Ecological and conservation insights from reconstructive studies of temperate old-growth forests

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Reconstructive studies that use paleoecological, dendroecological, historical and other approaches in order to interpret long-term ecosystem dynamics are increasingly generating valuable insights for ecologists, conservationists and foresters who are interested in the ecology, protection and management of old-growth forests. In most cases, the historical context provided by these studies reveals a long-term pattern of change that challenges assumptions about the pristine condition of these systems. Ironically, it is the history of environmental fluctuations, natural disturbance processes, and subtle, often indirect, human impacts that is revealed by reconstructive work that may shape the characteristic structure, composition and ecosystem processes of old-growth forests, and that will certainly provide the greatest challenge to their future conservation and management.

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Long studied by foresters and ecologists interested in natural ecosystem structure, composition and process, old-growth forests have attracted increasing investigation as a source of basic and applied information in conservation biology (Box 1). Considerable focus has centered on boreal, montane, temperate coniferous and tropical biomes, where relatively large areas of old-growth forest persist but which are threatened by current logging and development practices[1]. Attention has also been directed towards evaluating the status and role of old-growth and primary forest in the historically impacted temperate forest regions of eastern North America and northwestern Europe – the focus of this review[2,3]. As surveys have documented surprisingly large numbers of mostly small old-growth stands, for example, in the densely populated eastern USA, research efforts have turned to long-term studies and historical reconstruction in an effort to understand, to preserve and to restore these forests[4].

Retrospective studies that elucidate long-term patterns of ecosystem development have been conducted in a wide range of temperate old-growth forests and their surrounding landscapes[5,6]. By extending the temporal perspective from decades to millennia, forest reconstruction enables the assessment of infrequent events, long-term trends and gradual environmental change, which provide essential insights into modern conditions and fundamental ecological processes, and which also afford the background for informed management decisions. In this article, we review the motivations and techniques for temperate old-growth reconstructions and highlight the relevance of results to ecology and conservation (Box 2). One general theme that emerges is that retrospective studies bring new insights to the interpretation of ecological processes and consequently form an inherent part of ecological science and natural resource management.

Motivations for old-growth reconstructions

Old-growth reconstructions have been pursued as a source of basic and applied information. Due to the low frequency and intensity of human disturbance, old-growth ecosystems provide an unusual opportunity to investigate natural disturbance processes, forest dynamics, soil development, biogeochemical cycling, and species-site relationships[1,2]. The presence of old trees, accumulated woody debris, and undisturbed sediments and soil horizons, enable the development of long-term site histories and climate records using dendrochronological and paleoecological approaches[5,11]. The unusual physical structures and uncommon species and assemblages of organisms on old-growth sites also attract intensive ecological investigation[10,15,16].

Foresters have traditionally used old-growth studies to develop a natural or ecological system of forest management in which silvicultural practices are guided by native species biologies and natural ecosystem dynamics[17–19]. Consequently, and ironically, foresters were among the early activists responsible for studying and preserving well-known, old-growth forests across North America[17]. More recently, this perspective has promoted the prescription of managed disturbance regimes to preserve existing old-growth characteristics and to restore such features to second-growth forests[12,20]. Meanwhile, silviculturalists have used studies of natural disturbance processes to design ecologically sensitive and landscape-based harvesting systems[21,22].

Ecological insights

The most important insight from the retrospective study of old-growth forest is recognition that these ecosystems are often highly varied and dynamic in structure, composition and landscape pattern (Fig. 1). Early old-growth studies in temperate hardwood forests documented that many stands had undergone major structural or compositional reorganization following natural disturbance by fire, wind or pathogens[15,17,19]. Consequently, these old-growth areas often contain even-aged cohorts of seral species in inherently ephemeral communities that continue to change, even in the absence of ongoing disturbance. The perpetuation of these forest types requires infrequent disturbance and adequate land area to support both the necessary disturbance processes and an array of successional forest patches[17,22].

Elsewhere, forest dynamics are less dramatic[5]. However, the understory and overstory composition of many old-growth forests has shifted owing to long-term changes in the physical or biotic environment or disturbance regime (Fig. 2)[23,24]. Forests undisturbed by human impacts are sensitive indicators of changes in factors such as moisture

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Box 1. Old-growth forest – what is it?

