What Is Natural? The Need for a Long-Term Perspective in Biodiversity Conservation

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Ecosystems change in response to factors such as climate variability, invasions, and wildfires. Most records used to assess such change are based on short-term ecological data or satellite imagery spanning only a few decades. In many instances it is impossible to disentangle natural variability from other, potentially significant trends in these records, partly because of their short time scale. We summarize recent studies that show how paleoecological records can be used to provide a longer temporal perspective to address specific conservation issues relating to biological invasions, wildfires, climate change, and determination of natural variability. The use of such records can reduce much of the uncertainty surrounding the question of what is "natural" and thereby start to provide important guidance for long-term management and conservation.

Paleoecological records (e.g., fossil pollen, seeds and fruits, animal remains, tree rings, charcoal) spanning tens to millions of years provide a valuable long-term perspective on the dynamics of contemporary ecological systems (*1*). Such studies are increasingly becoming part of community and landscape ecological research (*2*). In contrast, conservation-related research largely ignores paleoecological records. For example, there are no temporal records spanning more than 50 years included in any of the key biodiversity assessments published over the past 7 years (*3*). Paleoecological records have been considered too descriptive and imprecise, and therefore of little relevance to the actual processes of conservation and management. Such criticisms may have been valid 30 years ago, but there is now a wealth of information in paleoecological records providing detailed spatial and temporal resolutions (*1*, *4–7*) that match in detail most records currently used in conservation research.

The potential of paleoecological records in conservation biology has been highlighted several times, including their application to biodiversity maintenance, ecosystem naturalness, conservation evaluation, habitat alteration, changing disturbance regimes, and invasions [e.g., (*8–14*)]. Conservation of biodiversity in a changing climate (*15*) and the relevant temporal and spatial scales for ecological restoration (*16*) have also been considered to warrant a longer-term temporal perspective. Most of these studies are descriptive and provide little practical application. A number of recent applied paleoecological studies, however, have begun to provide direct management information for biodiversity conservation at local, regional, and global scales. These include recommendations relating to biological invasions, wildfires, climate change, and conservation management within thresholds of natural variability. The overriding message from these studies is that such temporal perspectives are essential for meaningful modeling, prediction, and development of conservation strategies in our rapidly changing Earth.

Biological Invasions

Biological invasions are of critical concern to conservation organizations worldwide, with a general perception that many invasives are responsible for widespread community change and even extinctions (*17*). At the Rio Earth Summit Convention on Biological Diversity in 1992, for example, binding signatories were made "to prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species" (*18*). However, biological invasions are complex. Some regions are more prone to invasion, certain species are more successful invaders than others, and sometimes it is even unclear whether a species is alien or native. The importance of the historical record in improving our ability to predict the outcome of

non-native introductions has been acknowledged [e.g., (*13*, *14*)], but several recent paleoecological studies provide direct guidelines for the identification and management of invasives.

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 area of evolutionary origin and/or whether human agency is responsible for its current distribution. In the absence of a temporal record to assess a species history, the distinction can often become blurred (*16*). For example, in a reexamination of the British flora, several discrepancies between published records were found, with the same species being classified as "alien" or "native" depending on personal interpretation (*19*) (Table 1). There is also the question of how far back one takes "human" activity in determining whether a species is native or alien. When using evidence of first occurrences of species based on paleoecological records to reassess "doubtful natives" in the British flora, Preston *et al.* (*19*) determined that at least 157 plant species had been introduced to Britain by humans, intentionally or unintentionally, from the start of the Neolithic period (about 4000 years ago) to 500 years ago, yet the terminology used for their classification according to different floras is highly variable (Table 1). Preston *et al.* proposed that such species should be classified separately as "archaeophytes." They acknowledged, however, that this causes problems with their conservation status because this "non-native" label excludes them from the British Red Data Book of threatened or near-extinct species, and automatically deems them to be of lower conservation value—even though some are in serious decline and have been part of the British flora for at least 500 years.

