive clearance associated with European settlement. In some examples forests have regenerated after intensive cutting just 200 years ago (McLachlan *et al.* 2000). Moreover, former land use and disturbance history in these areas continues to affect forest succession (Foster 2000). In North America many conservationists also assumed that prior to European settlement, forests were stable and 'natural' or 'pristine' (without human influence), and that this state could return if human activities were carefully controlled (for a discussion see e.g. Hunter 1996; Proctor 1996; Spies & Turner 1999). But historical studies suggest that Native Americans used low intensity, frequent burns to create a mosaic of forest, shrubland and grassland in some areas (Chambers *et al.* 1999b; Keeley 2002; Gallant *et al.* 2003). They also encouraged the growth of useful species (Anderson 1999) and may have reduced the density of herbivores (Kay 1997).

Human influence on non-forested landscapes

Heathland communities in New England are highly valued for aesthetic and recreational purposes and there is a strong conservation movement to preserve them. Paradoxically, however, long-term studies indicate that these communities are a legacy of previous human activities and that in order to preserve them, traditional management techniques need to be maintained or restored (Motzkin & Foster 2002; Foster & Motzkin 2003). Bearberry–scrub–oak heaths, for example, are associated with formerly ploughed grazed or otherwise severely disturbed sites, and intensive management will be needed to maintain what is essentially a secondary vegetation phase (Motzkin *et al.* 2002).

Similarly, in the UK, many rare plants are associated with human disturbances like hay meadows and mining spoil, and the conservation of these species demands long-term knowledge of disturbance history, and a continuation of these activities (e.g. Squires 1978). Many English hedgerows were planted in the 18th Century in response to the Enclosures Act, and are now valued for their cultural significance as well as their biodiversity; some (but not all) 'ancient woodland indicator' species are now found in British hedgerows, a testament to their importance as wildlife corridors (McCollin *et al.* 2000).

Human activities are also important in maintaining biodiversity in savannas. In Australian savannas, historical evidence indicates that Aboriginal management involved small-scale, low intensity burning throughout the dry season (Preece 2002). This maintained the savannas as heterogeneous mosaics, and skilful manipulation of burning could protect fire-sensitive species like the native conifers *Callitris intratropica* and retain cover for species like kangaroos (Price & Bowman 1994; Bowman 1998). Replacement of low intensity patchy burns with high intensity late dry season fires since European settlement may have reduced habitat heterogeneity and contributed to the decline and extinction of many small mammals (Burbridge & McKenzie 1989). Restoration of traditional fire management might help to prevent species loss and reduce the risk of wildfires in the savannas of Australia (Russell-Smith *et al.* 1998; Yibarbuk *et al.* 2001; Russell-Smith *et al.* 2002).

CLIMATE–VEGETATION INTERACTIONS ON BIODIVERSE LANDSCAPES

Climate instability and ecosystem change

Climatic change is far too often neglected in conservation practice and planning, leading to unrealistic expectations of ecosystem stability. Global climatic changes over the past millennium have affected ecological processes like tree recruitment, causing changes that are still apparent in the ecosystems of today. For example, trees that are more than 150 years old germinated in the colder conditions of the Little Ice Age (which lasted from *c.* AD 1590 to 1850); the composition of some of today's old-growth forests reflects the recruitment conditions of times past (Millar & Woolfenden 1999). It is, therefore, probably unrealistic to expect species composition in old-growth forests to remain stable, and the failure of older trees to replace themselves might in some cases be a reflection of the changes in climate since the Little Ice Age, rather than any present-day problem of tree-recruitment failure.

Another example of a climatically driven ecosystem change is revealed in a study of the heather moorlands of Europe. In the 1990s, experimental control methods involving chemical treatments, burning and grazing were introduced in several regions of Britain where purple moor grass (*Molinia caerulea)* was apparently degrading Callunetum moorland (Berendse *et al.* 1994; Chambers *et al.* 1999a). Combined pollen and macrofossil analysis on Exmoor (UK) revealed, however, that the heather moorland was itself derived from grass moorland, and that over the past 1000 years, vegetation dominance has alternated between Callunetum and grass moor containing at least some *Molinia* (Chambers *et al.* 1999a). These shifts were probably driven by climatic change, in combination with changes in grazing regime. This innovative study by Chambers *et al.* has demonstrated that previous conservation targets – specifically the elimination of *Molinia* – do not have an ecological basis. Their palaeoecological work is helping to guide future management of these sensitive areas, and the success of the Exmoor project has already led to similar techniques being applied for management of heathland in Wales and elsewhere.