Definitions for old-growth forest are as diverse as the motivations for studying them, but they often include criteria relating to the age, size and successional status of the overstory trees, the stability of the forest community, the degree of human disturbance, a minimum forest area, and other stand or site characteristics. In this article, we adopt the very broad definition given by Spies and Franklin[1] in a recent review of temperate coniferous old-growth forests, namely 'an ecosystem distinguished by old trees not necessarily (1) in a late successional condition and (2) free of evidence of human activity.' This broad definition is quite compatible with the conclusions of many retrospective studies that old-growth forests are often quite dynamic through time, and that direct and indirect human impacts have been pervasive even when not obvious in the modern landscape.

balance, browsing intensity or fire frequency, and over time, subtle shifts in regeneration may have major cumulative impacts on stand composition[20] (Fig. 3). Some old-growth forests, such as the Sylvania Wilderness Area in upper Michigan, USA have demonstrated remarkable broad-scale constancy in composition over hundreds to thousands of years (Box 3)[5,16]. Yet, even within many of these areas there are landscape-level changes in the size and distribution of forest patches, ongoing dynamics as a result of canopy gap formation, and pronounced changes in growth and patterns of mortality[4,25].

Box 2. Approaches to old-growth reconstruction

Techniques ranging from the analysis of tree-rings, site and stand structure to the investigation of fossils and historical sources are used to reconstruct forest and landscape dynamics. When combined, these approaches yield extensive information on forest development in the context of environmental change.

Dendroecology: analysis of annual tree rings yields age-structure and tree-growth chronologies that describe reproductive patterns and changing stand conditions related to disturbance, stand development or climatic variation[7,8]. Cross-dating the chronologies of dead and living trees makes it possible to extend stand histories beyond one generation of trees and a single disturbance event. Analysis of annual rings at regular intervals along the height of a tree yields stem-height reconstructions, a three-dimensional chronology of stand development, and insights on the interactions among neighboring individuals[9].

Structural information: the abundance, distribution, composition and orientation of downed wood provide information on forest dynamics over the previous 25–100 years, such as the occurrence of logging or fire, the direction and impact of windstorms, and changes in community characteristics[6]. The cumulative impact of windthrows creates soil mound-and-pit topography. Determination of the age and orientation of these features, either by aging the trees that are growing on them or by evaluating the process of soil development, may reveal the timing and spatial pattern of wind events many centuries ago[9]. Soil analyses may uncover fossils, including charcoal, preserved plant remains, and soil horizons resulting from natural disturbance and human activity.

Stand-level pollen records: stratigraphic analysis of pollen in soil organic layers and woodland hollows has been used extensively in the reconstruction of European forests but has only been used recently in the USA[5,10]. This approach relies on paleoecological method and theory supported by empirical evidence that the pollen composition of hollows and forest soil is strongly correlated with that of trees within 20 to 50 m. On acid or moist sites organic soil stratigraphies may cover hundreds of years; nearly complete post-glacial sequences may exist in some hollows[11].

Historical records: information on early forest and landscape conditions comes from such diverse historical sources as township or regional surveys, journals and legal documents, regional histories, and long-term permanent plots[11–13].

Computer modeling and geographical analysis: information on long-term forest dynamics can be included in computer models to test our understanding of the mechanisms behind historical trends, to predict future developments, and to explore management scenarios. Geographic Information Systems (GIS) may be used to analyze the relationships between historical and modern landscapes and forest composition, to describe landscape transitions including the loss of old growth, and to develop predictive models of old-growth distribution[14].

Integrative approach: the most balanced and comprehensive retrospective approach synthesizes results obtained using different techniques, each with its strengths and limitations. Historical information may be biased or incomplete, palynological data often lacks taxonomic resolution and over-emphasizes wind-pollinated taxa, and dendrochronological techniques are restricted to surviving or decay-resistant trees. Individually each technique is incomplete; however, together they yield remarkable detail on forest dynamics.