A similarly conflicting conservation message was reached in an applied paleoecological study on the origin of an invasive form of the common reed (*Phragmites australis*) in the marshes of the inland wetlands of Lake Superior, North America (*20*) (Fig. 1). Over recent decades, *P. australis* populations have expanded rapidly throughout the coastal wetlands of North America, creating substantial changes in community structure and composition. In this study, paleoecological and genetic analyses were used to determine when the common reed became established in this region and whether the source was from a native or non-native

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Table 1. Classification of 157 species of British plants that were probably introduced more than 500 years ago (archaeophytes) according to three published floras (*54–56*).

Published flora	Native	Doubtful native	Introduced	Probably introduced	Uncertain or untreated	Total
Dunn, 1905 (*54*)	31	—	103	—	23	157
Clapham et al., 1952 (*55*)	85	19	30	10	13	157
Stace, 1991 (*56*)	77	27	39	14	0	157

population. A 4000-year paleoecological record indicated that reeds were not part of the local flora until very recently (several decades), and that their recent expansion was probably linked to changes in water levels in the wetlands and human-induced changes to the landscape. The simple conservation message from this study is therefore to eradicate or control reed populations, because the expansion was recent and is likely to cause serious changes to the wetlands community. However, genetic data from these reed populations add another level of complexity because they indicate that the reeds are a native variety, raising the question of whether this is an exotic or natural invasion.

Fig. 1. Native (?) common reed (*Phragmites australis*) growing in Bark Bay Slough on Lake Superior, North America [photo: E. A. Lynch]; rattlesnake (*Crotalus mitchellii stephensi*) in the warm desert of western North America [photo: Blake L. Thompson]; wood grouse or western capercaillie (*Tetrao urogallus*) in the Cantabrian Mountains, northern Spain [photo: E. Menoni].

Oceanic islands are particularly liable to invasions, and it is often difficult to assess whether particular species are native or introduced. The invasive ornamental club moss *Selaginella kraussiana*, for example, is widely planted in the Neotropics, southern United States, Australasia, and western Europe. It is common on the Azores Islands in a range of habitats, but is it native there? Paleoecological records (*21*) (Fig. 2) clearly show that *S. kraussiana* had been present on Flores in the Azores for several thousand years before Portuguese discovery and Flemish settlement in the 15th century, thereby establishing beyond doubt its native status on Flores Island. Paleoecology again helped here to resolve a question in biodiversity conservation.

Another key question is whether invasive species are the triggering mechanism for ecosystem change, or merely opportunists taking advantage of environmental change caused by other biotic or abiotic factors? Also, are there particular factors that make a habitat more susceptible to invasion? A study of the colonization and spread of invasive shrubs in native shrublands and early successional forests in the northeastern United States, for example, found that prevalence of agricultural fields (historic and present-day) was the most influential factor affecting the colonization and spread of invasive shrubs (*22*). These native shrublands and early successional forests currently have high conservation status because of their diversity of terrestrial vertebrates. By considering the temporal dimension, the authors argue that it should be possible to identify those early successional habitats that may be especially prone to exotic invasion and ought to be of higher conservation

Fig. 2. Simplified pollen diagram from Lagoa Rasa, Flores Island, Azores, for the past 3000 years showing the percentage of tree, shrub, and herb pollen and of *Selaginella kraussiana* spores before and after human occupation of the island. [Modified from (*21*)]

priority. This study used only 40 years of temporal data, but studies incorporating longer temporal time scales have also illustrated persistent legacies of ancient land use that may influence the vulnerability of a site to invasion (*12*), including differences in soil pH, C, and N values. These imprints can last for decades to centuries. The identification of former land use by paleoecological records can thus be a tool for understanding and determining a habitat's vulnerability to invasion.