Climatic thresholds

Predicting ecosystem responses to climatic change is complex because species respond individualistically and furthermore species response may be affected by other forms of disturbance. Palaeoecological studies can help in determining the position of species-specific critical climatic thresholds; in south-central Spain, for example, analysis of fossil pollen, microfossils and charcoal revealed rapid transitions between pine, deciduous oak and evergreen oak. The authors concluded that ecosystem inertia and stability was punctuated by periods of change, which occurred when ecological thresholds were crossed (Carrión *et al.* 2001).

An example of dramatic ecosystem change in northern Quebec also illustrates how the position of ecological thresholds can change in response to disturbance patterns. Studies of tree remains in a sub-arctic peatland showed that Black spruce (*Picea mariana*) forest regenerated successfully after major fires in 350 and 10 BC, but vegetation shifted to a open stunted spruce after a fire in AD 1568. The authors suggest that a climatic threshold had been crossed, which inhibited regeneration after the AD 1568 fire (Arseneault & Payette 1997).

The interaction of climate and ecological thresholds becomes more complex when also considering human disturbance. Human disturbances may exacerbate the effects of climate change, effectively lowering ecological thresholds. In the Segura Mountains of southern Spain, for example, palaeoecological studies have revealed that abrupt changes in vegetation were probably climatically driven, but grazing pressure may have pushed vegetation beyond a critical threshold for change (Carrión *et al.* 2001). Similarly, in the Appalachian Mountains (southeastern USA), ecotones between alpine, boreal and temperate ecosystems shifted dramatically when critical thresholds of both temperature and disturbance were passed (Delcourt & Delcourt 1998).

SCALE, CLIMATE AND PEOPLE

In New England (USA), comprehensive palaeoecological, archaeological, historical and ecological studies are now beginning to disentangle human influences from other environmental variables like soils, geomorphology, topography, climatic change and natural disturbance by hurricanes, fire and native pathogens (Foster 2002; Foster & Motzkin 2003). The landscape of New England today is a mosaic of more and less modified habitats; the effects of European settlement and land-use changes are underlain by older patterns of Native American land-use, while disturbance history and ongoing climatic change continue to affect ecological processes like recruitment and succession. In many tropical ecosystems, there are not yet enough data to say with certainty whether ecosystems have been influenced by humans, and the absence of evidence is not equivalent to evidence of absence (Gott 2002). Nevertheless, results are now emerging which parallel interpretations of the New England Landscape; in Puerto Rico, up to 90% of lowland 'primary' forest was either deforested or secondary vegetation, and the forest mosaic of today results from a complex interaction between natural disturbance (especially hurricanes), human activity, and environmental gradients such as elevation (Foster *et al.* 1999).

These examples illustrate how landscape complexity is determined by a multiplicity of interacting factors, which influence ecological processes at different spatial scales. Using the palaeo-record to compare vegetation change at local and regional scales can help to elucidate how the effects of human disturbance can interact with other factors. The causes of rainforest contraction in Queensland, Australia, for example, are hotly disputed. Some authors maintain that Aboriginal burning is the main cause of rainforest loss (Kershaw 1986, 1994), and that it is the reduction in Aboriginal impact that has allowed the re-expansion of rainforest in some areas (Harrington & Sanderson 1994). Others suggest that rainforest re-expansion was triggered by wetter conditions from 4000 BP and is still ongoing (Hopkins *et al.* 1996). A third hypothesis, (Bowman *et al.* 1999) argues that localised rainforest contraction in the late Holocene was caused by tropical cyclone damage and the subsequent severe fires associated with storm debris, rather than regional climate change or aboriginal burning regimes. According to this hypothesis, therefore, Aboriginal management of rainforest may have helped to maintain forest cover, and it was European settlers who caused its decline (Hill *et al.* 2000). Some of the incompatibility between these apparently contradictory hypotheses might be resolved by a rigorous consideration of palaeoecological data at varying spatial scales. Climatic trends (Hopkins *et al.* 1996), for example, would be most readily observable at the regional scale whereas hurricanes and fires (Bowman *et al.* 1999) associated with storm debris may affect smaller spatial scales. The activities of humans would imposed a still finer scale patterning of vegetation change (Hill & Baird 2003).

This importance of scale in understanding disturbance is further illustrated by elegant palaeoecological work from European forests. Migrations of *Fagus sylvatica* and *Picea abies*, though broadly controlled by climate at the continental scale, are also influenced by other factors; small-scale ground fires and changes in grazing regime might have facilitated the invasion of these species into existing forests, possibly contributing to the displacement and local extinction of *Quercus robur* and *Tilia cordata* (Björkman & Bradshaw 1996). It is the interaction between small-scale disturbance and broad-scale climate change that probably drove species migration and changed the composition of forests in Sweden.