Retrospective studies provide one of the few opportunities for examining disturbance regimes and vegetation dynamics across major cultural boundaries (e.g. European settlement in North America; the industrial revolution). Thus the importance of broad-scale human impacts on major ecosystem attributes, and local human impacts on the remaining old-growth forests[11,20], can be assessed. Techniques such as pollen analysis of humus soils, comparison of early settlement land surveys with modern surveys, and dendroecological reconstructions, have shown that natural ecosystems are extremely sensitive to human impacts, including changes in the landscape, regional and even global context of stands. Several conclusions emerge from this work: (1) essentially all ecosystems studied exhibit some response to past human activity; (2) the rate of change in disturbance processes and associated ecosystem attributes is frequently greatest in the historical period; and (3) many present-day old-growth forests comprise anomalous or unique assemblages relative to their historical counterparts[11,23,26,27].

The low frequency of direct human impact to most old-growth forests enables the detection of rather subtle stresses, such as changes in disturbance regimes or shifts in herbivore populations[1,28]. The scale and effect of these changes are ecosystem and region specific depending, for example, on the prior role of natural disturbance processes, the nature of the anthropogenic modifications, and the species composition. At the broadest scale, tree-ring records of numerous sites indicate that there is a close responsiveness of growth, reproduction and competitive balance to changes in the moisture balance, which is controlled by temperature and precipitation patterns. Ongoing climate change, whether natural or anthropogenically controlled, will continue to generate changes in protected old-growth forests. At a regional scale, human impacts ranging from alteration of cloud and precipitation chemistry to the introduction or elimination of species have exerted a dramatic and irreversible impact on forest ecosystems, including most old-growth forests. For example, across higher elevations of temperate eastern Europe and northeastern North America, mortality in mixed conifer and hardwood forests is positively correlated with the atmospheric deposition of nitrogen and other compounds, which have been enhanced in concentration by human activity[29]. In addition, a succession of introduced pathogens, including chestnut blight, Dutch elm disease, beech bark disease and hemlock woolly adelgid have removed or reduced important temperate forest species in eastern North America[26]. A final, poorly quantified regional impact is the loss or change in abundance of animal species such as the passenger pigeon, moose or beaver that may have had an important impact on forest structure and regeneration.

At a sub-regional scale, human impacts have indirectly modified natural disturbance regimes and altered densities of major grazing animals. With the exception of the northern hardwood forest, most mixed forests have shown major changes in species composition, age structure and vertical forest structure as a consequence of changes in the fire regime[4,30]. In examining the largest virgin forest reserve in eastern North America, located at the temperate boreal forest ecotone in the Boundary Waters Canoe Area Wilderness (BWCAW) of northern Minnesota, USA, Frelich[12] concludes that the modern forest pattern and community characteristics are substantially different from those at the time of European settlement owing to the effective suppression of fires that were caused by lightning (Fig. 3). Intensive studies of eastern hardwood forests document that an initial post-settlement increase in fire frequency was often associated with regional logging, clearing and industrial activity, followed by a decline in fire frequency resulting from control measures introduced during the 20th century[23]. The result was a peak in the establishment and eventual dominance of fire-tolerant species such as oak and pine followed by a modern trend towards a decline in those species and increase in mesic and shade-tolerant hardwoods such as maple, birch, beech and hemlock (Fig. 2). The lack of congruence between overstory and understory in these stands is both an indicator of change as well as a major concern for conservation and natural resource managers[20]. Parallel differences in tree regeneration and overstory composition in other old-growth forests have arisen due to changes in the population density of major herbivores. The resulting impacts on age structure, vertical structure and overstory composition can persist for more than a century[24].

Finally, changes in the matrix of forest communities in the landscape encompassing old-growth stands may have important consequences. Many old-growth ecosystems are enmeshed in a landscape of second-growth and anthropogenic communities that are strikingly different in species composition and structure. Abrupt changes and discontinuities in forest structure may enhance the susceptibility of the tall, old forests to disturbance, especially wind. Meanwhile, the very different species composition in surrounding second-growth and human-dominated landscapes may alter the seed rain in old-growth forests or enable the incursion of second-growth or domesticated wildlife[8,14,22].

