

Human impacts on genetic diversity in forest ecosystems

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Ledig, F. T. 1992. Human impacts on genetic diversity in forest ecosystems. – *Oikos* 63: 87–109.

Humans have converted forest to agricultural and urban uses, exploited species, fragmented wildlands, changed the demographic structure of forests, altered habitat, degraded the environment with atmospheric and soil pollutants, introduced exotic pests and competitors, and domesticated favored species. None of these activities is new; perhaps with the exception of atmospheric pollution, they date back to prehistory. All have impacted genetic diversity (i.e., species diversity and genetic diversity within species) by their influence on the evolutionary processes of extinction, selection, drift, gene flow, and mutation, sometimes increasing diversity, as in the case of domestication, but often reducing it. Even in the absence of changes in diversity, mating systems were altered, changing the genetic structure of populations. Demographic changes (i.e., conversion of old-growth to younger, even-aged stands) influenced selection by increasing the incidence of disease. Introduction of exotic diseases, insects, mammalian herbivores, and competing vegetation has had the best-documented effects on genetic diversity, reducing both species diversity and intraspecific diversity. Deforestation has operated on a vast scale to reduce diversity by direct elimination of locally-adapted populations. Atmospheric pollution and global warming will be a major threat in the near future, particularly because forests are fragmented and migration is impeded. Past impacts can be estimated with reference to expert knowledge, but hard data are often lacking. Baselines are needed to quantify future impacts and provide an early warning of problems. Genetic inventories of indicator species can provide the baselines against which to measure changes in diversity.

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Is there a thing of which it is said, "See, this is new?"
Ecclesiastes 1:10

Human impacts on forests date back to antiquity and even to prehistory (Behre 1988). Human societies have displaced and exploited forests for millennia. Not even the stresses caused by atmospheric pollutants are new, although their effects are more widespread than ever before. However, documenting human impacts on genetic diversity in forest trees and other wildland plants is a difficult matter; little quantitative data exist. Most evidence is anecdotal, and only in the extreme case of extinction can we unequivocally demonstrate a reduction in diversity. In most cases we are forced to speculate, to guess at what the ecological stage was like for

the evolutionary play. Nevertheless, experience can lead us to intelligent guesses.

In this paper, the term "genetic diversity" will be used to include the entire continuum in gene diversity and genetic variance from the intraspecific levels (within populations and among populations) to the interspecific level. Changes in gene frequencies and genotype frequencies are examples of changes in diversity, and so are alterations in the species composition of forest stands. Furthermore, changes in species composition may change the competitive environment, modifying the selection regime and resulting in intraspecific changes in gene frequencies.

There are several ways to organize a survey of human impacts on the genetic diversity of forests. One is by the

Accepted 1 July 1991

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effect: e.g., has diversity been increased or decreased, have populations diverged or converged, etc. Another is by process: e.g., what is the evidence for human impacts on evolutionary processes such as selection, migration, drift, recombination, hybridization, and mutation. Neither of these suit my purpose, and I have chosen to organize the paper by activities that influence genetic diversity and the structure of diversity: i.e., deforestation, exploitation, habitat fragmentation, alteration of habitat, demographic change, movement of organisms, pollution, and domestication. These categories overlap to a great degree and in any particular case several influences may be invoked at once. Another layer of organization is superimposed on these topics: some of these influences are historic, almost all are occurring now, and some, like global warming, are projected for the future. In general, I have followed a sequence from those for which we have virtually no data on the genetic impacts to those for which we can make assured inferences.

Impacts on the forests are increasing as a result of the fantastic growth of human populations and the global spread of pollutants. In a few cases of anthropogenic pollutants, changes in gene frequency have been documented. Changes under domestication are the easiest to quantify, as might be expected, and many tree species are now in a stage of semi-domestication. Some of the best-documented impacts have been the result of human-mediated biological invasions. Introduced diseases have resulted in selective changes within populations and widespread planting of exotics has resulted in hybridization of previously isolated congeners. Even worse, introduced diseases and predators have attacked native species and competitors have displaced them, resulting in extinction. The local or global extirpation of species has changed community structure. The impacts of deforestation, exploitation, and fragmentation on genetic diversity are much more difficult to quantify. However, every human action, every aspect of forest management, has ecological and genetic effects, and we must try to determine what those effects are if we are to maintain healthy ecosystems.

Recognizing the paucity of evidence for changes in genetic diversity is important in itself – it is a cry for new programs to develop the baseline data against which we can monitor future changes. Research is particularly needed to document changes in allele frequency under various types of forest management; very few studies exist on the impact of harvest methods on genetic diversity. We must also consider impacts on the mating system and how this affects genotype frequencies. Another area that is in need of solid, statistical data is the impact of deforestation on the loss of local populations, and its meaning in terms of genetic losses. Novel approaches may be needed to measure the changes resulting from widespread land clearing for agriculture and subsequent recolonization from remnants of the original vegetation. Genetic surveys and genetic monitoring

should be institutionalized to track the impacts of human-driven environmental changes, so that corrective action will be possible.

Deforestation

Day by day they forced the forests higher up the mountains, making them give way to fields and farmlands.

Lucretius (fl. 1st century BC)

Forest clearing, primarily for agriculture, has always accompanied cultural development. Deforestation invariably began at low elevations and moved upslope, perhaps sparing the highest elevations and most rugged terrain. In some cases, forest lands were cropped for short periods until yields began to decline, and then allowed to revert to forest. Such was the case for traditional swingle systems in the tropics. Agricultural lands also reverted to forest in temperate regions, such as the eastern United States; e.g., only 27% of Connecticut was forested in 1880, but this had increased to 66% by 1970 as a result of agricultural abandonment (Carroll 1973), and in central New York, forested area increased from 8% in 1930 to 40% in 1980 (Nyland et al. 1986). As long as a nearby seed source remained to facilitate natural regeneration, the impact on genetic diversity was often not noticed. Nevertheless, the cycle of deforestation and subsequent regeneration from forest remnants was not totally without effects, which are discussed below and in sections on forest fragmentation, demographic change, and habitat alteration.

In many cases, forests were unable to re-establish because farming and overgrazing by domesticated animals led to erosion, and timber harvest and goats or cattle eliminated all potential seed sources that could have recolonized the site. Deforestation was permanent in many dryer areas, such as southern Europe and the Middle East. Historical records refer to the existence of forests in the Greek and Roman empires where none now occur (Hughes 1982). Climatic change, erosion, agricultural decline, and the collapse of societies followed removal of the forest. Ancient ruins mark the sites.

No part of the world – Europe, Asia, North or South America, or Africa – has been spared. For example, the story of ancient Greece and Rome has been repeated more recently in Scotland (Carlisle 1977), Mexico (Jasso 1970), Japan (Totman 1989), Madagascar (Green and Sussman 1990), Ethiopia (Pohjonen and Pukkala 1990), and elsewhere. Scots pine (*Pinus sylvestris* L.) forests mentioned in historical texts have disappeared since 1600, victims of timber harvest followed by grazing and burning to promote grazing (Carlisle 1977). Conifer and hardwood forests covered 40% of Ethiopia around 1900; by 1985 only 2.7% of the native forest



Fig. 1. Deforestation and loss of local populations occurred even when forests were not converted to agriculture. On many sites in California, chaparral replaced low-elevation ponderosa pines after destructive logging in the early twentieth century.

remained, on the most remote uplands (Pohjonen and Pukkala 1990). Famine continually stalks the country.

Deforestation is proceeding at a more rapid rate in the tropics than in the temperate zones, a general increase from north to south. The British Columbia Ministry of Forests' Strategic Studies Branch (1984) estimated that the province's loss of productive forest to roads, railways, residences, and agriculture will be less than 0.04% in the 25-yr period that began in 1979. In California, losses in the 25-yr period from 1952 to 1977 was 1.2% (Bolsinger 1980). In Mexico, deforestation from 1981 through 1984 was 5.2% (Office of Technology Assessment 1984), an order of magnitude greater than the loss in California and several orders of magnitude greater than the loss in British Columbia. But in the tropics, forest destruction is even greater; in one exceptionally bad year, 20 million ha of Brazil's Amazonian forest was burned (Setzer and Pereira 1991), an area equal to the entire productive forest area of California. Most of the destruction in Latin America is a result of land-clearing for cattle ranching (Leonard 1987).

Forests have also been razed in war, to deprive an enemy of strategic materials or cover. This pattern is also ancient and repetitive. Demosthenes set fire to the forest on Sphacteria to harry the Spartans during the Peloponnesian Wars in 435 B.C. (Thucydides), and the United States sprayed herbicides in Vietnam to defoliate 1.1 million ha (about 10% of the country) of dense inland forest during the Second Indochina War (Westing 1984). Although a single spray resulted in only a modest kill of 10% of the forest dominants, 34% of the area was sprayed at least twice, and nutrient dumping, fire, and erosion exacerbated the effects. Much of the forest will require an estimated 8 to 9 decades to return to something like pre-war conditions, and even then, forest composition may be altered. Of even greater impact, 41% (124000 ha) of all the true mangrove (ge-

nus *Rhizophora* L.) type was sprayed, and resulted in total mortality of the herbicide-sensitive mangrove and the taxonomically diverse species that made up the mangrove community. Loss of the mangrove forest will lead to a 3 to 4% loss of indigenous species.

The impact of deforestation on genetic diversity is difficult to document. In most cases, baseline data are not available, so estimates of change are merely guesses. What is obvious is that cities and agricultural fields have permanently displaced forest over most of the world, but often we do not even know the extent of the original forests. In the worst cases, maquis now grows where forests once stood in the Mediterranean (Hughes 1982), the Caledonian pine forests were converted to heathland in Scotland (Carlisle 1977), and chaparral replaced ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) at lower elevations in the western United States (Shoup 1981).

Extinction, the most extreme reduction in genetic diversity, can be one consequence of deforestation. Endemism is generally higher in the tropics than in temperate climates, so deforestation such as that in Amazonia could have major impacts on species' survival (Gentry 1986). Conversion of lowland rainforests for subsistence agriculture in Madagascar poses an especial threat because Madagascar has 8000 endemic species of flowering plants (Freen and Succman 1990).

Less obvious is the reduction in within-species genetic diversity when local populations are eliminated. Jasso (1970) worried about the loss of gene pools in Mexican pines because the most rapidly growing, low-elevation forests were replaced by potato and maize fields; however, genetic losses are not documented. In Caledonian Scots pine, levels of genetic diversity are as high as those measured on the continent, even though climatic change, exploitation, grazing, and burning have restricted the species to less than 11000 ha in Scotland, divided among isolated pockets containing as few as 29 trees (Kinloch et al. 1986). Most tree species exhibit clinal patterns of variation correlated with environmental gradients. If one end of the cline was eliminated, it would reduce the range of adaptive genetic variance. If an interior segment of the cline was eliminated, its genotypes might never be regenerated in any realistic time frame, even though no alleles were lost (Anderson 1949).

