Insights from Paleoecology to Community Ecology

D.R. Foster, Peter K. Schoonmaker and S.T.A. Pickett

Ecologists and paleoecologists have become increasingly aware that the temporal and spatial scales of the two disciplines overlap considerably and provide complementary information. Pollen and macrofossil evidence from thousands of radiocarbon-dated sites worldwide indicate that species respond to environmental change independently, that communities are relatively open assemblages, and that instability and change characterize Quaternary environments and biotas. The extended temporal view provided by paleoecology also enables detection of the occurrence, intensity and changing frequency of periodic and unique events such as disturbances and environmental fluctuations. As these insights contribute to our understanding of a dynamic environment and biota, they may help to increase our ability to anticipate future changes in communities.

Ecologists have recently re-emphasized the importance of scale in understanding community organization and dynamics[1]. Paleoecology brings major insights to community theory as a result of its expanded temporal perspective and its ability to integrate a broad range of spatial perspectives (Fig. 1). Organisms experience environmental fluxes on scales that range from milliseconds to thousands of years and from 10^{-6} to 10^{14} m^2.

Ecologists generally study organisms on a time-scale of less than 100 years and often are limited to the duration of an experiment, field season, or grant. Many paleoecological studies cover a period of 1000–20 000 years with a temporal resolution of 10–200 years. Spatially, studies based on pollen analysis are sensitive to vegetational changes on a scale of hundreds of meters to hundreds of kilometers. The use of carefully selected basins and fine-resolution sampling of sediments in conjunction with other historical techniques can yield temporal and spatial resolution similar to that employed in community analysis (Box 1).

Community ecology can benefit from the expanded perspective provided by paleoecology because: (1) it enables the investigation of important ecological processes that are difficult to address in a short time-frame, (2) it provides many additional observations from which to derive ecological principles, (3) it clarifies community response over a range of temporal and spatial scales, (4) it compares the characteristics and dynamics of biological systems in periods before extensive human activity with periods of anthropogenic influence, and (5) it evaluates taxon response to environmental changes of magnitudes that are beyond historical values but within the range of projected global changes[6,7].

One fundamental message from paleoecology to community ecology is a better understanding of the nature of the 'community' and of the nonequilibrium conditions that organisms have been living with over the past two million years. Specifically, paleoecological studies provide information on the individualistic nature of species behavior, community organization, and community stability and change.

Species behavior

Species have responded individualistically to paleoenvironmental change in both time and space. For example, in pollen diagrams from the northeastern USA, individual tree taxa appear sequentially in the pollen record and rise to levels of abundance independently of other taxa[8]. In the face of species-specific disturbances, e.g. the chestnut blight and the apparent pathogenic attack on hemlock 4500 years ago, a broad group of other species increased to replace the affected species[9].

Spatially, the individualistic nature of species response is even more striking. Distribution maps of major tree taxa over the past 15 000 years in the northeastern United States show that genera that