In all studies of changing composition, structure and disturbance regime, it is clear that the modifications are often quite subtle and would be difficult to detect without a very sensitive and long-term record of forest attributes. Often direct impacts, such as intensive cutting or clearance in past centuries, or grazing and selective cutting during this century, are quite imperceptible in the modern forest[11]. It is not surprising to learn that many remaining old-growth forests are not broadly indicative of pre-settlement forests or landscapes[12,26]. Rather, they tend to be located on inaccessible sites that may be unusual with respect to environmental conditions and species composition, structure and productivity. Thus, although highly instructive and valuable, the lessons learned from old-growth forests need to be applied cautiously to the broad landscape.

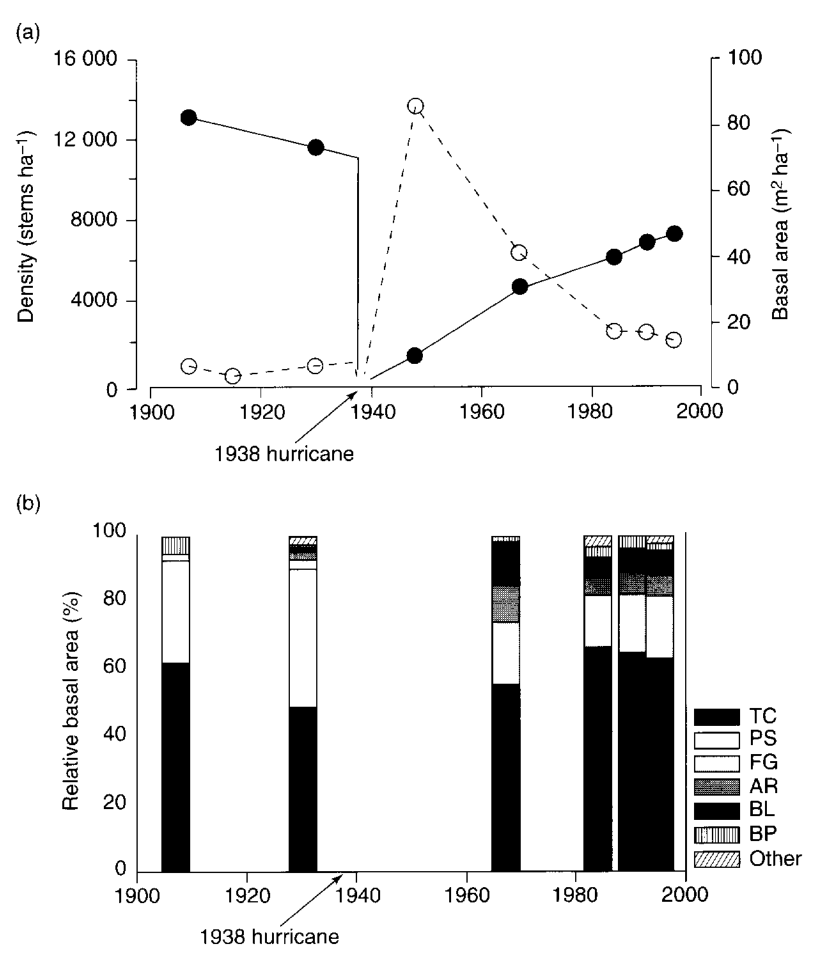


Fig. 1. A long-term study of the old-growth forest on the Harvard Pisgah tract in southern New Hampshire, USA discloses the types of major changes in (a) structure and (b) composition that may occur following catastrophic windthrow[13,15]. In (a) open circles represent density (stems per hectare) and filled circles represent basal area (m^2 per hectare). In the early 1900s, the 300-year-old forest was dominated by white pine (*Pinus strobus*; PS), which is typically 75–125 cm in diameter, and the slightly smaller hemlock (*Tsuga canadensis*; TC). The forest overstory was nearly completely windthrown by the hurricane of 1938; the ensuing vegetation includes hemlock and beech (*Fagus grandifolia*; FG) and an even-aged component of red maple (*Acer rubrum*; AR), birch (*Betula lenta*; BL, *B. papyrifera*; BP) and chestnut (*Castanea dentata*), but no white pine. This compositional shift has been long-lasting and will exert an enduring impact on the development and structure of the next old-growth forest on the site. The substantial differences in dominant species that may occur following disturbance is an important lesson from the studies of old-growth forest, and highlights the importance of preserving and studying intact as well as disturbed stands. *Modified from Ref. 13.*