COMPLEXITY AND CONSERVATION

Applying long-term data in conservation planning and practice

Comparing ecosystem responses to past climate change can help in predicting the ecological consequences of current and future climate change, in order to plan conservation strategies for warmer climates. Climate Change-integrated Conservation Strategies (CCS) require collaboration between palaeoecologists, ecologists and biogeographers in order to model interactions between vegetation, climate and land-use and to plan conservation strategies which consider these interactions (Hannah *et al.* 2002b). Palaeoecological research in the tropical Andes, for example, has helped to identify which species are most sensitive to climate change, and this information is informing Climate Change-integrated Conservation Strategies (Hannah *et al.* 2002a,b). These strategies include planning protected area networks which maximize altitudinal range and local environmental heterogeneity, thereby accommodating migrational shifts as well as preserving the range of micro-climates which facilitate the persistence of meta-populations (Hunter *et al.* 1988; Bush 2002; Hannah *et al.* 2002b).

As the examples from the tropical Andes illustrate, the future distribution of species will depend not only on the available climate space, but also many other factors, such as topography, land-use change and biotic interactions (Delcourt & Delcourt 1988; Bush 1996; Davis *et al.* 1998; Delcourt & Delcourt 1998; Lawton 2000; Pearson & Dawson 2003). As well as modelling broad-scale shifts in biomes, a much finer scale approach to conservation planning is therefore required if vulnerable species are not to slip through the conservation net (Hunter *et al.* 1988). Palaeoecological studies have demonstrated that species respond individualistically to changing climate and disturbance; in the southern Appalachian Mountains, for example, palaeoecological studies revealed the effects of Holocene climate change on the position of ecotones between alpine, boreal and temperate ecosystems (Delcourt & Delcourt 1988). These studies identified the presence of critical thresholds of temperature and disturbance, and enabled the authors to predict the possible effects future climate change scenarios on ecotones; they suggest that future rapid climate warming could result in geomorphic instability and increased habitat heterogeneity, alterations which will favour disturbance adapted species (Delcourt & Delcourt 1998). Thus it seems that both a 'coarse filter' (community level) and a 'fine filter' (species level) approach to are needed to ensure species survival in a changing climate (Hunter *et al.* 1988).

Syntheses of palaeoecological data can also be used to test predictions of the effects of climate change on ecosystem processes, and to model interactions between climate, fire and humans (Cowling *et al.* 2001; Lischke *et al.* 2002). For example, comparisons of a dynamic forest patch model with paleoecological data have shown that species immigration responses can lag behind climatic changes by centuries to millennia (Lischke *et al.* 2002). Outputs from another forest model were compared against the palaeorecord in order to evaluate the relative importance of climate, species immigration, fire and human impact throughout the Holocene (Keller *et al.* 2002). The results showed increasing impact of fire and humans from 7000 BP to the present, suggesting that fire may be an especially important determinant of forest composition in the future, when warming temperatures will probably increase fire frequency. Similarly, Cowling *et al.* (2001) tested the robustness of a forest gap model by comparing the simulated biomass trends for *Picea*, *Pinus* and *Betula* with a local pollen record. They also used a 1500-year palaeoclimate reconstruction, based on tree-rings, to assess the importance of climate on the decline of *Tilia* during the Little Ice Age, and concluded that present day dominance of *Fagus* is probably because of anthropogenic rather than climatic factors.

Species are more likely to persist in protected areas which incorporate local environmental heterogeneity, because they are provided with a range of conditions which allows them to adjust their local distribution in response to environmental change (Hunter *et al.* 1988; Bush 1996). However, a heterogeneous environment does not guarantee the survival of species or landscapes that are associated with a particular form or pattern of disturbance. In the 20th century, fire suppression has affected the composition of some temperate forests, and has increased or homogenised the fuel-base thereby encouraging severe fires (Polakow & Dunne 1999; Stephenson 1999). In south-western USA, dendrochronological techniques and historical records were used to reconstruct past fire disturbance regimes over the past 500 years, and the results were used to restore pre-Anglo-American settlement forest structure in ponderosa pine forests (Fulé *et al.* 1997; Moore *et al.* 1999). However, these fire restoration programmes cannot replicate past conditions; they are complicated by the differing expectations of ecosystem managers, and by the effect of changing climate (Fulé *et al.* 1997; Moore *et al.* 1999; Swetnam *et al.* 1999). Climate affects how much fuel is available, its combustibility, how quickly fire spreads, and the fire return interval (Polakow & Dunne 1999; Parshall & Foster 2002). As will be discussed in the following section, the success of ecological restoration projects depends on understanding how ecosystems respond to environmental changes, rather than mimicking past reference conditions (Millar & Woolfenden 1999).