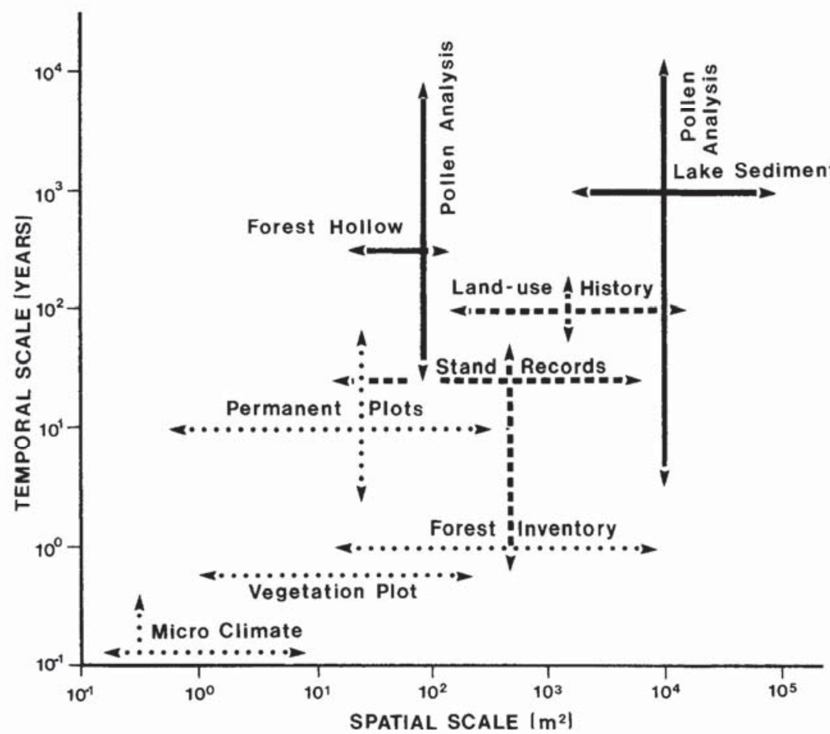

Fig. 1. The relationship of temporal and spatial scales in ecological and paleoecological studies. The source of the information is distinguished as field studies (dotted lines), historical data (dashed lines), and paleoecological studies (solid lines).

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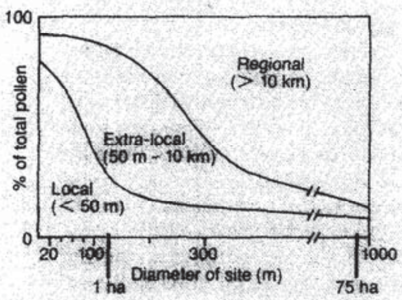
Box 1. Spatial and temporal resolution in paleoecology

Paleoecologists utilizing pollen analysis can control spatial and temporal resolution through the careful selection of study sites and sampling techniques. For example, basin size determines to a large degree the source area of pollen arriving at the site: the diagram (redrawn from Ref. 2) shows *one theoretical relationship* between the size of a lake site with no inflowing stream and the relative proportion of pollen originating from different areas around the site.



Moderate-sized lakes (10–100 ha) receive pollen mainly from within a 20–30 km radius, and basins with very small canopy openings (0.1–0.5 ha) still detect *some extra-local and regional pollen*[2,3]. Small forest hollows protected by a continuous canopy may receive more than half their pollen from the surrounding 50 m, with the remainder coming from more distant sources, depending on the individual dispersal characteristics of pollen taxa in the surrounding forest[4].

Fine sampling of sediments at intervals of 1 cm or less often yields a temporal resolution of 5–20 years per sample, and annual laminations in lake sediments provide yearly records of vegetation change[5].

broadly overlap in their current geographic distributions (e.g. *Picea*, *Pinus* and *Betula*) have undergone quite independent range movements and expansions in the past[10,11]. A similar individualistic response occurs across trophic levels. Beetles and other insects appear to migrate rapidly and independently of structural and compositional characteristics of the vegetation[12]; mammals move rapidly, perhaps primarily in response to structural rather than compositional changes in the vegetation; and different components of the flora (e.g. aquatic plants and upland species) migrate at different rates[13,14]. The results suggest that species have behaved individualistically due to inherent differences in responses to environmental complexes and due to differential dispersibility, growth and reproduction[15,16].

Community organization

The individualistic nature of species responses implies that communities are relatively open, and that the well-defined and apparently coherent assemblages of today are transient and have no long-term history in the Quaternary.

For decades paleoecologists have recognized that many fossil assemblages have no close modern analogs[17,18]. These 'disharmonious' groupings of fossils are accepted as representing faunal and plant communities that were shaped by unique past climatic, biotic and edaphic conditions[14,19]. At no time were the assemblages as unusual as during the Late Glacial period (14000–10000 years BP)[20]. In northern Minnesota this period is characterized by spruce (*Picea*) forest – but one that lacked *Pinus* and *Abies*, and included temperate genera such as *Fraxinus*, *Quercus* and *Ulmus*, and prairie genera such as *Artemesia* and *Ambrosia*. No such forest assemblage occurs today. Evidently the Late Glacial vegetation formed in response to a climate, characterized by mild winters and cool summers, for which there is no modern analog in North America[14,21].