Management implications

Insights from forest reconstructions reveal that strategies for the preservation, management and restoration of old-growth forests must be based on the acceptance and anticipation of change. Managers can use the results of reconstructive studies to understand the history and extent of change and to guide their decisions. Much of the preservationist sentiment guiding the protection of old-growth appears to be based on the assumption of stasis and the motivation to preserve 'original' conditions. However, recognition of the often significant impact that natural disturbance, environmental change and humans have had on all ecosystems forces an acceptance of past dynamics, an anticipation of future change, and acknowledgment of novel conditions[31]. Coupled with these perspectives comes the recognition that current composition and structure may provide an incomplete indication of past history. Although suites of species (e.g. 'Atlantic bryophytes'; 'ancient woodland indicators'; 'primary forest species'[10,32,33]) or specific structures (e.g. coarse woody debris; mounds and pits) often associated with old-growth forests may indicate a general absence of intense or recent human impact, their specific value in identifying natural conditions is dubious[27].

The maintenance of many natural ecosystems requires the protection not only of current old-growth areas, but also of naturally disturbed forests that represent future old-growth[22,34]. To ensure the continued presence of old growth, these areas must be maintained within a landscape that is adequate in size to allow for the continuing mosaic of disturbance and for the dispersal of organisms and processes among patches[12]. The protection and value of naturally disturbed old-growth patches is often a point of controversy among natural resource managers, conservationists and ecologists[34]. Many of the most intensively studied and revered old-growth forest areas have been recently disturbed in catastrophic ways (for example, in the USA: Tionesta Scenic Area in Pennsylvania, Cathedral Pines in Connecticut, Five Ponds Wilderness Area in New York's Adirondack Park). Pressure to salvage-log such areas to reduce fire hazard or to recoup economic loss is often intense and yet preservation of damaged old-growth ecosystems provides important ecological lessons and forms a critical element in old-growth research and preservation[4,15,16].