Introductions of non-native species often appear to fail a number of times before they eventually succeed; therefore, there is a lag between first colonization and population expansion of the invasive species (*23*). The reasons for resistance to invasion are complex and can have as much to do with environmental variables and extreme events as with demographic and biotic factors (*6, 7*). A study using paleoecological records has shown that consideration should be given to biological inertia (*24*), whereby a native community occurs where environmental conditions are no longer optimal but will remain in situ without any triggering mechanism (e.g., hurricanes, windthrow, etc.) to "remove" this resident population. Thus, the life history characteristics and biology of the resident species, and not the properties of the invading species, are responsible for invasion lags. This phenomenon is particularly apparent in forest ecosystems. In many current old-growth forests in western North America, paleoecological studies have shown that these stands were established during the cooler and moister climate of the Little Ice Age (about 650 to 150 years ago) and therefore reflect recruitment responses to former climate conditions (*25*). Such information about ecological legacies (*1*) is directly relevant to conservation because such forests may be at a critical threshold and may be particularly vulnerable to invasion after a disturbance event, either natural or human-induced.

Wildfires

Wildfires have been important in shaping the structure and function of fire-prone communities throughout Earth's history (*26*). Of particular concern to conservationists, however, are changes in the frequency, severity, and extent of burning from those perceived as the "norm" (*27*). What processes are driving this change (human or climate)? How will it affect the composition of plants and animals in ecosystems, in particular those already identified as vulnerable? And are there particular management techniques
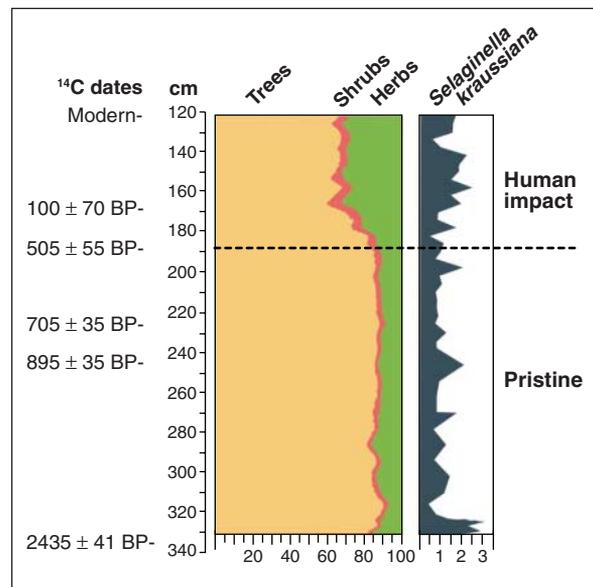
that can be implemented to alter fire regimes? Fundamental to these questions is establishing the natural variability of wildfires so that this can be used as a benchmark against which to evaluate contemporary conditions and future alternatives (28). Assessments based on short-term records (<50 years) can easily lead to misguided management plans (29).

Although climate change and human activities have long been acknowledged as drivers of wildfires, results from recent paleoecological studies show that these relationships are complex. For example, although it is not unreasonable to assume that an increase in aridity would result in more fires, several studies indicate otherwise. In the Alaskan boreal forest, fires occurred more frequently under wetter climatic conditions (30). A similar conclusion was reached in a paleoecological study of fire cycles in the Northern Great Plains grasslands of North America (31). Here, the highest charcoal flux occurred during past moist intervals when grass cover was extensive and fuel loads were high. Shifts in fuel quantity and quality can cause changes in fire regimes. Both studies show that there is a complex climate-fuel-fire relationship determining the variability of wildfires (32). Such studies (33) should be taken into account when predicting future ecosystem change within climate change conservation strategies.