Stability and change

An important consideration of community organization is the relative stability of community composition through time. Many early ecologists assumed a great continuity of plant assemblages through time – in part because of their belief in the evolutionary development of biotic associations, and in part because they underestimated the profound global environmental changes that had occurred[22]. There are some notable examples of long-term stability in the pollen record: for instance, two sites in northern Georgia show little variation in the amounts of spruce and jack pine (*Pinus banksiana*) abundance over a nearly 10000 year period ending in 13500 BP (Ref. 23). In other sites the vegetation also displays a certain inertia or resilience to change in the face of climate change or disturbance[24,25].

However, from 13500 years ago to the present, the history of biotic communities has been one of pervasive and continual change. Although the rate has varied, there is a remarkably widespread record of change in the composition of vegetation assemblages and underlying environmental factors. This has been best illustrated through comparative studies of pollen records from lake basins across the eastern United States[10] (Fig. 2). These records indicate essentially no periods of sustained homogeneity. Rapid and synchronous changes across most of the region at three discrete times (13500, 12300 and 10000 years BP) evidently signal major alterations in broad atmospheric circulation patterns, whereas continuous changes are a response to progressive modification not only of climate but also of soils, fire regimes and biotic interactions[8,10].

Even the archetype of sustained, homogeneous environmental conditions – the equatorial tropics – has undergone major transformations, as shown by the paleoecological record. For example, lowland areas of Guatemala were more xeric during the Late Wisconsin (11000–10000 years BP)[26], and dramatic altitudinal shifts in equatorial forests have been documented at all but the lowest elevations in South America, Africa and Southeast Asia[27]. This evidence reinforces the point that plant communities are highly dynamic entities and raises major doubts concerning the relationship between species diversity and long-term stability in tropical ecosystems.

Factors shaping community organization: climate, disturbance and man

The long temporal perspective of paleoecology clarifies the character and history of the factors that control community change, including climate, natural disturbance and human activities. A major conclusion derived from global climate models and biotic history during the Quaternary is that climate changes continuously on all temporal scales and that these climatic variations produced environments that are unknown in modern times[21,28].

A significant problem in the modern investigation of disturbance is that the low frequency or episodic occurrence of events may make it difficult to derive enough samples to yield generalizable results. Most ecologists increase their sample number by extending the spatial extent of their study area – thereby relying on a sometimes problematic substitution of space for time[29]. As shown by Clark[30] in an elegant study of fire and vegetation processes in northern Minnesota, such an approach may lead to highly erroneous results. By linking modern, historical and paleoecological data in a study with very fine resolution, Clark arrived at two major conclusions: (1) under changing climate and vegetation the disturbance regime of the area changed continuously during the past 2000 years; and (2) due to the longevity of the tree species, the disturbance (fire) regime of the modern landscape is not the same as the disturbance regime that gave rise to the modern vegetation pattern. The vegetation is not in equilibrium with the current disturbance regimes and therefore modern studies may provide little insight into the actual environmental variance that affects even a single generation of trees.

Clark and others make another relevant point, namely, that all current ecological studies of disturbance and other processes must contend with the unknown complication of widespread human alteration of ecosystems. In most regions of the world the vegetation has been directly and extensively altered by anthropogenic activities[31,32]. In all regions, indirect effects have occurred that are difficult to assess: for example fire suppression, introduction of pathogens, alteration of species abundance including herbivore numbers, and global alteration in atmospheric inputs[6]. In fact, a major contribution of paleoecology is its ability to address these changes by contrasting periods of low human activity to later periods of extensive change[33].

Paleoecology and applied ecology

The lessons from the historical perspective of system response to environmental change before and after extensive human impact have direct bearing on restoration ecology, management of natural areas and ecosystems, and prediction of system response to stress phenomena.