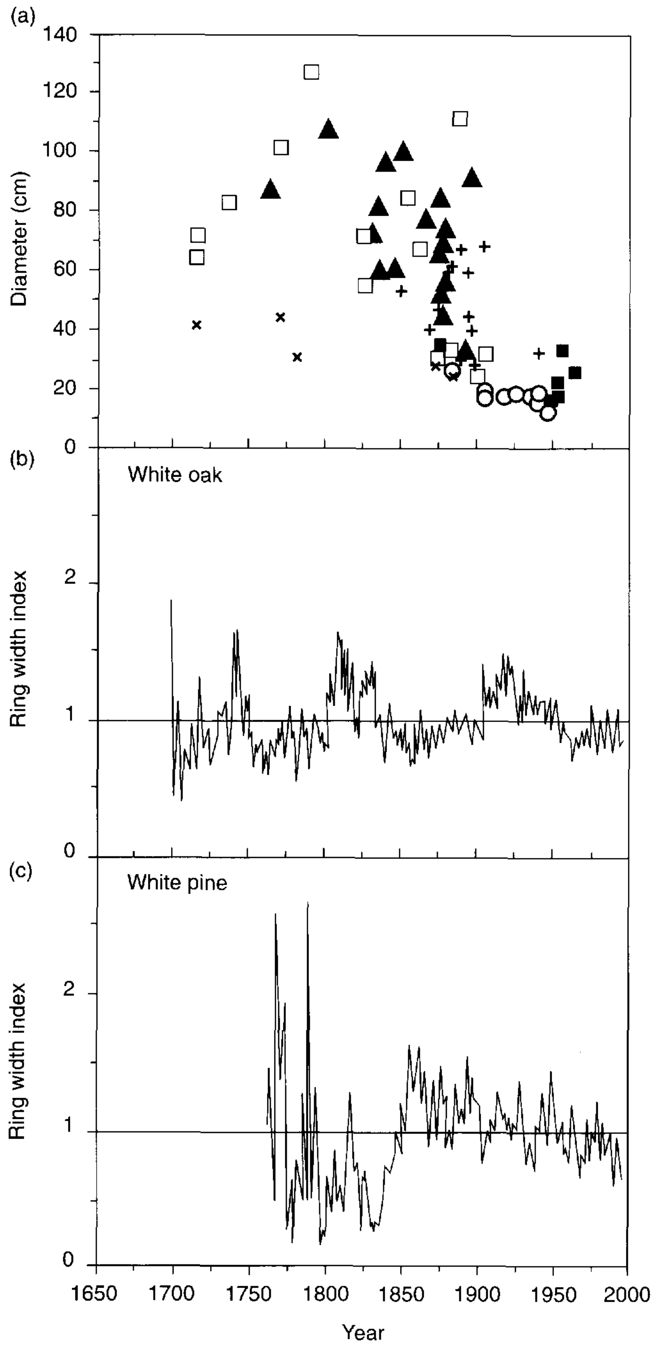


Fig. 2. Developmental history and successional dynamics derived from the coupling of species' 'current-day age versus diameter' relationships with (a) radial growth patterns of the oldest trees in an old-growth pine–oak stand[23]. Growth chronologies derived from the four oldest (b) white oak and (c) white pine trees indicate alternating periods of localized disturbance (seen as peaks in the ring-width index). Overstory species became established immediately following disturbances in the early and mid-1800s and in the early 1900s. Temporal changes in species establishment patterns included white oak from 1700–1900, white pine from 1830~1900, and red and black oak in the 1880s. Mixed-mesophytic species became established after 1900, a period of active fire suppression. White pine (*Pinus strobus*) (filled triangles); white oak (*Quercus alba*) (unfilled squares); red oak (*Q. rubra*) (pluses); black oak (*Q. velutina*) (pluses); red maple (*Acer rubrum*) (unfilled circles); sugar maple (*A. saccharum*) (filled squares); hemlock (*Tsuga canadensis*) (filled squares); beech (*Fagus grandifolia*) (filled squares); pignut hickory (*Carya glabra*) (crosses); black gum (*Nyssa sylvatica*) (crosses); and chestnut oak (*Q. prinus*) (crosses). *Modified from Ref. 23.*

Reconstructions do provide essential guidelines for managers. For managers interested in following a 'natural' management option (i.e. no intervention), reconstructions provide an assessment of baseline conditions and developmental history, which can help to anticipate ongoing dynamics and future conditions[16,19]. For managers intent on maintaining or developing structures and composition through the implementation of disturbance regimes, the long-term perspective can provide guidance on type, frequency and intensity of prescribed disturbance and the old-growth characteristics that form the management objective. Such is the approach taken in many fire-dependent ecosystems and it is a direction advocated by Frelich[12], who supports duplicating the natural pattern of tree-fall gaps in the restoration of old-growth northern hardwood forests from a matrix of second-growth stands. Finally, one ambitious option for managers is to work at the broad scale to design old-growth landscapes containing the mixture of communities, processes and structures that are characteristic of natural conditions[1,35]. Here, the collective historical and ecological insights can be used to evaluate current conditions and to identify desirable attributes and changes. In this, as in other management considerations, it is clear that retrospective insights provide guidelines and framework rather than absolute criteria on which to base decisions. Ultimately, conservation objectives must be recognized and selected as cultural values.