One way of estimating the loss of genetic diversity resulting from deforestation is to extrapolate from our knowledge of the present genetic structure of forest trees. Ponderosa pine will serve as an example. Ponderosa pine varies in significant ways over the altitudinal gradient in the Sierra Nevada of California, based on comparisons in common environments (Conkle 1973). If the genetic variance among populations in height at 29 yr is divided by the length of the gradient, 2% of the total genetic variation is associated with every 100 m change in elevation. The low-elevation limit of ponderosa pine is now about 600 m, but it grew at 40 m only

150 yr ago. In the past, destructive logging practices without regard for forest regeneration resulted in invasion by chaparral (Fig. 1) on many low elevation sites (Shoup 1981): "Brush vegetation ... often coincides quite clearly with areas which were clearcut in the early decades of the 20th century". Extrapolation suggests that, locally, 6% of the original genetic diversity in height growth has been lost in areas where low-elevation ponderosa pine were eliminated. Because the pattern of variation is unique to the species and characteristic under consideration, diameter growth, bud-break phenology, and other meristic traits might result in different estimates. With present knowledge, it is not possible to determine whether unique alleles were lost or whether populations characteristic of the original, low-elevation populations can ever re-evolve in a practical time frame.

Exploitation

The timber of the country grows straight and tall ...
William Wood (1634)

In this section I consider humans in their role as predator. Most predators concentrate on the weakest individuals, the young, old, or sick, whether the predator-prey system is wolves and moose or bark beetles and ponderosa pine. However, technology has allowed human predators to be more catholic in their choice of prey. Prehistoric hunters are credited by some with the extinction of megafauna in North America because they removed animals in their reproductive prime (Martin 1967). More recently the elephant seal and the bison were nearly eliminated in North America. Currently, exploitation threatens the existence of elephants and rhinoceroses in Africa.

I know no examples of the global extinction of exploited forest trees, but local extirpation has occurred. Pitch pine (*Pinus rigida* Mill.), for example, was eliminated from Nantucket and other islands off the coast of the northeastern United States because of the need for fuelwood in the eighteenth century (Lewis 1924, Dunwiddie 1990). However, pitch pine may not have been completely eliminated if the islands had not also been overgrazed with sheep. We do not know how much intraspecific genetic diversity was lost, but since pitch pine has differentiated along environmental gradients (Kuser and Ledig 1987), it will probably take considerable time to regenerate the original structure.

Many tropical timbers have become exceedingly scarce because of overharvest and thus face economic extinction (Oldfield 1988), but few are in danger of biological extinction. Those threatened as a result of exploitation are mostly island endemics: only one tree of Mauritius ebony (*Diospyros hemiteles* L.) remains and both St. Helena ebony (*Trochetiopsis melanoxylon*)

and St. Helena redwood (*Trochetiopsis erythroxylon* L.f.) are endangered. In a survey of exploited woody legumes (National Research Council 1979), the only species threatened with biological extinction was afro-mosia (*Pericopsis elata* [Harms] van Meeuwen). However, many tropical species are overexploited and have been completely logged out of major parts of their native ranges; e.g., ceiba (*Ceiba pentandra* [L.] Gaertn.), which was overharvested for plywood manufacture along the Amazon of Peru (Gentry and Vasquez 1988). It is not clear whether ceiba will reproduce itself and achieve its former importance in the community or not, but ceiba of non-commercial size remain, and genetic diversity is probably not irreparably damaged. Teak (*Tectona grandis* L.f.) is another species that has been overexploited, which accounts in part for an 80% decrease in teak production in Thailand between 1973 and 1985 (Gajasen and Jordan 1990).

Predation can have a genetic impact on populations if it is selective, and sometimes human exploitation has degraded the resource for the very uses for which it was exploited in the first place. The best examples come from fisheries and wildlife. Opening and closing dates for the fishing season in Alaska were established by 1928 to regulate harvest of the Pacific salmon runs. The opening date was so early that it provided no protection to the first part of the run, but early closure protected the latter part. By 1945 it was apparent that the runs were appearing later each year, a logical outcome of predation on early migrants, and catches were declining (Vaughan 1947).

In timber harvest, the historical pattern in North American temperate forests was to remove species of high value in the first wave of exploitation. Later generations removed increasingly lower-valued species. This pattern is currently being repeated in tropical forests. However, timber harvest scenarios may be interpreted as ranging from selection against the most valuable forms to selection for the poorest. For example, after colonization of the northwestern United States, intensive selection removed the truly exceptional, largest, straightest, white pine (*Pinus strobus* L.) for masts. William and Mary reserved all such trees within 3 miles of water for the English crown in 1691 (Kawashima and Tone 1983). At the other end of the spectrum was "high-grading" during the nineteenth and earliest twentieth centuries, in which forests were clear-cut, leaving isolated, commercially-valueless stems – small, crooked, diseased, or rotten. Seedlings and saplings were largely destroyed by destructive logging practices, and the defective trees were left to seed and regenerate the population.

The changes in genetic diversity as a result of selective logging have not been quantified. Some authorities have felt that "creaming" can lead to genetic degradation (e.g., Roche and Dourojeanni 1984), and Styles (1972) claimed that mahogany (*Swietenia mahogani* [L.] Jacq.) had been reduced to a multi-stemmed shrub in

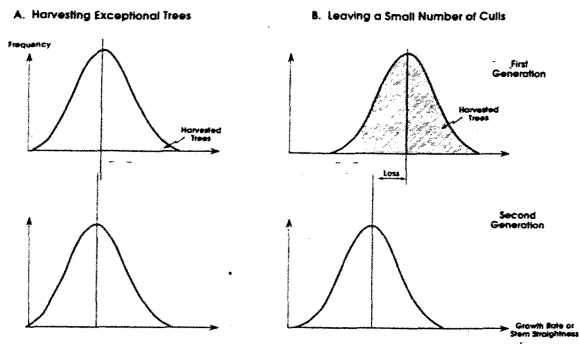


Fig. 2. A. Paradoxically, when loggers were very "selective" and exploited only the very highest quality stems, the genetic impact was likely to be minor, because change after selection depends on selection intensity, measured by the proportion of the population surviving and reproducing. B. When only culls were left following harvest, as in commercial clearcuts in the late nineteenth and early twentieth centuries, the potential for genetic change was great.

much of the Caribbean because of selective harvesting of the larger, well-formed trees. However, novel approaches will be necessary to demonstrate change because the baselines against which to compare present levels and patterns of diversity do not exist or are equivocal.

In North America, one of the most intensively harvested ecosystems was the New Jersey Pine Barrens, an area between New York and Philadelphia; the pinery was cut over for three centuries at an estimated 20-yr interval to provide fuelwood for iron smelting, domestic heating, glass-making, brick-making, and, later, the railroads (Sims and Weiss 1955). Such famous colonial glassworks as those on Cape Cod and in New Jersey were established because of the combined resources of silica sand and fuel. Bog iron from the New Jersey Pine Barrens supplied the colonies and the army during the American Revolution, and smelting required immense quantities of charcoal. Fuelwood is not a demanding use, but it seems obvious that the slowest-growing trees would stand a better chance of being left to reproduce following successive harvest cycles than the most rapidly growing. Put another way, slow-growing trees are less likely to reach harvest size than rapidly-growing trees between cutting cycles. And those that were limby would be less preferred than those with a single, straight bole because the latter are easier to cut and trim. The poor form of pitch pine in the Pine Barrens may be partially the result of dysgenic selection and, perhaps, even the dwarf forms found in scattered Pine Plains may owe their origin to inadvertent selection, but this is purely speculative.

We can examine the possibility of change, at least in a qualitative way, based on estimates of heritability and assumptions about the intensity of selection resulting from timber harvest. Genetic variance as a result of

additive gene effects is the predominant expression of diversity in forest trees. Change in a trait under selection depends on the additive genetic variance. The expression is:

$$C = ih^2\sigma_p,$$

where i is the intensity of selection, h^2 is the heritability of the trait in the population under consideration, and σ_p is the phenotypic standard deviation resulting from all environmental and genetic causes. Heritability is the ratio of additive genetic variance to total variance.

The two different harvest scenarios, exemplified by removal of only the finest white pine versus removal of everything but the very poorest pitch pine for fuelwood, will have different effects. In the case of removing only the finest, the change will be negligible, even over several generations, because the group left to reproduce is, in effect, scarcely reduced by selection (i.e., intensity, i , is low; Fig. 2A). On the other hand, leaving a small, residual group of defective trees could rapidly degrade form and growth rate and increase susceptibility to disease and rot because i is high (Fig. 2B). In fact, the less demanding the loggers were about what they harvested (i.e., the more complete the utilization, short of a silvicultural clearcut, which means taking absolutely everything), the greater the dysgenic effects. The greatest change would occur if only the very worst trees were left. Some reproduction would probably escape damage so that not all mortality was selective, and dysgenic change would be dampened. However, the accumulation of dead and downed fuel in early logging practice often lead to fires that destroyed all reproduction, sparing isolated culls (Holbrook 1938).

Another consequence of leaving relatively isolated trees to seed clearcuts is an increase in inbreeding. The lasting effect on adaptive genetic diversity would not be serious, but reproductive output and viability might be reduced for the next one or two generations. In pines, for example, selfing reduces seed yields 40 to 90% in most species. In the second generation many crosses will take place between neighboring trees that are likely to be siblings, and sib matings also reduce seed yields; e.g., by 15 to 30% in slash pine (*Pinus elliottii* Engelm.), depending on whether matings are between half-sibs or full-sibs (Squillace and Kraus 1963). Height growth is also reduced in inbreds and they are more likely to succumb to stress than outcrossed trees (Franklin 1970). Red pine (*Pinus resinosa* Ait.), which has almost no measurable genetic diversity, is an exception, showing neither reduction in seed yield or height growth after inbreeding. However, most tree species have high levels of genetic diversity and reductions in fecundity and viability create situations in which demographic stochasticity becomes critical. Despite the reduction in reproductive capacity or fitness, inbreeding actually increases genetic variance by exposing recessive alleles; thus it is also a route to rapid evolutionary change.