In the restoration of human-altered systems, paleoecology can define the pre-disruption conditions of the area or ecosystem and thereby provide a target condition to aim for. This information can concern state variables (e.g. the species composition or depth of an aquatic system) or processes

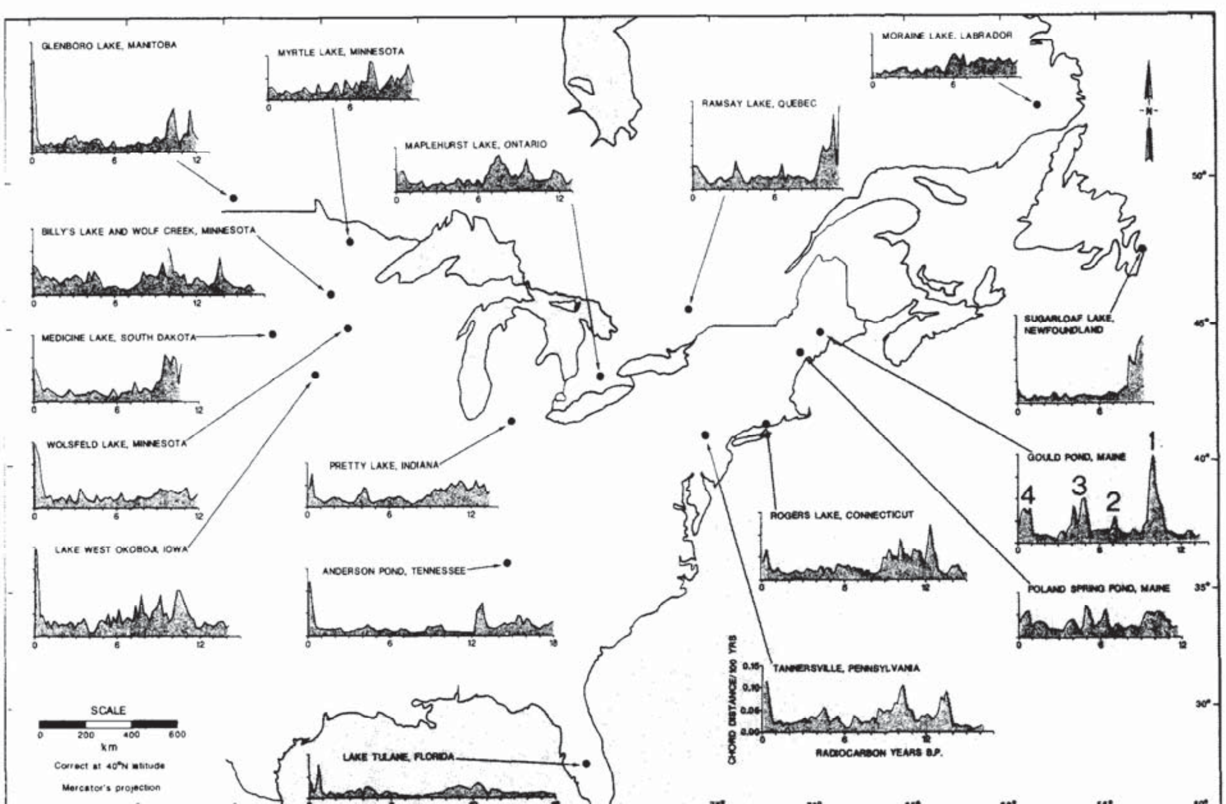


Fig. 2. The rate of vegetational change in continuous pollen-stratigraphic sequences at 17 sites in eastern North America. The rate is calculated by measuring the multivariate distances between adjacent pollen spectra interpolated to represent even time intervals. These multivariate distances per unit time provide a quantitative measure of the rate of palynological change, which is a proxy for the amount of vegetational change. A plot of the increments of change over long periods shows the rate of vegetational change[10]. Greater distances indicate greater changes in pollen spectra in 100 years. 'Chord distance/100 years' is a measure in ordination space along the first axis (using correspondence analysis) between successive pollen assemblages from a pollen diagram at one site. The pollen assemblages were taken from 100 year intervals, hence the 'distance/time' measurement. High rates of change at one site (Gould Pond, Maine) are associated with: (1) population expansion and decline of *Picea*, (2) expansion of *Tsuga*, (3) decline and recovery of *Tsuga* from pathogenic attack, and (4) decline of *Fagus* and *Tsuga*, expansion of *Picea* and modern cultural disturbance. *Redrawn from Ref. 6.*