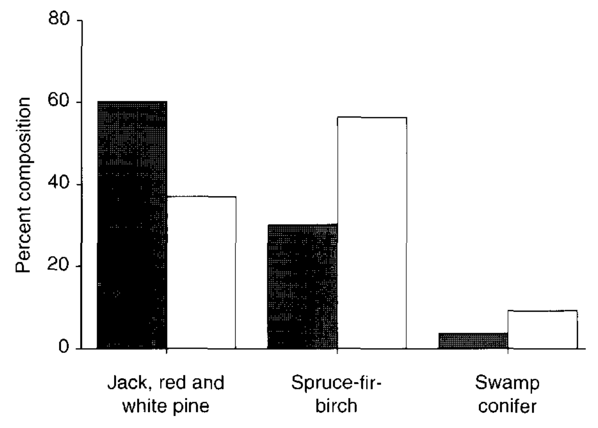
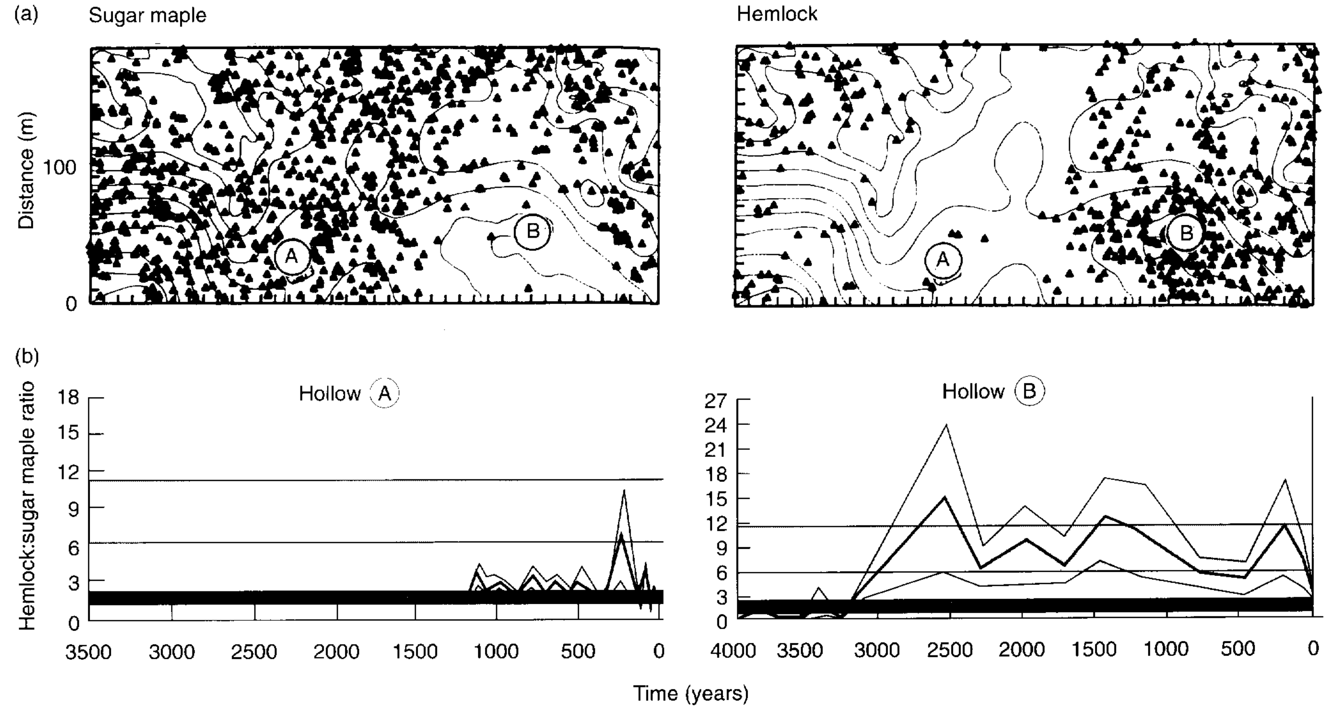


Fig. 3. General Land Office surveys conducted at the time of European settlement in northern Minnesota, USA provide an estimate of the natural forest of the Boundary Waters Canoe Area Wilderness[12]. The presettlement landscape pattern of vegetation (shaded bars) was maintained by periodic, broad-scale lightning fire. As a consequence of effective fire suppression during the 20th century, the fire-prone and maintained forest types have decreased, whereas late-successional, shade-tolerant and fire-sensitive species and forest types have increased. Although this region has not received extensive direct impact from human activity, the present-day landscape pattern and composition (unshaded bars) is changing dramatically as an indirect consequence of human decisions and actions. *Modified, with permission, from Ref. 12.*

Box 3. Long-term stability of old-growth forest mosaics at Sylvania Wilderness, Upper Michigan, USA



In contrast to the disturbance-mediated dynamics evident in other records of long-term forest development, the hemlock–northern hardwood forests of Sylvania Wilderness appear to have been dominated by autogenic successional processes since the climatically driven invasion of hemlock 3200 years ago[5]. Stand-level fossil pollen records suggest that discrete patches dominated by hemlock (*Tsuga canadensis*) and sugar maple (*Acer saccharum*) that established during this period have been maintained ever since. The determination that systematic associations exist between overstory trees and conspecific understory trees led to the development of a Markov simulation model, which illustrated that this mechanism is sufficient for the creation of such patches and their maintenance over long time-periods[16].