Prehistoric and historic human-induced wildfires are often assumed to have caused changes in ecosystem structure and degradation, especially in tropical forests where natural fires are rare and tend to be limited in extent. Management plans to control such fires are usually implemented, however, without paleoecological evidence to confirm such an assumption. One such example is in the tropical dry forests of the southern Ratanakiri Province, northeastern Cambodia (34). Here, regional conservation policy is based on the premise that burning by humans has degraded the dense forests and resulted in the present open forest–savanna mosaic. However, a paleoecological study shows that present-day fire activity is now lower than it has been for the past 9300 years (Fig. 3). Rather, the forest-savanna shift is probably a consequence of monsoonal activity, and the high-frequency but low-intensity fires caused by humans may, in fact, conserve forest cover. In this case, the current conservation management plan is clearly at odds with evidence from the paleoecological record.

Interesting conclusions have also emerged from studies examining ecosystem composition in response to fire regimes. One of the main findings of the work on the North American grasslands described above, for example, is that fire is not necessarily a universal feature of this ecosystem but oscillates through time with climate (31). The impact of such variability in burning regimes through time on ecosystem composition can have conservation implications. This is well illustrated in a study on the long-term record of fire and open canopy in a forest in southern Sweden that contains an exceptionally large number of endangered species of beetle (35). Of the 105 beetle species recorded at this site living on or in rotting wood that are in the Swedish Red Data Book of threatened or near-extinct species, many are associated with open forest, forest fires, or structures created by fire. Yet a site-scale paleoecological study indicates that the forest is more closed today than at any time in the past 2500 years; although
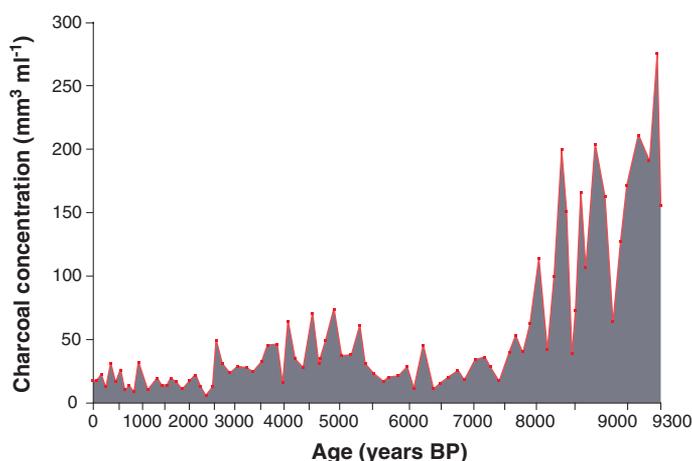

Fig. 3. Reconstructed fire regimes in northeastern Cambodian monsoonal forests over the past 9300 years, using microfossil charcoal concentration from a dated sedimentary sequence (34). The record indicates that present-day charcoal input is the lowest of the entire period. Conservation policies that suggest that human burning has increased and resulted in the open forest–savanna mosaic in this region are clearly misguided, as are management recommendations for fire suppression.

there had been a significant amount of burning in the past, there has been a large reduction in fires over the past 200 years. The authors concluded that openness of the site in the past as a consequence of burning is an important explanation for the high conservation value of the site today (35). To conserve the diverse beetle assemblage of this site, they suggested that open forest conditions needed to be restored and that prescribed burns would be the most appropriate way to achieve this.

Climate Variability

Most conservation organizations have developed climate change conservation strategies [as described in (36)] designed to conserve biodiversity in a changing climate. Two questions central to current conservation strategies arise. Where will biota move to in response to future climate change? Which species and regions are most at risk from future climate change? Underlying these questions are key management and planning issues—for example, ensuring that reserve boundaries allow for potential species-range shifts (37) and that the species and regions most at risk are identified and protected (38).