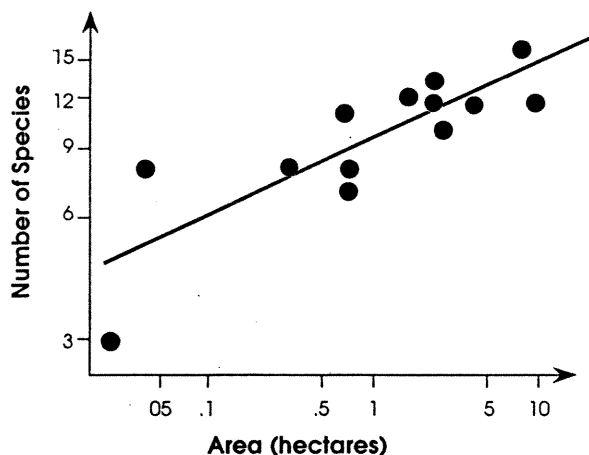


Fig. 3. Species-area relationship (transformed to logarithmic scales) for arctic-alpine plant species in the Adirondack Mountains, New York (after Riebesell 1982). The smaller the area of a fragmented ecosystem, the fewer the species, because the chance of local extinction increases as a result of demographic stochasticity and the chance of replacement by immigration decreases since there is less likelihood of dispersants finding a small patch of habitat than of finding a large patch.

Fragmentation

And all the King's horses and all the King's men
Couldn't put Humpty together again.

Traditional

Fragmentation of the natural environment by agriculture and urban development has two major impacts; it subdivides populations into small units and it imposes barriers to migration. In extreme cases of subdivision and isolation, inbreeding may be a problem in the forest remnants, but demographic stochasticity leading to local extinction is a more immediate concern (Lande 1988). Fragments of small area will have fewer species than fragments of large area (Fig. 3), even if they began with the same biota (e.g., Riebesell 1982, Harris 1984). This positive relationship between species and area occurs because the rate of extinction is higher in small fragments due to chance factors affecting survival and reproduction, and because small fragments tend to intercept fewer colonists than large fragments, other things (i.e., degree of isolation) being equal (e.g., Wilcox 1980).

Loss of populations because of fragmentation and demographic stochasticity represents an erosion of genetic diversity almost as bad as loss of species because it may signal the destruction of a complex structure of locally adapted populations. Even within a small watershed, Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) is genetically structured: subpopulations diverge in relation to elevation, slope aspect, and other microenvironmental factors (Campbell 1979). In balsam

fir (*Abies balsamea* [L.] Mill.), segments of a continuous population on the same mountainside have evolved differences in photosynthetic temperature optima over distances of less than 0.8 km (Fryer and Ledig 1972) and subpopulations of sugar maple (*Acer saccharum* Marsh.) have diverged in leaf morphology and photosynthetic rate along the same short gradient (Ledig and Korbobo 1983). Linkage tends to hold locally adapted gene complexes together, but it also makes it difficult to re-evolve similar, locally adapted complexes within any practicable time period if segments are removed (Clausen and Hiesey 1960).

Fragmentation generally means the imposition of barriers to migration among fragments and this precludes the possibility of species tracking environmental change by dispersal. Tree species have survived environmental change by dispersing to more hospitable environments during innumerable episodes in the geologic past. The palynological record shows that red spruce (*Picea rubens* Sarg.), for example, retreated to high elevations during the hypsithermal 8000 yr B.P. and reappeared at mid-elevations about 2000 yr B.P. In the late eighteenth century it composed 29 to 45% of the mid-elevation forest in New England but today its frequency is only 5 to 7% in the same area (Hamburg and Cogbill 1988). The role of dispersal in species survival is especially noticeable from shifts in timberline as a response to changes in climate (Scuderi 1987). Although species still may be able to retreat upslope in the event of global warming, dispersal in latitude is extremely unlikely in today's fragmented, temperate forests (Peters 1990). For many species, evolutionary change is the only remaining, viable option for tracking the environment.

In fragments of very small size, inbreeding and drift may affect the distribution and level of genetic variation. The immediate effect of inbreeding will be a reduction in fitness and fecundity in most tree species, as mentioned above. Inbreeding will also increase phenotypic variance by exposing recessive alleles. Total variance will be increased because drift will lead to divergence among subpopulations. Barriers to migration among fragments can have two consequences. The short term effect is to reduce recombination, which may make it difficult for species to evolve in response to multiple stresses. In the longer term, fragmentation is the route to population divergence; the predominant paradigm for speciation is speciation in geographic isolation. By eliminating migration between populations, each is able to adapt more closely to local conditions; however, in the current context, speciation is too long a process to concern us, and local extinction through demographic stochasticity is a much more likely outcome, which will lead to genetic erosion.

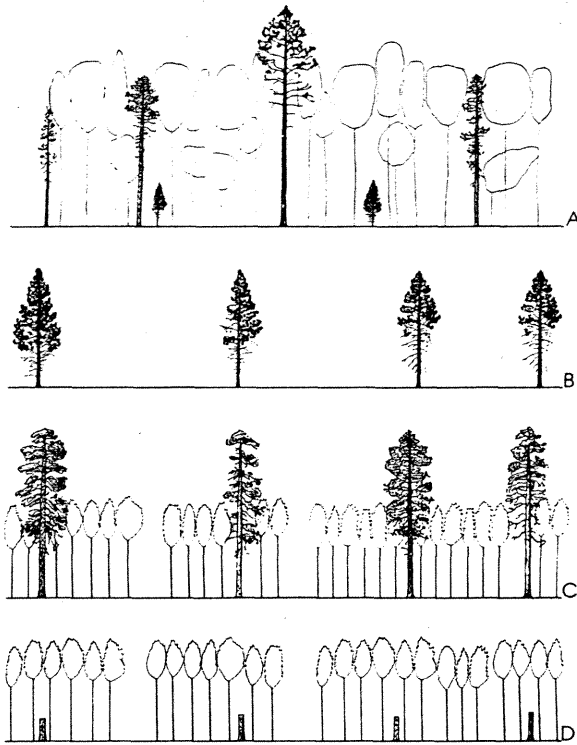


Fig. 4. Change in demographic structure of eastern white pine from the pre-colonial New England forest until recently. A. Eastern white pine occurred as scattered trees in the pre-colonial forest. B. Following conversion of forest to agriculture, some white pine remained in fencerows and woodlots, and spread from there to colonize abandoned agricultural land in the late nineteenth and early twentieth centuries. C. The initial, widely-spaced colonists matured and filled in the gaps, forming a two-aged stand of older dominants in a matrix of their progeny. D. Some managed stands were selectively thinned to remove large-limbed, poorly-formed, weeviled trees, which invariably included the original old-field colonists.

Demographic alteration

Old-growth forests, with their ... high age class diversity, are less conducive to pest outbreaks than are the simplified forests created through current harvest and regeneration practices.

T. D. Schowalter and J. E. Means (1988)

Demographic change influences selection, the mating system, and the generation of novelty through mutation, but is one of the least appreciated human impacts on the forest. In general, forests have gotten younger because old-growth was exploited while it lasted, leaving seedling stands in its wake. Management of second-growth forests and forest plantations is dictated by economic considerations and economics inevitably reduces the time between harvests, the rotation age.

Most harvest practices still result in drastic swings in population size and simplify age structure. All silvicultural

harvest methods, except the selection method, result in even-aged stands. In the seed-tree method, isolated trees (usually 2 to 25 per ha) are left to regenerate following harvest (Smith and Hawley 1954). In addition to creating an even-aged stand, the method creates a bottleneck, because of the reduced number of parents and non-overlapping generations. However, seed of some species may persist in the soil for several yr or even decades (e.g., Marks 1974), and germinate after harvest, which effectively overlaps generations and prevents a bottleneck. The genetic impact of harvest methods is largely uninvestigated; but certainly, the demographic structure created by even-aged silviculture favors pest outbreaks and, therefore, selective change.

The California Gene Resources Program (1982) identified the impact of harvest practices on Douglas-fir genetic resources as a priority research item, but few studies have addressed the challenge. One study of regeneration following a shelterwood cut in Douglas-fir found no significant changes in gene or genotype frequencies (Neale 1985). However, in the shelterwood method of regeneration, many more trees contribute to reproduction than is the case in the seed-tree method. Changes in mating system parameters suggested that the shelterwood cut had reduced the inbreeding that results from mating among relatives in closed stands (Neale and Adams 1985). Mating systems should be investigated in leave-trees at various densities to determine the point at which reduced density affects outcrossing rate.

Many diseases are diseases of regeneration to which mature trees are resistant. The conversion of the mature forest to younger age classes has converted diseases that were merely "mycological curiosities" to widespread epiphytotic (Kinloch 1972). Thus, diseases such as fusiform rust of southern pines in the United States have changed from endemic to epidemic and, therefore, become much more potent selective forces than they were in the precolonial forest. White pine blister rust is another disease that is more damaging to young seedlings or saplings than to mature trees (Patton 1961). When blister rust was first discovered in western North America in the early years of the century, only 1 to 2% of seedling progeny of western white pine (*Pinus monticola* Dougl. ex D. Don) were resistant, but by 1964, 20% of the progeny from stands decimated by the disease were resistant (Hoff et al. 1976), indicating the possibility of rapid, directional changes in gene frequency from exposure to an epiphytotic. Note that directional changes are not necessarily a reduction in gene diversity, but the reduction in population size may reduce genetic variation in the long-term.

The pattern of land and forest exploitation, by changing the demographic structure of forest trees, has also affected their mating systems. Eastern white pine is a model (Ledig and Smith 1981). In the precolonial forest, eastern white pine occurred as a scattered tree in the forest canopy. Conversion of forest to agriculture

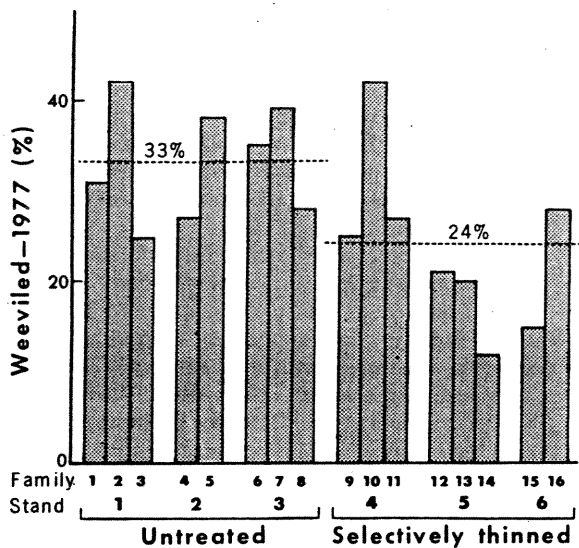


Fig. 5. Progeny from old-field stands of eastern white pine selectively thinned to remove weeviled trees were apparently more weevil resistant than progeny from unthinned stands, and this was consistent with expectations based on estimates of heritability for weevil resistance (after Ledig and Smith 1981).

restricted the remnants to small woodlots or fencerows. Following widescale abandonment of farmland in the late nineteenth and early twentieth centuries, the winged seeds of white pine were spread by the wind and colonized the old fields. Typically, these first old-field stands would be understocked with widely-spaced trees (Fig. 4). As they matured the early colonists crossed among themselves and filled in the gaps. Such old-fields were essentially two-aged: scattered older dominants in a matrix of their progeny. When the progeny reached reproductive maturity, two types of crosses predominated: crosses among nearest neighbors, who were often sibs, and pollination of parent by offspring. The inbreeding coefficient of sib mating is $1/8$ and of parent-offspring mating, twice as great – $1/4$.