Applying long-term data in restoration ecology

A long-term perspective raises particularly interesting challenges for restoration ecology: which point in time should be chosen as a benchmark for restoration (Sprugel 1991)? If multiple pathways of succession are possible (Fastie 1995; Turner *et al.* 1998), which is the 'right' one? Should locally extinct species be re-introduced or replaced? How will changing environmental conditions today affect ecosystem processes? Are human disturbances 'natural' (Hunter 1996)? Should traditional management practices be re-introduced, and if so at what level? Can the desire for 'wilderness' be reconciled with necessary management and restoration interventions? (Moore *et al.* 1999).

Some of the most successful examples of the use of palaeoecology in restoration ecology can be found in wetland ecosystems; past levels of acidity and salinity can be inferred from fossil diatoms preserved in lake sediments, providing a lake-specific history which can be used as a basis for lake management and restoration (Anderson 1995). Similarly, palaeoecological evidence of change and response in lake ecosystems can be used to identify the thresholds of tolerance to pollutants (Smol 2002). The Balkan Lake Dojran, for example, has high conservation value because of its endemic species and importance to wetland birds, but is threatened by eutrophication and water abstraction. Palaeoecological data from ostracods and diatoms indicate that it is not too late to act; ecological changes are as yet quite localised, but the ecosystem might be approaching an ecological threshold, beyond which larger changes could be expected (Griffiths *et al.* 2002).

Palaeohydrology and palaeoecology are also being used in the restoration of rivers and floodplains in Europe.

Evidence suggests that prior to deforestation of floodplains and subsequent channelization of rivers, the ecology of rivers and floodplains was probably dynamic; most rivers were multi-braided, rather than single channels, and the surrounding vegetation was a mosaic consisting of woodland and more open areas (Brown 2002). Brown (2002) therefore suggested that using palaeohydrological and palaeoecological data to guide river and floodplain restoration projects might not only enhance biodiversity, but could also reduce future flood defence expenses by restoring the river channel's capacity to respond to flood events (Brown 2002).

An innovative approach to wetland ecosystem restoration is also being implemented at the Oostvaardersplassen reserve, in the Netherlands. Here, long-term data have been used to restore ecosystem processes and thus re-create variability over time and space. Management plans included allowing water levels to fluctuate naturally and emergent plant communities to return. Furthermore, disturbance patterns were restored by the re-introduction of deer, ponies, cattle and beavers (Sutherland 2002).

Apart from in the case of very recent anthropogenic disturbance, it will rarely be possible to return ecosystems to a former state or nearby reference condition, because ecosystems are unique in time and space (Pickett & Parker 1994; White & Walker 1997; Foster 2000). Restoration ecology is therefore inherently experimental, but knowledge of long-term variability can guide the design of management experiments, by defining the boundaries of ecosystem variability and the sensitivity of ecosystems to environmental change (Walters & Holling 1990; White & Walker 1997). Studying the effect of large, infrequent disturbances, for example, can help to define the extremes which can be tolerated by an ecological system (Landres *et al.* 1999). Such information helps in making reasonable predictions of ecosystem response to management actions, and knowledge of the rates of change in ecosystems can provide a temporal framework for monitoring and adjusting management and restoration plans.

CONCLUSIONS

New conservation approaches are developing that incorporate long-term data to understand, manage and conserve ecosystem variability and biodiversity (e.g. Birks 1996; Landres *et al.* 1999; Foster 2000, 2002). Whereas traditional approaches to wilderness conservation were underpinned by the assumption that ecosystems should be stable and pristine, contemporary ecological paradigms recognize that nature is in flux (Pickett *et al.* 1992; Pickett & Ostfeld 1995). Experimental and adaptive conservation approaches aim to conserve ecological processes by applying knowledge of ecosystem variability over a range of temporal and spatial scales (Bowman 2001; Biggs & Rogers 2003; Rogers 2003). There is, therefore, a potential for productive collaboration between ecologists, palaeoecologists and conservationists, in order to integrate a long-term perspective into the management of dynamic ecosystems. The challenge is to develop a conservation ethic that uses a knowledge of the history and variability of ecosystems to understand the thresholds of their resilience, while still delivering a strong conservation message (Pickett *et al.* 1992; Pahl-Wostl 1995; Cronon 1996; Trudgill 2001). Ecosystems are unique in time and space; how we proceed today does not have to mimic the past, but should be informed by it.

ACKNOWLEDGEMENTS

We thank Keith Bennett and three anonymous reviewers for helpful comments on the text, and the Trapnell Fund for financial support.

REFERENCES

Anderson, N.J. (1995). Using the past to predict the future: lake sediments and the modelling of limnological disturbance. *Ecol. Model.*, 78, 149–172.

Anderson, M.K. (1999). The fire, pruning and coppice management of temperate ecosystems for basketry material by California Indian tribes. *Hum. Ecol.*, 27, 79–113.

Arseneault, D. & Payette, S. (1997). Reconstruction of millennial forest dynamics from tree remains in a subarctic tree line peatland. *Ecology*, 78, 1873–1883.