(e.g. the changing forms and accumulation rates of organic carbon, phosphorus, nitrogen, sulfur and cations)[34]. Paleoecological perspectives have been most useful in aquatic systems, e.g. in mitigating eutrophication or assessing acidity changes[35,36], but may have direct relevance to wetland and upland situations.

Baseline and background information derived from paleoecological studies should be a standard part of land management programs. This is true whether the objective is to maintain or restore natural conditions or processes (e.g. in National Parks), to assess the desirability of acquiring land for preservation, or to retain cultural landscapes in their present conditions[37]. Largely on the basis of historical and paleoecological reconstructions, fire has been reintroduced into the management program of many National Parks in the United States[38]. There is also a growing interest in preserving landscapes that have arisen through extensive human activities, such as increasingly rare heathlands, which generally develop in coastal, sandy environments as a result of intensive deforestation, grazing, burning and mowing[39].

Finally, it has been estimated that the earth's environment will undergo global changes as a result of human activities, especially the alteration of atmospheric chemistry[40]. Although some of these projected changes are novel (e.g. inputs of organic pollutants or acidification of aquatic and terrestrial ecosystems), the magnitude, if not the rate, of projected climate changes driven by enhanced atmospheric CO_2 concentrations may be within the range of past, natural changes. The observations, and particularly the models developed and calibrated using paleoecological data (e.g. Refs 17 and 28), will provide a major source of information for predicting future changes[6].

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Conclusion

Ecologists recognize the importance of long-term studies to assess the variability inherent in biological systems and to investigate ecological phenomena that occur slowly or over long time-scales[41,42]. Although current long-term studies are directed towards understanding prospective changes, paleoecology provides a retrospective view of biotic and environmental history over temporal scales relevant to modern ecologists. This historical approach has contributed greatly to improving current concepts of community organization, evaluating climate dynamics and understanding disturbance processes. As a result, we may increase our ability to anticipate future changes in community composition and dynamics.

Acknowledgements

The development of this paper has been greatly improved by the comments of G. King, T. Sipe, G. Whitney and H.E. Wright, Jr. This work has been supported by National Science Foundation Grant BSR-8811764 to the Long Term Ecological Research program at the Harvard Forest and BSR-8906135 to SP and DF.

References

1 O'Neill, R.V., DeAngelis, D.L., Waide, J.B. and Allen, T.F.H. (1986) *A Hierarchical Concept of Ecosystems*, Princeton University Press

2 Jacobson, G.L. and Bradshaw, R. (1981) *Quat. Res.* 16, 80–96

3 Jackson, S.T. (1989) *Bull. Ecol. Soc. Am.* 70, 154

4 Calcote, R.R. and Davis, M.B. (1989) *Bull. Ecol. Soc. Am.* 70, 75

5 Berglund, B.E., ed. (1986) *Handbook of Holocene Palaeoecology and Palaeohydrology*, J. Wiley & Sons

6 Davis, M.B. (1988) in *Towards an Understanding of Global Change*, pp. 69–106, National Academy Press

7 Prentice, I.C. (1988) *Trends Ecol. Evol.* 3, 343–345

8 Davis, M.B. (1976) *Geosci. Man* 8, 13–26

9 Allison, T.D., Moeller, R.E. and Davis, M.B. (1986) *Ecology* 67, 1101–1105

10 Jacobson, G.L., Webb, T. and Grimm, E.C. (1987) in *The Geology of North America: North America and Adjacent Oceans during the Last Deglaciation* (Ruddiman, W. and Wright, H.E., eds), pp. 277–288, Geological Society of America