In the evaluation of predictive models to determine the biogeographic effects of climate change, several studies have used paleoecological records for backward prediction (hindcasting) to assess errors potentially inherent in species-envelope bioclimatic modeling (39). This involves running models for past intervals of time, using present-day species data but modeling the species' response to climate change against paleoclimatic data as opposed to present-day climatic data. The predicted distributions are then tested against the distribution of the species apparent in the fossil record for the time interval covered by the paleoclimatic data to assess model robustness (40). In a study of 23 extant mammal species in the United States (39), for example, an ecological niche model was run backward for the time interval of the Last Full Glacial (14,500 to 20,500 years before the present) and predicted distributions were compared to actual distribution records obtained from the FAUNMAP fossil database (41). The model was also run in reverse (i.e., using fossil data and paleoclimatic data to predict present distributions) and similar comparisons were made. Results indicated that for nine species the model was able to predict accurately the Pleistocene distributions from the present-day data, and vice versa. Not only did this confirm that the model was robust for these species, it also provided a test for the underlying assumption of these models that the species' ecological niche characteristics have remained constant through time. A similar pattern was recently found for several North American plant species (42). The remaining species, however, either had significant predictions only one way but not the other (nine species) or were not significant in either direction (five species).

The question of why some species' distributions cannot be accurately predicted by species-climate modeling can also be answered, at least for some species, from paleoecological studies. A study of the spread of *Picea abies* (spruce) and *Fagus sylvatica* (beech) over the past 4000 years in southern Scandinavia, for example, showed that at the local-stand scale the spread of *Picea* closely tracked the changing area of suitable regional climate, whereas the spread of *Fagus* was more directly linked to anthropogenic activities and disturbance by fire (43). Thus, caution may be needed in using the results of

predictive species-envelope models in conservation planning, because the distributions of some species today or in the past may be poorly predicted.

Bioclimatic models are particularly relevant to conservationists in determining and understanding the dynamics of the leading edge of species-range margins and the potential space that will be needed for future reserve boundaries (40). There is also a considerable literature on modeling to determine which species will go extinct [e.g., (38)]. However, there are few studies of the likely fate of rear-edge populations, that is, the source populations from which the leading-edge populations migrate (Fig. 4) (44). A key conservation objective should be the preservation of conditions necessary for speciation (45). Evidence from paleoecological and genetic records indicates that the maintenance of populations in these rear-edge regions could, in fact, be critical for conservation of long-term genetic diversity (44). Evidence also suggests that these regions tend to be where plants and animals were geographically and genetically isolated in refugia during the cold stages of the Pleistocene. In Europe, for example, refugial localities have been recognized in Iberia, the Balkans, and Italy and in mountain ranges such as the Carpathians (46–48).

With the use of a combination of paleoecological and genetic evidence, other such regions have been identified, and this information is feeding into conservation policy. For example, in a study on Eurasian populations of western capercaillie (grouse)—a keystone species of Palearctic boreal and high-altitude coniferous forests (49)—a combined genetic and temporal record enabled the identification of two regions that should be classified as ecologically significant units (ESUs) because of the genetic distinctiveness of the populations within them from the rest of Europe. The distinctiveness of the populations in these ESUs, located in the Pyrenees and Cantabrian Mountains (Fig. 1), is almost certainly related to their Pleistocene refugial isolation. Similar historically related genetic patterns have been identified in these two regions for a number of plants and animals, and this knowledge is now leading to international recognition of the conservation importance of these areas (49).

In the United States, a similar approach using a molecular and deep-time historical perspective as a primary mechanism to frame biodiversity reserves (50) has been applied to a number of groups of plants and animals. Distinctive patterns of genetic diversity related to geological events in deep time (Pliocene/Miocene) and to Pleistocene refugial isolation have been demonstrated, for example, in four rattlesnake species (Fig. 1; genus *Crotalus*) in the warm deserts of western North America (50). Here it is argued that an approach that seeks to understand the causation of genetic patterns would be more effective in encapsulating biodiversity than

current measures (based on the use of geological features as a surrogate for diversity) and that such studies should be routinely used in developing integrated regional conservation policies (50).