Balmford, A., Green, R.E. & Jenkins, M. (2003). Measuring the changing state of nature. *Trends Ecol. Evol.*, 18, 326–330.

Bayliss-Smith, T., Hviding, E. & Whitmore, T. (2003). Rainforest composition and histories of human disturbance in Solomon Islands. *Ambio*, 32, 346–352.

Berendse, F., Schmitz, M. & de Visser, W. (1994). Experimental manipulation of succession in heathland ecosystems. *Oecologia*, 100, 38–44.

Biggs, H.C. & Rogers, K.H. (2003). An adaptive system to link science, monitoring, and management in practice. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds du Toit, J.T., Rogers, K.H. & Biggs, H.C.). Island Press, Washington, DC. pp. 59–82.

Birks, H.J.B. (1996). Contributions of quaternary palaeoecology to nature conservation. *J. Veg. Sci.*, 7, 89–98.

Björkman, L. & Bradshaw, R. (1996). The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. *J. Biogeogr.*, 23, 235–244.

Botkin, D.B. (1990). *Discordant Harmonies: A New Ecology for the Twenty-First Century*. Oxford University Press, Oxford, UK.

Bowman, D.M.J.S. (1998). Tansley review no. 101: the impact of aboriginal landscape burning on the Australian biota. *New Phytol.*, 140, 385–410.

Bowman, D.M.J.S. (2001). Future eating and country keeping: what role has environmental management in the management of biodiversity. *J. Biogeogr.*, 28, 549–564.

Bowman, D.M.J.S., Panton, W.J. & Head, J. (1999). Abandoned Orange-footed Scrubfowl (*Megapodius reinwardt*) nests and coastal rainforest boundary dynamics during the late Holocene in monsoonal Australia. *Quatern. Int.*, 59, 27–38.

Brown, A.G. (2002). Learning from the past: palaeohydrology and palaeoecology. *Freshwat. Biol.*, 47, 817–829.

Burbridge, A.A. & McKenzie, N.L. (1989). Patterns in the modern decline of Western Australia's vertebrate fauna: causes and conservation implications. *Biol. Conserv.*, 50, 143–198.

Bush, M.B. (1996). Amazonian conservation in a changing world. *Biol. Conserv.*, 76, 219–228.

Bush, M.B. (2002). Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecol. Biogeogr.*, 11, 463–473.

Carrión, J.S., Munuera, M., Dupre, M. & Andrade, A. (2001). Abrupt vegetation changes in the Segura Mountains of southern Spain throughout the Holocene. *J. Ecol.*, 89, 783–797.

Chambers, F.M., Mauquoy, D. & Todd, P.A. (1999a). Recent rise to dominance of *Molinia caerulea* in environmentally sensitive areas: new perspectives from palaeoecological data. *J. Appl. Ecol.*, 36, 719–733.

Chambers, J.C., Vander-Wall, S.B. & Schupp, E.W. (1999b). Seed and seedling ecology of pinon and juniper species in the pygmy woodlands of Western North America. *Bot. Rev.*, 65, 1–38.

Chatty, D. (2003). Environmentalism in the Syrian badia. The assumptions of degradation, protection and bedouin misuse. In: *Ethnographies of Conservation. Environmentalism and the Distribution of Privilege* (eds Anderson, D.G. & Berglund, E.). Berghahn Books, New York and Oxford, pp. 87–99.

Conservation International (2004). Conservation strategies: tropical wilderness. URL: http://www.conservation.org/xp/CIWEB/strategies/tropical_wilderness/tropical_wilderness.xml.

Cowling, S.A., Sykes, M.T. & Bradshaw, R.H.W. (2001). Palaeovegetation-model comparisons, climate change and tree succession in Scandinavia over the past 1500 years. *J. Ecol.*, 89, 227–236.

Cronon, W. (1996). The trouble with wilderness: or getting back to the wrong nature. In: *Uncommon Ground. Rethinking the Human Place in Nature* (ed. Cronon, W.). W.W. Norton, New York, pp. 69–91.

Davis, A.J., Jenkinson, L.S., Lawton, J.L., Shorrocks, B. & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786.

Day, S.P. (1993). Woodland origin and 'ancient woodland indicators': a case-study from Sidlings copse, Oxfordshire, United Kingdom. *Holocene*, 16, 45–53.

Delcourt, H.R. & Delcourt, P.A. (1988). Quaternary landscape ecology: relevant scale in space and time. *Landscape Ecol.*, 2, 23–44.

Delcourt, H. & Delcourt, P. (1991). *Quaternary Ecology: A Paleoecological Perspective*. Chapman and Hall, New York, NY.

Delcourt, P.A. & Delcourt, H.R. (1998). Paleoecological insights on conservation of biodiversity: a focus on species, ecosystems, and landscapes. *Ecol. Appl.*, 8, 921–934.