11 Webb, T. (1988) in *Vegetation History* (Huntley, B. and Webb, T., eds), pp. 385–414, Kluwer Academic Publishers

12 Coope, G.R. (1967) in *Quaternary Paleoecology* (Cushing, E.J and Wright, H.E., eds), pp. 359–380, Yale University Press

13 Iversen, J. (1960) *Dan. Geol. Unders.* 4, 1–32

14 Wright, H.E. (1984) *Quat. Sci. Rev.* 3, 91–131

15 Chapin, F.S. and Shaver, G.R. (1985) *Ecology* 66, 564–576

16 Davis, M.B. and Botkin, D. (1985) *Quat. Res.* 23, 327–340

17 Cushing, E.J. (1967) in *Quaternary Paleoecology* (Cushing, E.J. and Wright, H.E., eds), pp. 135–148, Yale University Press

18 Wright, H.E. (1964) *Ecology* 45, 439–447

19 Graham, R.W. (1986) in *Community Ecology* (Diamond, J. and Case, T.J., eds), pp. 300–313, Harper & Row

20 Overpeck, J.T., Webb, T. and Prentice, I.C. (1985) *Quat. Res.* 23, 87–108

21 Kutzbach, J.E. and Guetter, P.J. (1986) *J. Atmos. Sci.* 43, 1728–1759

22 Braun, E.L. (1947) *Ecol. Monogr.* 17, 213–219

23 Watts, W.A. (1970) *Ecology* 51, 17–33

24 Gorham, E. (1957) *Q. Rev. Biol.* 32, 145–166

25 Grimm, E.C. (1984) *Ecol. Monogr.* 54, 291–311

26 Binford, M.W. and Leyden, B. (1987) *Quat. Sci. Rev.* 6, 77–92

27 Walker, D. and Chen, Y. (1987) *Quat. Sci. Rev.* 6, 115–128

28 COHMAP Members (1988) *Science* 241, 1043–1052

29 Pickett, S.T.A. (1989) in *Long-term Studies in Ecology: Approaches and Alternatives* (Likens, G.E., ed.), pp. 109–135, Springer-Verlag

30 Clark, J. *Ecol. Monogr.* (in press)

31 Cronon, W. (1983) *Changes in the Land*, Hill & Wang Publishers

32 Birks, H.H., Birks, H.J.B., Kaland, P.E. and Moe, D., eds (1989) *The Cultural Landscape: Past, Present and Future*, Cambridge University Press

33 Behre, K.E., ed. (1986) *Anthropogenic Indicators in Pollen Diagrams*, A.A. Balkema

34 Binford, M., Deevey, E.S. and Crigman, T.L. (1983) *Annu. Rev. Ecol. Syst.* 14, 255–286

35 Engstrom, D.R. and Wright, H.E. (1984) in *Lake Sediments and Environmental History* (Haworth, E.Y. and Lund, W.G., eds), pp. 11–67, University of Minnesota Press

36 Davis, R.B. (1987) *Quat. Sci. Rev.* 6, 147–164

37 Patterson, W.A., Saunders, K.E. and Horton, L.J. (1983) *Fire Regimes of Cape Cod National Seashore*, US Department of Interior, National Park Service

38 Pyne, S.J. (1984) *Introduction to Wildland Fire*, Wiley-Interscience

39 Odgaard, B. (1989) in *The Cultural Landscape: Past, Present and Future* (Birks, H.H., Birks, H.J.B., Kaland, P.E. and Moe, D., eds), pp. 311–320, Cambridge University Press

40 Committee on Global Change (1988) *Towards an Understanding of Global Change*, National Academy Press

41 Callahan, J.T. (1984) *BioScience* 34, 363–367

42 Likens, G.E., ed. (1989) *Long-term Studies in Ecology: Approaches and Alternatives*, Springer-Verlag