Determination of Thresholds Within Natural Variability

Variability through time is an inherent part of ecosystem behavior. It is thus essential to incorporate variability into management policies. To do this reliably in our rapidly changing world requires answers to several questions. What are the baseline or "reference" conditions before recent times? What is the range of natural variability? Under what conditions do negative impacts become apparent? How can thresholds be determined beyond which specific management plans should be implemented?

Gillson and Duffin (51) used paleoecological records from savannas in Kruger National Park, South Africa, to determine the natural variability of woody vegetation cover during the past 5000 years. They used this information to address whether woody cover has decreased below 80% of its "highest ever value"—a threshold set by ecosystem managers to define the upper and lower level of accepted variation in this ecosystem. Paleoecological results indicated that during the past 5000 years, the estimated woody vegetation cover had remained at about 20% of its "highest ever value," and therefore that management intervention in this part of the park is unnecessary at present.

Other examples where paleoecological records have been used to identify where natural thresholds have recently been exceeded include river ecosystems in Australia (52) and Colorado (53). The large deep billabongs in the middle reaches of the Murray River, Australia, for example, do not currently support submerged mac-

rophyte beds. Yet paleoecological analyses indicate that these were an important part of the ecosystem before the arrival of Europeans (52). In the Colorado delta ecosystem (53), paleoecological studies suggest that there has been a decline of up to 94% of shelly benthic macroinvertebrates over the past 75 years. This decline is probably associated with a reduction of fresh water and nutrients resulting from the diversion of the Colorado River by dams and irrigation projects. Both studies provide quantitative assessments of the relative health (4) of these river ecosystems and indicate thresholds that have been exceeded—information that is critical to their restoration and long-term conservation.

Conclusions

Conservation biology and nature management are primarily concerned with the present and increasingly with the future. Paleoecology primarily considers the past but can provide a historical perspective to the present (1). It can also contribute to key questions in conservation and management such as habitat naturalness, biological invasions, disturbance regimes, natural variability, and ecosystem health. With increasing amounts of paleoecological data of a high spatial and/or temporal resolution (4, 5), there is potential for synergy between conservation biology and paleoecology. There are, however, several research needs and challenges that need to be met before an effective synergy can fully develop. These include the following:

1) Paleoecological studies in biodiversity hotspots with a high density of species. At present there are few studies from these critical areas.

2) Improved taxonomic resolution of the fossils found, because improved resolution invariably enhances the biological value of fossil records (5, 21).
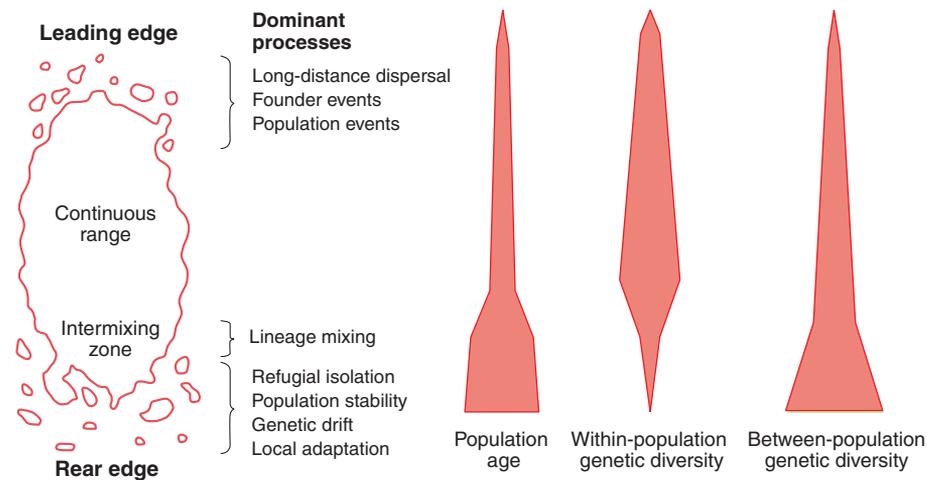

Fig. 4. Schematic representation of the leading and rear-edge populations in response to climate change (44). Paleoecological and genetic evidence suggests that the rear-edge populations may be extremely important in the conservation of long-term genetic diversity and that more attention must be given to modeling the impacts of future climate change on these populations and their protection.