A reduction in both vigor and in seed yield accompany inbreeding in pines (Franklin 1970) and is reflected by performance of the progeny of old-field white pine (Ledig and Smith 1981). We compared progeny from old-field stands to those from old-field stands where heavily-weeviled trees had been removed in thinning. The thinning included all trees in the older strata. Thinning improved weevil resistance in the progeny (Fig. 5), in agreement with expectations based on the heritability of weeviling and the selection intensity against weeviled trees. But it also led to a more rapidly growing progeny (Fig. 6), and this could not be explained by selection because the genetic variance for height growth was essentially zero. However, the increase was completely accounted for by a reduction in inbreeding – because parent-offspring matings were precluded by thinning. The initial demographic struc-

ture of old-field white pine will affect the genetic structure (i.e., distribution and frequency of genotypes) of local populations for a few generations, but eventually succession should restore the historic structure and return genotypes to Hardy-Weinberg frequencies.

Human-caused demographic changes also may influence the release and expression of genetic variation and the occurrence of novelties, or mutants. As forests were reduced to fragments, perhaps to isolated trees in fencerows, inbreeding must have become more common than in the original forest. Variability would be released as rare recessives were made homozygous in the array of progeny that reseeded abandoned farmlands. Even if these variants were mildly deleterious, they might survive under the conditions of reduced competition that were encountered in newly-abandoned fields. As early successional species expanded in population size, new mutants would be likely; the rate of occurrence for a particular mutation would not change, but the expectation of recovering a particular mutant would be finite rather than infinitely remote, as it is in populations of only a few individuals. Loblolly pine (*Pinus taeda* L.) provides an example of this scenario. The name, loblolly, refers to the pine's habitat when first encountered by early settlers; a loblolly is a mudhole or wet area. Loblolly pine was restricted to swamp margins and wet lowlands. However, it was so aggressive in colonizing abandoned farmland in the latter half of the nineteenth century that it became known by the common name of "oldfield pine" (Harlow and Harrar 1950).

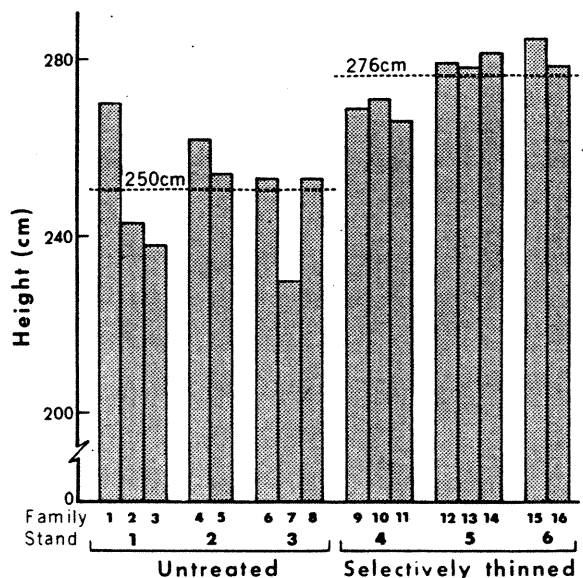


Fig. 6. Progeny from old-field stands of eastern white pine selectively thinned to remove weeviled trees grew more rapidly than progeny of unthinned stands (after Ledig and Smith 1981). This is not consistent with expectations based on the low heritability for height growth and the lack of selection for height during selective thinning. However, it is consistent with an expected reduction in parent-offspring mating.

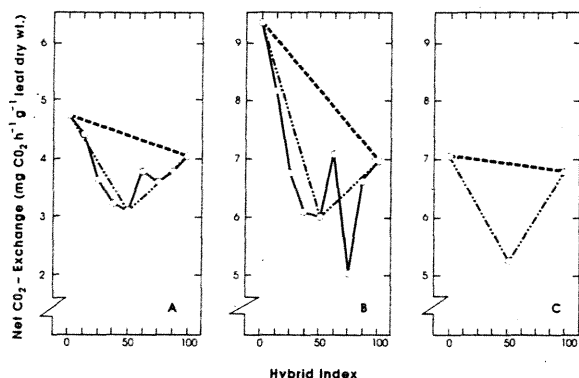


Fig. 7. Habitat alteration in the Canadian Maritimes probably reduced primary productivity by creating conditions suitable for large-scale hybridization of black and red spruce. In three different series of crosses in three different years (A, B, C), F_1 hybrids (hybrid index of 50) had rates of photosynthesis about 25% lower than either their black spruce (0) or red spruce (100) parents. Backcrosses, recurrent backcrosses, and other hybrid combinations fell below expectations based on a model of additive inheritance (after Manley and Ledig 1979). A. Mean of photosynthetic rates at several temperatures and light fluxes for seedlings grown under various acclimation conditions in growth chambers ($n = 132$). B. Photosynthetic rates at 3500 ft-c for greenhouse-grown seedlings ($n = 4$). C. Photosynthetic rates at 3000 ft-c for seedlings grown in growth chambers at 26°C day and 15°C night temperatures and 1000 ft-c ($n = 5$ to 9).

Loblolly pine expanded in numbers many orders of magnitude. The massive expansion in population as well as relaxation of selection may be one reason that it is the most variable eastern conifer (Conkle 1981) and produces such an array of mutant forms upon inbreeding (Franklin 1969).

Habitat alteration

It is red hills now, not high, ... and now and then a place where the second-growth pines stand close together if they haven't burned over for sheep grass, and if they have burned over, there are the black stubs. ... There were pine forests here a long time ago but they are gone. The bastards got in here and set up the mills and laid the narrow-gauge tracks and knocked together the company commissaries and paid a dollar a day ... Till, all of a sudden, there weren't any more pine trees.

Robert Penn Warren (1946)

In presettlement Mississippi, longleaf pine grew on the dry hills described by Robert Penn Warren, and loblolly pine grew in the bottoms. Sonderegger pines, the hybrid between longleaf (*Pinus palustris* Mill.) and loblolly pines, were recognized in the period 1910–1930, the period of greatest habitat disturbance. The hybrids were

invariably found on "cut-over lands which originally bore heavy stands of longleaf pine, and which ... [had] a few scattered seed trees left" (Chapman 1922). The pollen parents seemed to be loblolly pines. With time, backcrosses were observed, which tended toward loblolly pine on the lower slopes and longleaf on the upper, although most backcrossing seemed to go toward longleaf pine (Namkoong 1966).

Hybridization is often found in the wake of habitat disturbance, and hybridization is often followed by introgression; i.e., backcrossing to one or both of the parental species, resulting in an increase in diversity for the recurrent parent(s). The success of hybrids is often explained as a consequence of a "hybridized habitat", one intermediate in its demands to those in which the parental species evolved; a more likely explanation is that hybrids are able to succeed following disturbance because of reduced competition from parental types (Anderson 1949).

In the Maritime provinces of Canada, habitat alteration has resulted in hybridization on an extreme scale. Three centuries of logging followed by fires led to such extensive hybridization between black spruce (*Picea mariana* [Mill.] B.S.P.) and red spruce that many foresters doubted the existence of two species. Red spruce on the uplands were cut in large blocks of thousands of hectares, but isolated culls or small trees were left. Fires in the logging residue eliminated the understory vegetation. Black spruce in the bogs and along the rivers were not logged because of their small stature and because of the difficulty of harvesting the poorly drained bottomlands. Neither did the wet bottomlands burn. The scattered red spruce remaining after logging were swamped with black spruce pollen from the bottoms because spruce are monoecious and as the red spruce mature, they produce ovulate strobili before pollen strobili. The resulting hybrids regenerated easily in the absence of competition from competing vegetation.

On undisturbed sites, hybrids are found infrequently, even at the ecotone between black and red spruce, partially because of pollen competition or differential survival of zygotes during embryogenesis. If red spruce is pollinated with a 50:50 mix of black and red spruce pollen, few hybrids are produced, but the cross is easy to accomplish if black spruce pollen is applied alone (Manley 1975). Another reason hybrids are uncommon in undisturbed forest is because they are less fit than the parental types in several ways: e.g., reduced fertility, greater frequency of abnormal germinants, a high frequency of nanism (Manley 1975), and a rate of photosynthesis that is 25% lower than mid-parent values (Fig. 7; Manley and Ledig 1979). Likewise, longleaf $\times$ loblolly pine hybrids are less fit than the parental types because of slower growth and a combined susceptibility to both of the separate pests that plague the two parental species (Snyder et al. 1977). In the case of black and red spruce, the parental types diverge in their light and temperature response and no true "hybridized habitat"

exists. As succession proceeds, the hybrids and hybrid derivatives from backcrossing and intercrossing of the F_1 s tend to disappear and the frequency of trees with hybrid indices like red spruce increases on the uplands and those like black spruce, in the bogs (Manley 1972, Gordon 1976).

More subtle human impacts have led to hybridization in orioles and flickers and tree frogs. The eastern Baltimore oriole and the western Bullock oriole were kept separate by the Great Plains and hybridized to a limited extent along a few riparian corridors in the pre-disturbance West, but as trees were planted for windbreaks, along streets and roads, in farmsteads, and in city parks, the two came together over a broad front and introgression was noted far from the contact zone (Sibley and Short 1964). The situation is similar in the eastern yellow-shafted flicker and the western red-shafted flicker. In the green treefrog and the barking treefrog, the construction of farm ponds with well-mown margins had the curious effect of promoting hybridization. The male barking treefrog breeds in the water and the green treefrog on land. Because the pond margins are weed-free, the male green treefrogs can see the barking treefrog females as they head toward the pond, and intercept them (Mecham 1960).