Fairhead, J. & Leach, M. (1996a). *Misreading the African Landscape: Society and Ecology in a Forest-Savanna Mosaic*. Cambridge University Press, Cambridge, UK.

Fairhead, J. & Leach, M. (1996b). Rethinking the forest-savanna mosaic: colonial science and its relics in West Africa. In: *The Lie of the Land* (eds Leach, M. & Mearns, R.). James Currey, Oxford, UK, pp. 105–121.

Fastie, C.L. (1995). Causes and ecosystem consequences of multiple pathways of primary succession at Glacier Bay, Alaska. *Ecology*, 76, 1899–1916.

Fiedler, P.L., White, P.S. & Leidy, R.A. (1997). The paradigm shift in ecology and its implications for conservation. In: *The Ecological Basis of Conservation. Heterogeneity, Ecosystems, and Biodiversity* (eds Pickett, S.T.A., Ostfeld, R.S., Shachak, M. & Likens, G.E.). Chapman and Hall, New York, pp. 83–92.

Foster, D.R. (1992). Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *J. Ecol.*, 80, 753–772.

Foster, D.R. (2000). Conservation lessons & challenges from ecological history. *For. Hist. Today*, Fall 2000, 2–11.

Foster, D.R. (2002). Conservation issues and approaches for dynamic cultural landscapes. *J. Biogeogr.*, 29, 1533–1535.

Foster, D.R. & Motzkin, G. (2003). Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. *For. Ecol. Manag.*, 185, 127–150.

Foster, D.R. & Zebryk, T.M. (1993). Long-term vegetation dynamics and disturbance history of a Tsuga-dominated forest in New England. *Ecology*, 74, 982–998.

Foster, D.R., Fluet, M. & Boose, E.R. (1999). Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecol. Appl.*, 9, 555–572.

Fulé, P.Z., Covington, W.W. & Moore, M.M. (1997). Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecol. Appl.*, 7, 895–908.

Gallant, A.L., Hansen, A.J., Councilman, J.S., Monte, D.K. & Betz, D.W. (2003). Vegetation dynamics under fire exclusion and logging in a Rocky Mountain watershed. *Ecol. Appl.*, 13, 385–403.

van Gemerden, B.S., Olff, H., Parren, M.P.E. & Bongers, F. (2003). The pristine rain forest? Remnants of historical human impacts on current tree species composition and diversity. *J. Biogeogr.*, 30, 1381–1390.

Gott, B. (2002). Fire-making in Tasmania: absence of evidence is not evidence of absence. *Curr. Anthopol.*, 43, 650–656.

Griffiths, H.I., Reed, J.M., Leng, M.J., Ryan, S. & Petkovski, S. (2002). The recent palaeoecology and conservation status of Balkan Lake Dojran. *Biol. Conserv.*, 104, 35–49.

Hannah, L., Midgley, G.F., Lovejoy, T., Bond, W.J., Bush, M.B., Lovett, J.C. *et al.* (2002a). Conservation of biodiversity in a changing climate. *Conserv. Biol.*, 16, 264–268.

Hannah, L., Midgley, G.F. & Millar, D. (2002b). Climate change-integrated conservation strategies. *Global Ecol. Biogeogr.*, 11, 485–495.

Harrington, G.N. & Sanderson, H.D. (1994). Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest. *Pacific Conserv. Biol.*, 1, 319–327.

Heckenberger, M.J., Kuikuro, A., Kuikuro, U.T., Russell, J.C., Schmidt, M., Fausto, C. *et al.* (2003). Amazonia 1492: Pristine forest or cultural parkland? *Science*, 301, 1710–1714.

Hill, R. & Baird, A. (2003). Kuku-Yalanji rainforest aboriginal people and carbohydrate resource management in the wet tropics of Queensland, Australia. *Hum. Ecol.*, 31, 27–52.

Hill, R., Griggs, P. & Incorporated, B.B.N. (2000). Rainforests, agriculture and aboriginal fire regimes in wet tropical Queensland, Australia. *Aust. Geogr. Stud.*, 38, 138–157.

Hopkins, M.S., Head, J., Ash, J.E., Hewett, R.K. & Graham, A.W. (1996). Evidence of a Holocene and continuing recent expansion of lowland rain forest in humid, tropical North Queensland. *J. Biogeogr.*, 23, 737–745.

Hunter, H.J. (1996). Benchmarks for managing ecosystems: are human activities natural? *Conserv. Biol.*, 10, 695–697.

Hunter, M.L., Jacobson, G.L. & Webb, T. (1988). Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conserv. Biol.*, 2, 375.

Kay, C.E. (1997). Ungulate herbivory, willows, and political ecology in Yellowstone. *J. Range Manag.*, 50, 139–145.