The panels in part (a) of the figure show maps of canopy sugar maple and hemlock stems for a 7.2 ha area of Sylvania Wilderness. These illustrate the discrete patchiness of the forest and the sites of the pollen records described below (A and B). The compositional mosaic of the forest does not seem to depend upon patchy disturbances or patchy distributions of physical features in the environment[16].

The panels in part (b) of the figure show ratios of percentages of hemlock pollen to sugar maple pollen (95% confidence intervals) plotted against time (1200 and 4000 years), from two small forest hollows within the plot. The ranges that are characteristic of hemlock stands (6–11; light shading) and of hardwood stands (1–2; dark shading) were determined from ratios of modern pollen assemblages and are indicated here by shading. The long-term compositional constancy of these patches is remarkable, especially given the proximity of the two sites[5].

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Microsatellites, from molecules to populations and back

Philippe Jarne and Pierre J.L. Lagoda

Population genetics studies using microsatellites, and data on their molecular dynamics, are on the increase. But, so far, no consensus has emerged on which mutation model should be used, though this is of paramount importance for analysis of population genetic structure. However, this is not surprising given the variety of microsatellite molecular motifs. Null alleles may be disturbing for population studies, even though their presence can be detected through careful population analyses, while homoplasy seems of little concern, at least over short evolutionary scales. Interspecific studies show that microsatellites are poor markers for phylogenetic inference. However, these studies are fuelling discussions on directional mutation and the role of selection and recombination in their evolution. Nonetheless, it remains true that microsatellites may be considered as good, neutral mendelian markers.

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History sometimes takes ironical twists, and the history of science is no exception. Microsatellites have been detected in eukaryote genomes for over 15 years, though they were regarded as sequences of no particular interest. With the rise of PCR, it was realized in the late 1980s that microsatellites may be the most powerful mendelian markers ever found (see Boxes 1 and 2). They have since been widely studied in conjunction with some genetic diseases. They have also been used in mapping programmes, and by population biologists, for kinship investigations and for more classical studies of population genetic structure[1–4].

Another interesting trait of microsatellites is that we can relatively easily gain information on their molecular structure, and on their mutation rate as well. This has not escaped the attention of population geneticists, and information is increasing. Also, recent work[3,5–10] at the population level may shed light on the molecular forces acting on microsatellites. This switching between the molecular and population levels is proving extremely fruitful.

The structure and distribution of microsatellites

Where does the wealth of information come from?

In organisms for which genomic mapping or sequencing has been undertaken (e.g. humans, crops), microsatellites may be characterized by scanning genomic databases. Alternatively, the only access to microsatellites for organisms that are depauperate in sequence information is to characterize them directly, through the laborious phases of cloning, detection of microsatellites and sequencing, in order to determine flanking sequences that can then be used for defining locus-specific PCR primers[1]. An interesting spin-off of both procedures for population biologists are data on the types and families of the repeat sites (Box 3), their flanking regions, their distribution and association, as well as estimates of the density of microsatellites. However, there are some pitfalls (Box 4). In population studies, allele size of microsatellites may be known with an accuracy of one base pair, and alleles are subsequently characterized by their number of repeats at the locus analyzed (Box 2). They can be analyzed further through sequencing, although this is not always possible owing to lack of time and money. From this viewpoint, the use of microsatellites is more informative than allozyme polymorphism and less informative than sequence mutation analysis.

What do molecular approaches tell us?

General information on the most widely used types (di-, tri- and tetranucleotides) of microsatellites are given in Box 3. The frequent association in the same cloned insert between different types indicates a clustering of microsatellites[11].

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