Obviously, selection should also be affected by habitat alteration. In forage species, the creation of pastures and introduction of domestic livestock has resulted in selection for procumbent forms (Kemp 1937). Sweet vernal grass (*Anthoxanthum odoratum* L.) has evolved variants adapted to a range of soil pH and nutrient conditions in fertilizer-plot trials over distances as small as 30 m (Snaydon 1970, Snaydon and Davies 1972), and in annual bluegrass (*Poa annua* L.), golf course management has led to differentiation between fairway and green's populations (Lush 1989).

In forest management one of the most pervasive changes has been fire control, and it seems likely that this will have an effect on community structure and an influence on genetic variation through selection. Before European settlement of North America, native Americans burned the forest at frequent intervals (perhaps, 5 to 6 yr in some areas) both in the eastern (Hawes 1923, Dunwiddie 1990) and western (Arno 1980, Barrett and Arno 1982) United States. Fire frequency has decreased greatly, particularly in this century, although when they occur, fires are generally more intense. Adaptations (e.g., serotinous cones) to frequent fires, of moderate intensity, may be of negative value under the new regime. Serotinous cones may remain closed and retain seed for decades until they open in response to fire. In the absence of fire, it may be more adaptive to shed seed every year to maximize opportunities of encountering suitable substrate and climatic conditions for seed germination and seedling growth (Ledig and Little 1979). Givnish (1981) argued that the frequency of cone serotiny in pitch pine populations in the New Jersey Pine Barrens reflected fire history. Increased fragmen-

tation of the Pine Barrens has reduced the occurrence of fire (Gibson et al. 1988) and may lead to a decline in frequency of genes for cone serotiny. The serotinous cone also provides a mechanism for presenting a maximum of recombinants to the environment at any one time and for storing diversity over many decades. It may be reasoned that diversity per se would decline in the absence of serotiny, an apparently testable hypothesis.

Another pervasive change in the forest environment is the global increase in atmospheric carbon dioxide (Harrington 1987). The projected global warming resulting from increased levels of carbon dioxide and other greenhouse gases could lead to widespread forest decline and will be considered in the next section. However, an increase in carbon dioxide, per se, ameliorates the environment for plants, whose genesis dates to a period when the earth's atmosphere was much less oxidative than it is at present. A high level of carbon dioxide, by itself, could change competitive relationships among species and among individuals within species (Leverenz and Lev 1987). Among herbaceous species the advantage of C_4 -plants relative to those with the C_3 pathway for photosynthesis would decline. Plants that responded to moisture deficits by early closure of stomata would be less disadvantaged with regard to photosynthesis than they are at present because the carbon dioxide diffusion gradient would be greater. Therefore, photosynthesis would not be reduced by stomatal closure as much as transpiration.

Environmental deterioration

Coketown lay shrouded in a haze of its own ... You only knew the town was there, because you knew there could have been no such sulky blotch upon the prospect without a town. A blur of soot and smoke, now confusedly tending this way, now that way, now aspiring to the vault of heaven, now murkily creeping along the earth.

Charles Dickens (1854)

Environmental deterioration is habitat alteration, but differs in degree. The changes considered in this section are truly devastating because they increase stress and cause heavy mortality, in contrast to the examples above, which, as in the cases of hybridization, reduce selection pressure and permit high rates of survival. The evolution of insecticide resistance in mosquitos and flies, of antibiotic resistance in bacteria, and herbicide tolerance in weeds are recent examples of changes in genetic structure as a result of abrupt environmental changes. More pertinent to forests are the effects of atmospheric pollutants such as sulfur dioxide and ozone, and soil pollutants such as heavy metals and acid deposition.

As the quote from Charles Dickens indicates, indus-

Table 1. Percentage of leaves with evidence of oxidant injury in quaking aspen from areas with different ambient levels of atmospheric pollution, after fumigation with 180 ppb ozone for 6 h (after Berang et al. 1989).

Population origin	Mean ozone concentration at origin (ppb)	Leaves with injury (%)
Cuyahoga Valley National Recreation Area, Ohio	65	50
Saratoga National Historic Park, New York	49	58
Acadia National Park, Maine	52	60
Voyageurs National Park, Minnesota	26	71
Isle Royal National Park, Michigan	14	75

trial emissions have been with us for at least a century and a-half. In fact, Linnaeus described the devastating effects of smelter fallout on plants in 1734 (Cowling 1982). What is new is that these pollutants have become a truly global problem in this century. Some pollutants, such as the chlorofluorocarbons are relatively recent phenomenon. The chlorofluorocarbons are important for their secondary effects, notably the attenuation of the ozone layer and increase in ultraviolet-B radiation. Global warming, another secondary effect of human-induced atmospheric change, is not novel – global heating to above-present levels followed the Wisconsin glaciation – but the projected changes in the next century will occur much more rapidly than any in the paleoclimatic record.

Smog damage to trees around the Los Angeles Basin was noted between 1941 and 1945, although it was not diagnosed as such until later (Bolsinger 1980). In the half century since, changes in the forest community have been documented, and along with tests using controlled levels of ozone and sulfur dioxide, illustrate differential susceptibility of species to atmospheric pollutants (Miller 1973).

Many studies also have demonstrated intraspecific genetic variation in tolerance to atmospheric pollutants among populations, families, and clones (Karnosky and Steiner 1981, Larsen and Friedrich 1988, Larsen et al. 1988, and see review by Pitelka 1988) under controlled conditions. Therefore, pollutants may have an impact on the genetic structure of populations. Some studies suggest that selective changes have already occurred in natural populations, for example in quaking aspen (*Populus tremuloides* Michx.). Clones of quaking aspen were sampled from five areas that varied in levels of air pollution. Populations differed in the extent of leaf injury after fumigation with 180 ppb ozone or after exposure in field tests (Table 1), and tolerance was correlated with ambient levels of ozone at the population

origin (Berrang et al. 1986, 1989). Several investigators sought to relate pollution tolerance to isozyme frequencies or heterozygosity (e.g., Geburek et al. 1986) but results were equivocal. Heterozygotes may be favored under stress (Hattemer and Muller-Starck 1989), but this is to be expected if homozygosity is merely a reflection of inbreeding (Ledig 1986).

Smelters and mine spoils provide extreme examples of the effects of heavy metal pollution on plants. The effects are pronounced in the immediate vicinity of smelters, but they may be more widespread. At a distance 88 km downwind from a smelter site, tree rings showed an accumulation of heavy metals and a decline in growth for the years during which the smelter was operated (Baes and McLaughlin 1984). Differential sensitivity may lead to altered competitive relationships. Several herbaceous species have genetic variants able to survive normally-toxic levels of various metals, such as copper, zinc, and nickel. Tolerant populations have diverged from non-tolerant populations over distances as short as a few meters (Antonovics et al. 1971).

There are no reports of heavy metal tolerant races in trees; their long generations and general intolerance of inbreeding would make it difficult for metal-tolerant populations to evolve. Nevertheless, some woody species managed to persist adjacent to a copper smelter and brass manufactory in Connecticut (F. T. Ledig and M. L. Shea, unpublished data). Scattered gray birch (*Betula populifolia* Marsh.) were common and grew in soils with a lead concentration of over 450 ppm; accumulations in the leaves were over twice as high, 1130 ppm. Whether these trees were more metal-tolerant than ones from pristine environments, is not known, but it may be significant that gray birch is a very short-lived species, with a high reproductive output and light seed that is easily dispersed by wind (Harlow and Harrar 1950) – factors that might contribute to rapid evolution.

Acid deposition is blamed for the widespread die-back, or Waldsterben, of Norway spruce (*Picea abies* [L.] Karst.) and silver fir (*Abies alba* Mill.) in Europe. However, simulated acid deposition in relatively short-term field experiments generally results in a stimulation of growth because it supplies limiting nutrients, namely nitrogen. If acid deposition has a role in forest decline, it is probably through its effect on nutrient balance (Schulze 1989). Whatever the causes of Waldsterben, the effects are so serious for silver fir, Norway spruce, and Scots pine that an intensive conservation effort is needed to sequester the endangered genetic resources (Melchior et al. 1986).

The release of chlorofluorocarbons is the primary culprit in destruction of the ozone layer that screens the earth from biologically active ultraviolet-B (UV-B) radiation. The most pronounced attenuation of the ozone layer has been measured over Antarctica, but the effect is not restricted to the polar regions alone. An annual increase of 1% in UV-B has been detected in the Swiss Alps since 1981 (Blumthaler and Ambach 1990). The

effect of UV-B on plants was reviewed by Caldwell et al. (1989) who concluded that the main effect of projected increases in UV-B will be to push UV-B flux at high latitudes within the range presently encountered in the tropical latitudes. Nevertheless, this may require evolutionary adjustments in temperate-zone plants; various characteristics (e.g., wax deposits, anthocyanins) of tropical and high altitude species are interpreted as adaptations to protect against damaging effects of UV-B on chlorophyll, phytochrome, and other critical molecules (Lee and Lowry 1975, 1980). Genetic divergence within species may distinguish low- and high-elevation populations or low- and high-latitude forms (e.g., Robberecht 1980), suggesting that increases in UV-B will be perceived as a stress by plants and result in selection for protective characteristics.

UV-B can damage DNA, so in addition to becoming an agent of directed genetic change through selection, it may also result in increases in genetic variation by increasing the rate of mutation. Although most reproductive organs are shielded, somatic mutations can eventually lead to modified gametes in plants (Whitham and Slobodchikoff 1981). And pollen would be directly vulnerable to increases in UV-B, especially in anemophilous species like conifers and oaks.

Mutation rates may be affected by other agents of stress as well as UV-B. In flax (*Linum usitatissimum* L.) quantitative and qualitative changes in DNA occur under some conditions (Cullis 1987). These often take the form of increases in the highly repetitive and intermediately repetitive fractions of the nuclear DNA. DNA content increases with altitude in comparisons of rye species (genus *Secale* L.) or of populations of teosinte (*Euchlaena mexicana* Schrad.) according to Laurie and Bennett (1985), and this may reflect a gradient in UV-B radiation with altitude, although other stresses are also associated with high altitude. Stress is a less parsimonious explanation of the complex pattern of altitudinal variation in DNA content in landraces of maize (*Zea mays* L.) in the southwestern United States; DNA content increases to a maximum at ca. 1800 m and decreases again from 1800 m to 2134 m (Rayburn 1990). Water-borne pollutants also have resulted in increased rates of mutation, as demonstrated in ferns growing along floodplains of polluted rivers (Klekowski 1976).