Keeley, J. (2002). Native American impacts of fire regimes of the California coastal ranges. *J. Biogeogr.*, 29, 303–320.

Keller, F., Lischke, H., Mathis, T., Möhle, A., Wick, L., Ammann, B. *et al.* (2002). Effects of climate, fire and humans on forest dynamics: forest simulations compared to the palaeoecological record. *Ecol. Model.*, 152, 109–127.

Kershaw, A.P. (1986). Climatic change and aboriginal burning in north-east Australia during the last two glacial/interglacial cycles. *Nature*, 322, 47–49.

Kershaw, A.P. (1994). Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeogr. Palaeoclimato. Palaeoecol.*, 109, 399–412.

Knapp, S. (2003). Dynamic diversity. *Nature*, 422, 475.

Landres, P.B., Morgan, P. & Swanson, F.J. (1999). Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.*, 9, 1179–1188.

Lawton, J.L. (2000). Concluding remarks: a review of some open questions. In: *The Ecological Consequences of Environmental Heterogeneity* (eds Hutchings, M.J., John, E. & Stewart, A.J.A.). Cambridge University Press, Cambridge, UK.

Leach, M. & Fairhead, J. (2000). Fashioned forest past, occluded histories? International environmental analysis in West African locales. *Dev. Change*, 31, 35–39.

Lischke, H., Lotter, A.F. & Fischlin, A. (2002). Untangling a Holocene pollen record with forest model simulations and independent climate data. *Ecol. Model.*, 150, 1–21.

May, R. (1999). Unanswered questions in ecology. *Philos. T. Roy. Soc. B.*, 354, 1951–1959.

McCollin, D., Jackson, J.I., Bunce, R.G.H., Barr, C.J. & Stuart, R. (2000). Hedgerows as habitat for woodland plants. *J. Environ. Manag.*, 60, 77–90.

McLachlan, J., Foster, D.R. & Menalled, F. (2000). Anthropogenic origins of late-successional structure and composition in four New England hemlock stands. *Ecology*, 81, 717–733.

Millar, C.I. & Woolfenden, W.B. (1999). The role of climate change in interpreting historical variability. *Ecol. Appl.*, 9, 1207–1216.

Moore, M.M., Covington, W.W. & Fulé, P.Z. (1999). Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecol. Appl.*, 9, 1266–1277.

Motzkin, G. & Foster, D.R. (2002). Grasslands, heathlands and shrublands in coastal New England: historical interpretations and approaches to conservation. *J. Biogeogr.*, 29, 1569–1590.

Motzkin, G. & Foster, D. (2004). Insights for ecology and conservation. In: *Forests in Time. The Environmental Consequences of 1000 years of Change in New England* (eds Foster, D.R. & Aber, J.D.). Yale University Press, New Haven, CT, pp. 367–379.

Motzkin, G., Eberhardt, R., Hall, B., Foster, D.R., Harrod, J. & MacDonald, D. (2002). Vegetation variation across Cape Cod, Massachusetts: environmental and historical determinants. *J. Biogeogr.*, 29, 1439–1454.

Pahl-Wostl, C. (1995). *The Dynamic Nature of Ecosystems: Chaos and Order Entwined.* John Wiley & Sons Ltd, New York, NY.

Parshall, T. & Foster, D.R. (2002). Fire on the New England landscape: regional and temporal variation, cultural and environmental controls. *J. Biogeogr.*, 29, 1305–1317.

Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful ? *Global Ecol. Biogeogr.*, 12, 361–371.

Peterken, G.F. (1996). *Natural Woodland. Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge, UK.

Pickett, S.T.A. & Ostfeld, R.S. (1995). The shifting paradigm in ecology. In: *A New Century for Natural Resources Management* (eds Knight, R.L. & Bates, S.F.). Island Press, Washington, DC, pp. 261–278.

Pickett, S.T.A. & Parker, V.T. (1994). Avoiding old pitfalls: opportunities in a new discipline. *Restor. Ecol.*, 2, 75–79.

Pickett, S.T., Parker, V.T. & Fiedler, P.L. (1992). The new paradigm in ecology: implications for conservation biology above the species level. In: *Conservation Biology* (eds Fiedler, P.L. & Jain, S.K.). Chapman and Hall, New York, NY, pp. 50–65.

Polakow, D.A. & Dunne, T.T. (1999). Modelling fire-return interval T: stochasticity and censoring in the two-parameter Weibull model. *Ecol. Model.*, 121, 79–102.

Preece, N. (2002). Aboriginal fires in monsoonal Australia from historical accounts. *J. Biogeogr.*, 29, 321–336.

Price, O. & Bowman, D.M.J.S. (1994). Fire-stick forestry; a matrix model in support of skilful fire management of *Callitris intratropica* R.T. Baker by north Australian Aborigines. *J. Biogeogr.*, 21, 573–580.