3) Assessing terrestrial paleoecological data in terms of "ecosystem health" to provide an ecosystem's health history (*4*). Some taxa in paleoecological records are "indicators" of particular ecological conditions that can provide useful "symptoms" about the ecosystem's health. Paleolimnologists (*4*) have effectively applied the concept of ecosystem health to lakes in relation to critical loads of pollutants. The same concept could be usefully applied to forests, heathlands, grasslands, wetlands, tundra, and savannas.

4) Greater discussion and collaboration between paleoecologists and conservation biologists, so that the most pertinent and urgent research questions are addressed together and the most relevant paleoecological data are collected at the spatial and temporal scales of direct concern in conservation.

Paleoecology provides a historical perspective that can help put present and future conservation and management policies into context. The time is ripe for the two disciplines to work more closely together and to develop a common agenda for biodiversity conservation.

References and Notes

1. National Research Council, *The Geological Record of Ecological Dynamics: Understanding the Biotic Effects of Future Environmental Change* (National Academies Press, Washington, DC, 2005).
2. L. Graümlich, S. Sugita, L. B. Brubaker, V. M. Card, *Ecology* **86**, 1667 (2005).
3. K. J. Willis, L. Gillson, T. Brncic, B. Figueroa-Rangel, *Trends Ecol. Evol.* **20**, 107 (2005).
4. J. P. Smol, *Pollution of Lakes and Rivers—A Paleoenvironmental Approach* (Arnold, London, 2002).
5. H. J. B. Birks, *Grana* **44**, 1 (2005).
6. M. E. Lyford, S. T. Jackson, J. L. Betancourt, S. T. Gray, *Ecol. Monogr.* **73**, 567 (2003).
7. S. T. Gray, J. L. Betancourt, S. T. Jackson, R. G. Eddy, *Ecology* **87**, 1124 (2006).
8. H. J. B. Birks, *J. Veg. Sci.* **7**, 89 (1996).
9. P. B. Landres, P. Morgan, F. J. Swanson, *Ecol. Appl.* **9**, 1179 (1999).
10. T. W. Swetnam, C. D. Allen, J. L. Betancourt, *Ecol. Appl.* **9**, 1189 (1999).
11. L. Gillson, K. J. Willis, *Ecol. Lett.* **7**, 990 (2004).
12. D. R. Foster *et al.*, *Bioscience* **53**, 77 (2003).
13. G. M. MacDonald, *Adv. Ecol. Res.* **24**, 67 (1993).
14. S. T. Jackson, in *Assessment and Management of Plant Invasions*, J. O. Luken, J. W. Thieret, Eds. (Springer-Verlag, New York, 1997), p. 37.
15. L. Hannah *et al.*, *Conserv. Biol.* **16**, 264 (2002).
16. J. B. Calicott, *J. Biosci.* **27**, 409 (2002).
17. J. Gurevitch, D. K. Padilla, *Trends Ecol. Evol.* **19**, 470 (2004).
18. S. Henderson, T. E. Dawson, R. J. Whittaker, *Prog. Phys. Geogr.* **30**, 25 (2006).
19. C. D. Preston, D. A. Pearman, A. R. Hall, *Bot. J. Linn. Soc.* **145**, 257 (2004).
20. E. A. Lynch, K. Saltonsall, *Wetlands* **22**, 637 (2002).
21. J. F. N. Van Leeuwen *et al.*, *Neobiota* **6**, 27 (2005).