Global warming is another potential impact on genetic diversity. If projected increases of 2.5°C and associated climatic changes (Schneider 1989) materialize, extensive forest dieback will result (Peters 1990). Davis and Zabinski (1991) have modeled the ranges of several northeastern forest tree species following climate change; the models show near total elimination of beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton), and sugar maple from the United States. Range extensions at their northern limits would not completely compensate for losses at the southern end of their distributions.

I feel, however, that even these scenarios are optimis-

tic because almost all wide-ranging tree species that have been subjected to investigation are differentiated along latitudinal gradients. In a test of sugar maple from 37 different populations, drought mortality in the first season of growth was greater in seedlings from the northern part of the range than in those from the southern portion (Kriebel 1957); survival was positively correlated with average July temperature and maximum summer temperature at the population origin. In addition, the amount of winter chilling required by northern populations is greater than that needed by southern populations, and without adequate chilling, growth is not normal the following spring (Kriebel and Wang 1962). Thus, sugar maple and most other wide-ranging species might be able to survive in a warmer, northeastern United States *only* if the present populations were replaced with ones from the extreme southern margin of their present distribution. However, the complex of climatic changes associated with global warming may jeopardize successful transfers. Even if northern populations were able to survive, their net primary productivity probably would be reduced (e.g., Fetcher and Shaver 1990), and a reduction in rates of carbon-sequestering could become a positive feedback in a spiraling greenhouse effect.

Climatic changes of similar magnitude to those projected occurred at the end of the Pleistocene, and temperate forest trees adjusted by migration, in part (Ogden 1989, Critchfield 1984). As Critchfield (1984) and Ogden (1989) point out, they also adjusted through a restructuring of gene pools, including gene exchange by hybridization among related taxa. However, the Holocene climatic changes required millennia; the current climate models portend a crisis because the changes in global temperatures that they project will occur in a much shorter span of time, i.e., less than a century. Furthermore, barriers to migration (agricultural and urban development) will hinder or eliminate the possibility of unassisted migration in most forest tree species.

The projected change in climate will be accompanied by increases in disturbance (Overpeck et al. 1990). Higher surface temperatures will favor higher winds, greater drying, and more frequent thunderstorms. Hurricanes are likely to be strengthened, increasing fuel buildup by blowdown. Forest dieback will also increase fuel buildup. The increase in fuels, in drying, and in thunderstorms will lead to more frequent and more intense fires. Fire itself will change community structure toward fire-adapted species and will be a selective agent for features such as thick bark, basal sprouting, and serotinous cones and fruit. Increased disturbance may favor erosion and loss of nutrients, creating additional stress.

All of these stresses combined may create an intolerable load and could conceivably reduce diversity, reduce population size to levels where inbreeding might dominate even in outbreeding tree species, and, in some cases, lead to extirpation of affected populations. Al-

ready, an estimated 60% of mature red spruce in New England are in some stage of decline although no single factor can be isolated as the cause (Chevone and Linzon 1988).

Consider a hypothetical example of multiple stresses on sugar pine (*Pinus lambertiana* Dougl.) around the Los Angeles Basin, threatened by an introduced disease (white pine blister rust) and climatic change, and under stress from ozone pollution. Transplant studies indicate that movement of populations 4.5° south in latitude results in 21% mortality (R. D. Westfall, pers. comm.), and 4.5° latitude is equivalent to a change in temperature of roughly 2.5°C, according to Hopkins' Law (Hopkins 1938). A 2.5°C increase in temperature is within the range projected for the next century (Harrington 1987). Survivorship after global warming should be high, 79%, although a proportion of the survivors may exhibit reduced productivity and fitness. However, sugar pine is also threatened by white pine blister rust which is spreading southward. In the San Bernardino Mountains the frequency of a dominant resistance gene is only 3% (B. B. Kinloch, pers. comm.), so survivorship after combined global warming and the introduced white pine blister rust will be only 2.4%, assuming independent gene action. Drought and ensuing bark beetle epidemics are periodic in California and would be a natural impact almost certain to be imposed during the next 50 yr. The current drought in California is being credited with 25% mortality in the mixed-conifer type, depending on site. Survivorship from combined impacts of disease, global warming, and drought could be as low as 1.8%. Stand density in the California mixed conifer type is about 150 trees ha⁻¹, but sugar pine rarely constitutes as much as half of the stand, or 75 trees ha⁻¹. Therefore, fewer than 1.5 trees ha⁻¹ would survive multiple stresses, assuming independent action of genes for disease resistance, drought tolerance, and adaptation to a warmer environment. Obviously, gene frequencies would change at the loci under selection. More significantly, at population densities as low as this, selfing would increase, with a resulting decrease in seed production. Combined with demographic stochasticity, this may result in local extirpation.

Anthropogenically induced stresses may reduce diversity and, conversely, low levels of diversity may also predispose populations to damage. Most North American species of white pines (*Pinus* subgenus *Haploxylon*) carried some form of resistance to the introduced white pine blister rust. Although resistance genes were in low frequency, as indicated for sugar pine, white pines will survive the epidemic. American chestnut (*Castanea dentata* [Marsh.] Borkh.) was not as variable with respect to resistance to chestnut blight as white pines were with respect to blister rust, and it was eliminated as a forest tree. It would be interesting to compare gene diversity in chestnut to diversity in sugar pine. DeHayes and Hawley (1988) suggested that relatively low gene diversity in red spruce may be contributing to

its decline in the face of multiple stresses. Certainly, genetic uniformity was responsible for major epiphytotics in domesticated crops (U.S. Committee on Genetic Vulnerability of Major Crops 1972). An important objective for conservation biologists is to determine which species may be at risk because of low levels of diversity.

Translocation

Behold, evil shall go forth from nation to nation.
Jeremiah 25:32

The best documented and, perhaps, greatest impact that humans have had on the genetic structure of forest trees is through movement of plants, animals, and microorganisms – bridging barriers to migration, the converse of fragmentation which imposes barriers to migration. In the role of vector, humans have introduced competitors that threaten to eliminate native species, and diseases or herbivores that impose new selection pressures on species that had not coevolved with the pest. They have expanded the ranges of species of economic value, leading to genetic divergence, the origin of new ecotypes, and hybridization, and they have mixed divergent populations, contaminating local gene pools and homogenizing species structure. Movement of plants and animals has affected selection, drift, and the mating system of countless organisms.

Island floras have suffered most from the introduction of competitors, probably because island flora evolved as colonists in an environment relatively competition-free. The introduction of the invasive species guava (*Psidium guajava* L.) and quinine (*Cinchona succirubra* L.) in the Galapagos Islands has resulted in near-elimination of the native evergreen forest on the island of San Cristobal (Schofield 1989). Hawaii provides many other examples, such as the invasion of banana poka (*Passiflora mollissima* Bailey) into native forest (Cuddihy and Stone 1990). The subtropical flora of Florida is essentially insular, and the introduced species melaleuca (*Melaleuca quinquenervia* [Cav.] S. T. Blake), casuarina (*Casuarina equisetifolia* L.), and Brazilian pepper (*Schinus terebinthifolia* Raddi) have displaced native forest and grasslands (Harty 1986). The ultimate reduction in genetic diversity – extinction of native species – is feared in some cases.

North American species, relatively isolated from congeners in Europe and Asia, have suffered most from introduction of diseases, such as chestnut blight, white pine blister rust, and Dutch elm disease. Chestnut blight was probably introduced into New York City on Asian chestnut stock (*Castanea mollissima* Bl. or *C. crenata* Sieb. et Zucc.) about 1900 (Burnham 1988). By 1960 it had eliminated American chestnut throughout its native range in the eastern United States. Chestnut constituted 25% of the forest in much of the Appalachians, but

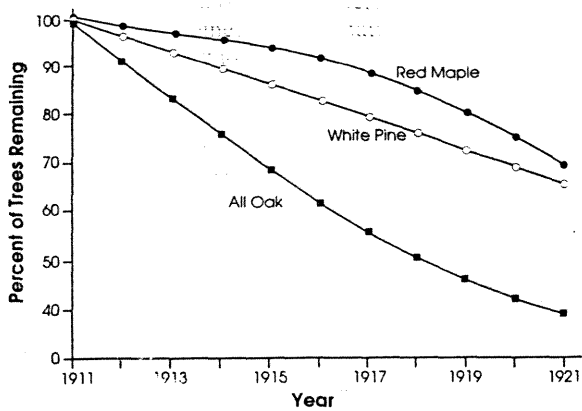


Fig. 8. Differential mortality following defoliation by the introduced gypsy moth changed community structure of New England woodlands (after Campbell and Sloan 1977).

today exists only as a shrub regenerated from old stumps, which continue to produce sprouts that are, just as often, killed back by the blight fungus. The breeding system has probably been changed because chestnut was an anemophilous forest dominant, and now is a scattered, sub-canopy shrub or small tree. Usually, the only bushes that flower are found along roadsides, where they are less shaded, so that the distribution of breeding individuals is now essentially "linear". The impact is not on chestnut alone; the loss of chestnut created a void that enabled other species to increase in importance, changing competitive relationships on a huge scale.

White pine blister rust, an introduced fungal disease, is now an important pathogen of eastern white pine, western white pine, and sugar pine. On the West Coast of North America, blister rust was apparently introduced near Vancouver, Canada on eastern white pine seedlings imported from Europe about 1910 (Mielke 1943). It is still expanding southward throughout the range of sugar pine in the southern Sierra Nevada of California. As with chestnut blight, the impacts of blister rust are manifold – on species composition of forests and on selection within the host population – but unlike chestnut, the white pine hosts were genetically variable with respect to resistance. The effects of natural selection have been documented in western white pine (Hoff et al. 1976) where mortality from blister rust has been greater than 80% on some sites. Early in the course of the epiphytic, less than 1% of the progeny of infected stands were resistant. However, after the initial mortality, the progeny of these heavily infected stands were 20% resistant. Florida Torreya (*Torreya taxifolia* Arn.) is another North American species threatened by introduced pathogens, at least in part (McMahan 1989).

The examples of chestnut blight and white pine blister rust illustrate transport of disease organisms across a major barrier to natural dispersion, but human activities

also threaten diversity by transfer of diseases among forest fragments within the range of single species. Phytophthora root rots are spread among jarrah (*Eucalyptus marginata* Donn. ex Sm.) stands in Western Australia and among stands of Port-Orford-cedar (*Chamaecyparis lawsoniana* [A. Murr.] Parl.) in the western United States by movement of off-road, logging vehicles and construction equipment (Shepherd 1975, Zobel et al. 1985). In both cases, the origin of the disease is uncertain. *Phytophthora lateralis* was not a native disease of Port-Orford-cedar. It was discovered on nursery and ornamental plants north of the tree's natural range and was transported south into natural stands about 1952. It now threatens the species' very survival.