Proctor, J.D. (1996). Whose nature? The contested moral terrain of ancient forests. In: *Uncommon Ground. Rethinking the Human Place in Nature* (ed. Cronon, W.). W.W. Norton, New York, pp. 269–297.

Rackham, O.R. (2003). *Ancient Woodland. Its History, Vegetation and Uses in England.* Castlepoint Press, Colvend.

Redford, K.H., Coppolillo, P., Sanderson, E.W., da Fonseca, G.A.B., Dinerstein, E., Groves, C. *et al.* (2003). Mapping the conservation landscape. *Conserv. Biol.*, 17, 116–131.

Rogers, K.H. (2003). Adopting a heterogeneity paradigm: implications for management of protected savannas. In: *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* (eds du Toit, J.T., Rogers, K.H. & Biggs, H.C.). Island Press, Washington, DC.

Russell, E.W.B. (1997). *People and the Land Through Time.* Yale University Press, New Haven and London.

Russell-Smith, J., Ryan, P.G., Klessa, D., Waights, G. & Harwood, R. (1998). Fire regimes, fire-sensitive vegetation and fire management of the sandstone Arnhem Plateau, monsoonal northern Australia. *J. Appl. Ecol.*, 35, 829–846.

Russell-Smith, J., Ryan, P.G. & Cheal, D.C. (2002). Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: frequency, interval, patchiness. *Biol. Conserv.*, 104, 91–106.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2003). The human footprint and the last of the wild. *Bioscience*, 52, 891–904.

Smol, J.P. (2002). *Pollution of Lake and Rivers. A Paleoenvironmental Perspective*. Arnold, London, UK.

Spies, T.A. & Turner, M.G. (1999). Dynamic forest mosaics. In: *Maintaining Biodiversity in Forest Ecosystems* (ed. Hunter, M.L. Jr). Cambridge University Press, Cambridge, UK, pp. 95–160.

Sprugel, D. (1991). Disturbance, equilibrium and environmental variability: what is 'natural' vegetation in a changing environment. *Biol. Conserv.*, 58, 1–18.

Squires, R. (1978). Conservation in Upper Teesdale: contributions from the palaeoecological record. *T. I. Brit. Geogr.*, 3, 129–150.

Stephenson, N.L. (1999). Reference conditions for Giant Sequoia forest restoration: structure, process, and precision. *Ecol. Appl.*, 9, 1253–1265.

Sutherland, W.J. (2002). Openness in management. *Nature*, 418, 834–835.

Swetnam, T.W., Allen, C.D. & Betancourt, J.L. (1999). Applied historical ecology: using the past to manage for the future. *Ecol. Appl.*, 9, 1189–1206.

Tipping, R., Buchanan, J., Davies, A. & Tisdall, E. (1999). Woodland biodiversity, palaeo-human ecology and some implications for conservation management. *J. Biogeogr.*, 26, 33–43.

Trudgill, S. (2001). Psychobiogeography: meanings of nature and motivations for a democratized conservation ethic. *J. Biogeogr.*, 28, 677–698.

Turner, M.G., Baker, W.L., Peterson, C.J. & Peet, R.K. (1998). Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems*, 1, 511–523.

Walters, C.J. & Holling, C.S. (1990). Large-scale management experiments and learning by doing. *Ecology*, 71, 2060–2068.

WCS (2004). WCS-Congo.org: the forests of Central Africa. URL: http://www.wcs-congo.org/

Weddell, B.J. (2002). *Conserving Living Natural Resources in the Context of a Changing World*. Cambridge University Press, Cambridge, UK.

White, P.S. & Walker, J.L. (1997). Approximating nature's variation: selecting and using reference information in restoration ecology. *Restor. Ecol.*, 5, 338–349.

Willis, K.J. (1993). How old is ancient woodland? *Trends Ecol. Evol.*, 8, 427–428.

Willis, K.J., Gillson, L. & Brncic, T. (2004). How 'virgin' is virgin rainforest. *Science*, 304, 402–403.

Wu, J. & Loucks, O. (1995). From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.*, 70, 439–466.

WWF (2004). Major habitat type 1: tropical and subtropical moist broadleaf forests. URL: http://www.panda.org/about_wwf/where_we_work/ecoregions/global200/pages/habitat/habitat01.htm.

Yibarbuk, D., Whitehead, P.J., Russell-Smith, J., Godjuwa, C., Fisher, A., Cooker, P. *et al.* (2001). Fire ecology and aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *J. Biogeogr.*, 28, 325–343.

Editor, Mark W. Schwartz
Manuscript received 6 April 2004
First decision made 1 June 2004
Second decision made 16 July 2004
Manuscript accepted 21 July 2004