22. V. S. Johnson, J. A. Litvaitis, T. D. Lee, S. D. Frey, *For. Ecol. Manage.* **228**, 124 (2006).
23. D. F. Sax, J. H. Brown, *Glob. Ecol. Biogeogr.* **9**, 363 (2000).
24. B. Von Holle, H. R. Delcourt, D. Simberloff, *J. Veg. Sci.* **14**, 425 (2003).
25. C. I. Millar, W. B. Woolfendon, *Ecol. Appl.* **9**, 1207 (1999).
26. W. J. Bond, J. E. Keeley, *Trends Ecol. Evol.* **20**, 387 (2005).
27. D. McKenzie, Z. Gedalof, D. L. Peterson, P. Mote, *Conserv. Biol.* **18**, 890 (2004).
28. P. Z. Fulé, W. W. Covington, M. M. Moore, *Ecol. Appl.* **7**, 895 (1997).
29. C. Whitlock, *Nature* **432**, 28 (2004).
30. J. A. Lynch, J. L. Hollis, F. Sheng Hu, *J. Ecol.* **92**, 477 (2004).
31. K. J. Brown *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 8865 (2005).
32. J. S. Clark, P. D. Royall, C. Chumbley, *Ecology* **77**, 2148 (1996).
33. J. S. Clark, E. C. Grimm, J. Lynch, P. G. Mueller, *Ecology* **82**, 620 (2001).
34. A. L. Maxwell, *J. Biogeogr.* **31**, 225 (2004).
35. M. Lindbladh, M. Niklasson, S. G. Nilsson, *Biol. Conserv.* **114**, 231 (2003).
36. L. Hannah, G. F. Midgley, D. Millar, *Glob. Ecol. Biogeogr.* **11**, 485 (2002).
37. M. B. Araújo, M. Cabeza, W. Thuiller, L. Hannah, P. H. Williams, *Glob. Change Biol.* **10**, 1618 (2004).
38. C. D. Thomas *et al.*, *Nature* **427**, 145 (2004).
39. E. Martínez-Meyer, A. Townsend Peterson, W. W. Hargrove, *Glob. Ecol. Biogeogr.* **13**, 305 (2004).
40. M. B. Araújo, C. Rahbek, *Science* **313**, 1396 (2006).
41. FAUNMAP Working Group, *Illinois State Mus. Sci. Pap. 25* (1994).
42. E. Martinez-Meyer, A. Townsend Peterson, *J. Biogeogr.* **33**, 1779 (2006).
43. R. H. W. Bradshaw, M. Lindbladh, *Ecology* **86**, 1679 (2005).
44. A. Hampe, R. J. Petit, *Ecol. Lett.* **8**, 461 (2005).
45. D. Jablonski, *Nature* **427**, 589 (2004).
46. K. D. Bennett, P. C. Tzedakis, K. J. Willis, *J. Biogeogr.* **18**, 103 (1991).
47. P. C. Tzedakis, I. T. Lawson, M. R. Frogley, G. M. Hewitt, R. C. Preece, *Science* **297**, 2044 (2002).
48. K. J. Willis, J. C. McElwain, *The Evolution of Plants* (Oxford Univ. Press, Oxford, 2002).
49. O. Duriez *et al.*, *Conserv. Genet.*, in press.
50. M. E. Douglas, M. R. Douglas, G. W. Schuett, L. W. Porras, *Mol. Ecol.* **15**, 3353 (2006).
51. L. Gillson, K. I. Duffin, *Philos. Trans. R. Soc. London Ser. B*, in press.
52. M. A. Reid, R. W. Ogden, *River Res. Appl.* **22**, 167 (2006).
53. M. Kowalewski, G. E. A. Serrano, K. Flessa, G. A. Goodfriend, *Geology* **28**, 1059 (2000).
54. S. T. Dunn, *Alien Flora of Britain* (West Newman, London, 1905).
55. A. R. Clapham, T. G. Tutin, E. F. Warburg, *Flora of the British Isles* (Cambridge Univ. Press, Cambridge, 1952).
56. C. A. Stace, *New Flora of the British Isles* (Cambridge Univ. Press, Cambridge, 1991).
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