Herbivores have also been transported to the detriment of genetic diversity. Goats were purposely introduced to many islands, where they have driven native plant species to extinction or the brink of extinction (e.g., Rieseberg et al. 1989, Schofield 1989). In 1968 Guadalupe Island off the coast of Baja California had a population of 383 pines (Libby et al. 1968), an isolated population of Monterey pine (*Pinus radiata* D. Don) worthy of subspecific rank and uniquely resistant to western gall rust (Old et al. 1986) and red band needle blight (Cobb and Libby 1968). By 1988, in only 20 yr, feral goats had reduced the number to 45 and the population seems doomed to extinction.

Ill-advised release of insect herbivores has also had disastrous impacts; for example, gypsy moth in North America. Gypsy moth was introduced at Medford, Massachusetts in 1869. Serious defoliation over wide areas began in the early twentieth century. Mortality of preferred species as a result of defoliation was very high in New England forests from 1911 to 1931 (Fig. 8; Campbell and Sloan 1977); e.g., 72% for white oak (*Quercus alba* L.), 33% for white pine, and 30% for red maple (*Acer rubrum* L.). Obviously, forest composition and competitive relationships must have changed because of differential mortality. Moreover, these values, especially for white oak, are high enough to produce selective changes if tolerance to defoliation or palatability have a genetic basis. Inventory on permanent plots showed that some trees were subjected to high levels of attack year after year, perhaps suggesting the influence of genetic factors. Mortality in European forest species is much less than that in New England, reflecting the coevolution of trees and herbivore in Europe. Under selection from the pest, North American trees may change in susceptibility; the percent defoliation in New England decreased from 1911 through 1921 and mortality rates differed among cohorts (Campbell and Sloan 1977).

Tree species themselves have been moved. The origin of many of our fruit and nut species is lost in prehistory because humans took their favored tree species with them as they migrated. In the process, selection, natural and human-directed, have adapted species to their new homes, leading to divergence among populations and

increasing overall diversity for at least some characteristics. In recent history, the ranges of species like Hinds walnut (*Juglans hindsii* Jeps. ex R. E. Smith) and black locust (*Robinia pseudoacacia* L.) have been modified and their original, pre-European patterns of distribution in North America are difficult to determine precisely (Detwiler 1937, Griffin and Critchfield 1972). Black locust has been transported around the globe and naturalized in Europe (Keresztesi 1980). Many tropical trees have been transported by humans and have naturalized on a pan-tropical scale, such as mango (*Mangifera indica* L.) and coconut (*Cocos nucifera* L.). The origin of coconut is uncertain, but it has undoubtedly been carried around the Pacific with human commerce (Ohler 1984). Its many distinct varieties reflect the action of both drift – the founder effect – and selection.

Afghan pine (*Pinus eldarica* Medw.) is an interesting example in conifers. Afghan pine occurs in scattered locations from Azerbaydzhan in the USSR to Pakistan, but appears to occur in natural stands only in Azerbaydzhan on a single mountain, Eliar-Ugi (Critchfield and Little 1966). Elsewhere it has probably been spread as a semi-domesticated selection or landrace, desirable because of its large seed. In fact, genetic evidence (Conkle et al. 1988) suggested that Afghan pine was simply a variant of Calabrian pine (*Pinus brutia* Ten.; therefore, Afghan pine is *P. brutia* ssp. *eldarica* [Medw.] Nahal) that owes its wide range to human transport along ancient trade routes. Genetic diversity in Afghan pine is only two-thirds that of Calabrian pine, which is interpreted as evidence of bottlenecking during selection and transport in cultivation.

In the process of introduction, new gene complexes evolve in local landraces, and geographic patterns of variation often mimic those of native species – e.g., latitudinal gradients in body size in European house sparrows introduced to North America (Johnston and Selander 1964). Differences among generations show the changes in progress; trees in the third generation of an expanding population of the common pear (*Pyrus communis* L.) had more rapid growth rates than their progenitors and differed from them in various morphological characteristics, suggesting adaptation to site and climate by selection (Waldron et al. 1976). In Europe, landraces of several European and North American conifers are recognized (de Vecchi 1970), and in the semi-arid tropics, landraces of mesquites (*Prosopis* L.) and acacias (*Acacia* Mill.) have led to taxonomic confusion (Palmberg 1981). Landraces, usually of unknown origin, often outperform any subsequent introductions; e.g., in New Zealand local plantations of European larch (*Larix decidua* Mill.) produced seedlings that were more rapidly growing than newly-imported, native seed sources (Miller 1964).

Hybridization occasionally follows translocation. Sympatric species-pairs have usually evolved mechanisms to prevent hybridization. The need for such reproductive isolating mechanisms is not necessary in con-

geners separated by geographic barriers. When geographic isolation is removed and they are brought together, hybrids are a common occurrence. Hybridization in botanical gardens or production plantations can create a bridge for the introgression of genes into a local species. Famous hybrids that arose spontaneously in cultivation are the Dunkeld larch (*Larix decidua* Mill. $\times$ *L. leptolepis* [Sieb. et Zucc.] Gord.; Henry and Flood 1919) and the London plane tree (*Platanus occidentalis* L. $\times$ *P. orientalis* L.; Santamour 1970). In a few cases, hybrids can spread and usurp the habitat of a parent species, as in the case of Townsend's grass (*Spartina* $\times$ *townsendii*; Huskins 1931). Mediterranean ecosystems have been disturbed since antiquity, and genetic evidence suggests that both ancient and modern transfers of Aleppo pine (*Pinus halepensis* Mill.) and Calabrian pine have led to hybridization and introgression (Schiller et al. 1986). Hinds walnut, a California endemic, has been largely displaced by cultivated walnut (*Juglans regia* L.) and pollen contamination from cultivated walnut may hybridize the remaining Hinds walnut out of existence (McGranahan et al. 1988).

The most massive movement of forest trees is a modern phenomenon, an aspect of reforestation. In California, for example, 13355 ha are planted every year on average, following harvest or wildfire (Kitzmilller 1990). Each site is replanted with native species grown from seed collected in the local seed zone; seed zone boundaries are drawn on the basis of natural patterns of genetic diversity and structure, when known. However, because genetic evidence is often lacking, seed zone boundaries use natural climatic and physiographic divisions as a surrogate for knowledge of genetic structure. When seed from the local seed zone is not available, seed from an adjacent zone is used. These rules are fairly enlightened relative to the historic practice of obtaining seed without regard to origin (Baldwin and Shirley 1936). Widespread plantation failures, obvious deformity, and loss of productivity lead to the recognition that "local" seed is often best or, at least, safest in the absence of knowledge to the contrary. Of course, exceptions are known; e.g., Scots pine seed must be transported south to obtain satisfactory survival in northern, interior Sweden (Eriksson et al. 1980).

Reforestation by planting certainly alters the genetic structure of natural stands, whether or not the present system of seed zones maintains productivity or not. Planting may eliminate local patterns of variation, it modifies the mating system, and it may impact adjacent, natural areas by pollen and seed migration from the non-local plantation. Populations of forest trees diverge over short distances, as mentioned above (e.g., Fryer and Ledig 1972, Campbell 1979), but seed zones are designed to accommodate activity on much larger scales. Consideration of seed and pollen dispersal patterns (Wright 1953) suggests that stands might be expected to have an internal structure of their own, with a high probability that adjacent trees are more related

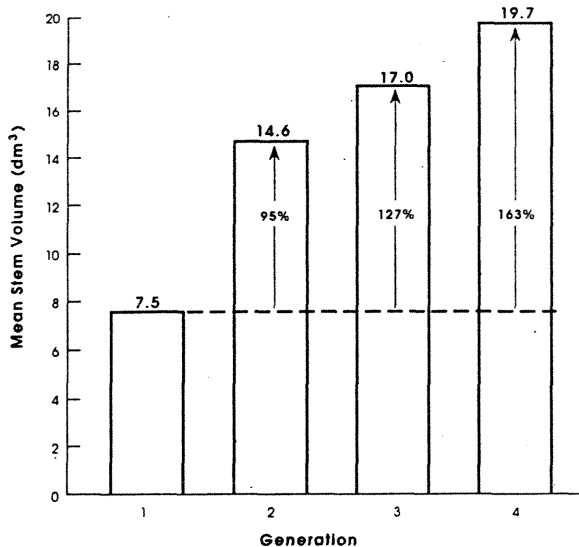


Fig. 9. Domestication of forest trees, has produced great changes, such as in flooded gum where average wood volume increased 163% in four generations, about 16 yr (after Meskimen 1983).

than distant ones (Ledig 1974). Crosses among neighbors likely predominate in nature, which means that the mating system in natural stands may be characterized by inbreeding (Neale and Adams 1985). This is supported by observations that controlled pollination of near neighbors results in a depression of seed yield, akin to what occurs from mating close relatives (e.g., Coles and Fowler 1976). However, this might not always be the case; Yazdani et al. (1989) observed no clustering of alleles in a stand of Scots pine, which is interpreted to mean that relatives are not clustered. In a planted stand, relatives are distributed at random, which should enhance outcrossing.

Contamination of natural stands by pollen and seed migration from plantations seems a logical consequence of reforestation, and needs more study. Non-local Monterey pines have been planted as ornamentals in two of the three endemic populations (i.e., at Monterey and Cambria), and non-local Bishop pines (*Pinus muricata* D. Don) have been planted at Sea Ranch in California, which is a unique meeting place of two divergent races of Bishop pine. Both situations have resulted in gene migration into the local stands; allozymes from the non-locals are already detectable in the local populations (Millar and Libby 1989). Even National Parks, areas established to maintain outstanding examples of natural ecosystems, are impacted; non-local redwood (*Sequoia sempervirens* [D. Don] Endl.), Douglas-fir, and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) have been aerially seeded in Redwood National Park, albeit before creation of the park. The consequence of this contamination on local populations is not known, but could be serious if non-locals disturb ecosystem function by low-

ering primary productivity and the flow of energy through the system. The many plantation failures from using non-adapted seed sources are all too obvious in the Sierra yellow pine type, and gene migration from the survivors into local populations could have long-lasting consequences.

Domestication

Man, in ignorance, made some mistakes during millennia of domesticating our crop plants and animals. We wish he had studied the ecology of the native ancestral populations before he changed them and replaced them with domestic varieties.

William J. Libby (1973)

Some forest species are in the early stages of domestication, but the whole continuum from truly wild to domesticated crop can be found within one species. At the one extreme are species that occur on wildlands that have never been cleared and are of little commercial value for wood or food and, therefore, have not been altered; e.g., in North America, high-elevation species like whitebark pine (*Pinus albicaulis* Engelm.).

Other species have been slightly modified by selection for desirable characteristics; e.g., Siberian stone pine (*Pinus sibirica* Du Tour). Seed yield is correlated with bark type in Siberian stone pine; trees with "pine tree-like bark" produce higher yields than those with "spruce-like bark" (Pravdin 1963). Near some villages in the Urals, the proportion of trees with pine tree-like bark is as high as 89%, which is higher than the highest frequency in more remote forests and "cannot be considered as accidental"; over a period of at least two to three centuries, high yielding stone pine have been favored, and the resulting forests may be considered an early step in their domestication.

Several examples of partially domesticated tree crops were mentioned in the preceding section. Loblolly and slash pines are at this extreme of the continuum, approaching the level of domesticated crops.

Domestication often involves movement. Examples of Afghan pine, mango, and coconut were referred to above. Loblolly and slash pines, prime examples of trees domesticated for wood and fiber production, have been moved around the globe, planted on 2800000 ha in Asia, Africa, and Latin America (McDonald and Krugman 1986). The domesticated populations will diverge from the wild-type, increasing total diversity within the species. And the vast expansion in numbers increases the opportunity for the occurrence and recovery of new variants. However, native vegetation may be displaced by the domesticated species, and the net result could be a loss in global diversity. For example, the wild ancestor of cultivated maize may have been driven to extinction partly because it was displaced by the domesticated

form. The sites where wild maize grew may well be the sites chosen by Native Americans for their earliest cultivation (Mangelsdorf et al. 1964)

Domestication involves conscious, directional selection and is very effective in causing divergence from wild-type. In four generations of selection, about 16 yr, breeders in Florida improved volume growth 163% in flooded gum (*Eucalyptus grandis* Hill ex Maid.), a non-native species (Fig. 9; Meskimen 1983). After only one generation of breeding, Australian breeders increased wood volume of 10- to 12-yr-old Monterey pine, an endemic of coastal California, 9 to 29%, depending on test site (Eldridge 1982). Trees in the improved line also responded to selection for straight stem form and small branches.

Very few studies have compared the level of variation in breeding populations to natural populations, but in those few, the reduction in diversity, as measured by isozyme polymorphisms, was small or nil. Cultivated Monterey cypress (*Cupressus macrocarpa* Hartw.) had fewer alleles at a leucine aminopeptidase locus and the same number of alleles but fewer heterozygotes at an alcohol dehydrogenase locus than the native populations on the Monterey Peninsula (Kafton 1976). Muller-Starck (1987) found that genetic distances among seed orchards of Scots pine, calculated from isozyme frequencies, were greater than those among natural stands in Germany; this may reflect the founder effect because the number of clones in seed orchards is much less than the effective population in natural stands.

In addition to the effect of directed selection on the distribution of genetic variation within and among populations, inadvertent changes can occur as the result of cultural practices. Germination may be delayed because the length of seed stratification was insufficient for some seedlots or the nursery environment was unsuitable. If germination is delayed, growth is suppressed and the seedlings are subsequently culled. Lifting date may not match requirements for all seedlings in a nursery bed, so that root growth capacity is poor and some seedlings fail to survive when outplanted (Jenkinson 1984). Some seedlings may not recover from transplanting shock as well as others (Beineke and Perry 1966), a stress to which they are never subjected naturally. To the degree that variation in response to seed collection, seed cleaning, stratification, fertilization, and irrigation regimes, lifting date, seedling storage, and transplanting technique are genetically determined, mortality or cull may be selective and reduce diversity; Campbell and Sorensen (1984). Theisen (1980) and Kitzmiller (1990), described the various opportunities for management practices to influence genetic diversity. Despite efforts to maintain high levels of diversity in planted stands, management can have inadvertent effects as a result of mortality at any of the many steps in the process of artificial regeneration. Even if every seed or seedling was saved in the nursery, changes from the native pattern of genetic variation would still result because selec-

tive deaths occur as a result of planting practices and even the year of planting; e.g., cohorts of sugar maple differ genetically, probably as a result of differences in selection resulting from year to year climatic fluctuation (Mulcahy 1975).

Finally, domestication may provide the incentive for the protection and conservation of genetic diversity in the face of exploitation. Breeders establish and maintain clone banks and seed orchards to facilitate breeding and the production of improved lines. For example, over 8,000 loblolly pine clones were preserved by just one breeding cooperative in the southern United States (McConnell 1980). However, only a few species in the entire world are adequately conserved in breeding programs.

Conclusions

In seeking rigidly to preserve an ecological status quo, conservationists inevitably collide with both natural and human forces.

Walter E. Westman (1990)

Humans have impacted forests even prior to recorded history, and it is likely that future forests will have to sustain impacts at least as great as those of the past. If the human population continues to grow, forests will exist only within the context of societal needs. However, the most basic of those needs is a functioning, global ecosystem, which depends largely on the forests. Therefore, it is in our best interests to maintain diversity and promote system redundancy and resilience. In order to do that, we must understand the consequences of our actions for genetic diversity in all its aspects, intraspecific and interspecific.

Deforestation and exploitation, habitat fragmentation and degradation, introduction of new plants, animals, and microbes, and, of course, domestication affect the evolutionary processes of selection, gene flow, genetic drift, and mutation. However, society has only the vaguest notion of how extensive these impacts are, partly because ecologists and evolutionary biologists often prefer to work with pristine systems. Thus, for much of this review, I have been forced to speculate on the impacts of human activities.

Human-mediated transport of diseases, herbivores, and forest trees themselves has had probably the greatest, and best-documented, impact on biodiversity – overwhelmingly negative. Several forest species in North America have been eliminated by introduced diseases or are threatened with extinction – chestnut, American elm, sugar pine, eastern white pine, western white pine, Port-Orford-cedar, Florida Torreya. Introduced goats and other browsers have destroyed large segments of insular floras, and introduced ornamentals have escaped and displaced native species.

Transport of important commercial species, like coconut or loblolly pine, beyond natural barriers to their distribution has had positive effects on their genetic diversity; e.g., by increasing the opportunities for genetic divergence among populations. However, increases in the range or numbers of favored species must, in many cases, result in the displacement of native species and threaten their genetic diversity. Transport across geographic barriers also has facilitated hybridization between previously separated congeners. Hybridization releases new variation through recombination but does so at the risk of homogenizing flora on the global scale.

Reforestation by planting within a species' native range is another example of human-mediated transport. The movement of seed without regard to its origin was common as recently as a half-century ago. If trees in off-site plantations cross with those in native populations, diversity may increase in the next generation but with negative consequences for local adaptation. Unfortunately, the consequences are difficult to document. Because records have been poorly kept, we cannot even tell how much "off-site" planting has occurred.

Environmental degradation is the secondmost important influence on genetic diversity, not so much for its impact in the past as for its future threat. Environmental degradation on regional and global scales is already responsible for forest decline and probably will affect genetic structure by directional selection. Genetic variation with respect to pollutants has been demonstrated, but long-lived perennials may be least able to respond to the multiple stresses of oxidants, heavy metals, and global warming. Monitoring efforts are needed to provide a warning of changes, which likely will be progressive and escape notice until well-advanced.

The process of domestication has obvious consequences for domesticated populations. It increases total variation by isolation of breeding populations and divergent selection. Selection, inadvertent and directed, has led to the origin of new land races, improved in economic value. However, domesticated lines impact conspecific native populations through gene migration or "contamination" of native gene pools. The consequences are not easily predicted.

Intuitively, deforestation must have impacted genetic diversity because it has occurred on such a broad scale over such a long period and has resulted in the extirpation of local populations. However, the genetic effects may be remediable unless entire species have been lost; given a few centuries or a millennium, trees may again invade abandoned fields and adapt to local environments. Forest flora has suffered similar massive disruptions in the geologic past as glacial ages waxed or waned in the temperate and boreal latitudes and as regional patterns of precipitation changed in the tropics (Prance 1978). Deforestation has often led to soil erosion and site deterioration, and alteration of habitat has created opportunities for invasion of new floras and,

most notably in the present context, to hybridization between related species previously separated by their environmental tolerances.

The effects of exploitation on forest trees is more ephemeral than deforestation. When animals, such as the elephant, are hunted, the effects of population reduction on behavior and reproduction can be disastrous. But when all the commercial *ceiba* are harvested along the Amazon of Peru (Gentry and Vasquez 1988), small trees still remain in the understory and gaps. Given the long life of forest trees, these will persist, and a century later may even fuel a new wave of exploitation. Local genetic structure may be altered by selection and by changes in demography and in the mating system, but, in all probability, gene diversity and geographic structure will be little affected.

Demographic changes under forest management have increased variation in some species; the great expansion in numbers for species favored because of their commercial value has increased the opportunity for mutation and the recovery of new variants. Changes in the age structure, almost invariably toward younger forests, has encouraged epiphytotics and, therefore, intensified selection for disease and pest resistance.

Fragmentation will have its most significant effect because of demographic stochasticity. Reduction in numbers per se will pose a danger for outbreeding forest-species. Although the breeding system of many is flexible enough to tolerate some inbreeding (Bannister 1965), inbreeding will drastically reduce reproductive output, increasing the chance of reproductive failure. If a species is eliminated from a forest remnant by chance events, it will be unable to recolonize from other fragments because migration corridors are blocked. On the positive side, genetic variance actually increases under inbreeding in early generations, which can lead to rapid evolutionary change.

Human impacts on forest composition, and probably on the genetic structure of forest species, is not new. What is new is the rapidity with which changes are now occurring, perhaps exceeding the capacity of most long-lived species to respond. If anything like the present level of biodiversity is to remain a century from now, society must actively intervene to reduce stresses and remove barriers to migration. Moreover, we must be more alert to the consequences of our technology than we have in the past.

However, we can scarcely demonstrate human impacts on forest diversity because there have been – and still are – few baselines against which to gauge the present condition. Perhaps, historical impacts on diversity could be quantified by comparing restriction fragment length polymorphisms in DNA from herbarium specimens or other preserved materials to extant populations. The tools to measure present levels of genetic diversity are readily available, and using them will provide an early warning of adverse impacts and a chance to take remedial action. We urgently need new,

institutionalized programs to inventory genetic diversity of forest species in both temperate and tropical forests, and then periodically monitor them to determine if and when intervention is necessary to protect their health – and society's.

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