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Review

Anthropogenic alterations of genetic diversity within tree populations: Implications for forest ecosystem resilience

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ABSTRACT

Healthy forests provide many of the essential ecosystem services upon which all life depends. Genetic diversity is an essential component of long-term forest health because it provides a basis for adaptation and resilience to environmental stress and change. In addition to natural processes, numerous anthropogenic factors deplete forest genetic resources. Genetic losses could be particularly consequential now because robust resilience is needed to respond to a growing number, variety, and frequency of stress exposures. Silvicultural management that selectively removes trees (and their genes) from forests may be another force reshaping forest gene pools. Although data concerning the influence of silvicultural management on genetic resources in temperate forests is somewhat mixed, through the genetic assessment of long-term silvicultural treatments within an eastern hemlock (*Tsuga canadensis*) forest, and computer-based simulated harvests of a genetically mapped eastern white pine (*Pinus strobus*) stand, we found that the selective removal of trees can alter gene frequencies. Due to an association with phenotypic characteristics used to guide harvests, the frequencies of rare alleles appeared particularly vulnerable to manipulation. Depending on the selection criteria used, rare allele frequencies either remained steady, decreased, or increased relative to study controls. Although harvest-associated genetic losses are possible, our data suggests that management can also sustain or enhance genetic richness. Similar to studies within temperate ecosystems, recent research in tropical forests underscores the potential influence of harvesting on the genetics of tree populations. In addition to efforts to reduce controllable sources of ecosystem stress (e.g., high pollutant exposures), management options should be evaluated that may bolster forest ecosystem resilience by preserving levels of genetic diversity within forests.

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1. The importance of ecosystem resilience

All terrestrial ecosystems are exposed to changes in climate, nutrient or chemical loading, habitat fragmentation, and biotic loss or harvest. These changes are often gradual and initiate smooth adjustments that provide for dynamic stability within existing communities or progressive transition to new assemblages. This capacity to adjust to environmental perturbation without meaningful loss of biological or ecological function is a defining characteristic of ecosystem resilience (Rapport, 1998). Despite inherent capacities to resist change, sudden and/or severe environmental perturbation can push ecosystems beyond their limits of resilience, and result in catastrophic shifts to alternative ecological states (Scheffer et al., 2001). These ecosystem shifts can cause marked losses of ecological and economic resources, and ecosystem restoration may require considerable and expensive intervention (Scheffer et al., 2001). Considering the potential consequences and costs of ecosystem disruption, prevention of this damage has become an important management objective. A major goal of ecosystem management has typically been the prevention of perturbations rather than the fostering of ecosystem resilience. However, this is not entirely a practical approach because stochastic events that trigger ecosystem shifts are usually difficult to predict or control. Furthermore, some disturbances (e.g., fire and hurricanes) are natural components of ecosystems and help promote diversity and renewal processes. In contrast, the maintenance of ecosystem resilience through thoughtful management could offer a more pragmatic approach for safeguarding ecosystems and the critical services they provide that support biological and social health (Costanza et al., 1997). This safeguard may be particularly beneficial now as ecosystems worldwide experience an ever-increasing burden of anthropogenic alteration. Indeed, the simultaneous erosion of factors that support resilience at the individual and population levels, combined with elevated stress exposure, may be a dual threat of unprecedented nature and scope (Fig. 1). Because genes are at the foundation of biological function and response, alterations of genetic diversity are uniquely consequential and worthy of analysis (DeHayes et al., 2000).

2. Genetic diversity and ecosystem resilience

Genetic diversity, including the presence of rare alleles, has repeatedly been shown to be important to the survival of a range of biological populations due to the development of resistance following exposure to a variety of selective forces. The increasing resistance of bacteria to antibiotics (Abramson and Sexton, 1999), insects to pesticides (Georghiou, 1991), herbaceous "weeds" to herbicides (Heap, 1997), and tree species to air pollution (Berrang et al., 1989) provide noteworthy examples of how humans are altering evolutionary trajectories (Palumbi, 2001). These cases also illustrate that, when the three requirements for evolution by natural selection are present (i.e., a species is genetically variable for a trait, that trait influences the survival or reproductive success of the species, and differences in that trait are heritable), then the presence of genetic variability provides the foundation for adaptation and long-term resilience within a population.

Although essential to the long-term health and survival of all biological populations, genetic diversity may be particularly critical to the health of forest trees, because they have limited mobility, are slow to reach reproductive maturity, and are likely to encounter significant environmental change during their long lifespans. Indeed, relative to the many organisms evaluated, trees are among the most genetically variable organisms on earth (Bush and Smouse, 1992).

3. Natural selection and genetic diversity

Although some have found little association between levels of heterozygosity and fitness (e.g., Linhart and Mitton, 1985; Savolainen and Hedrick, 1995), many studies have noted a positive

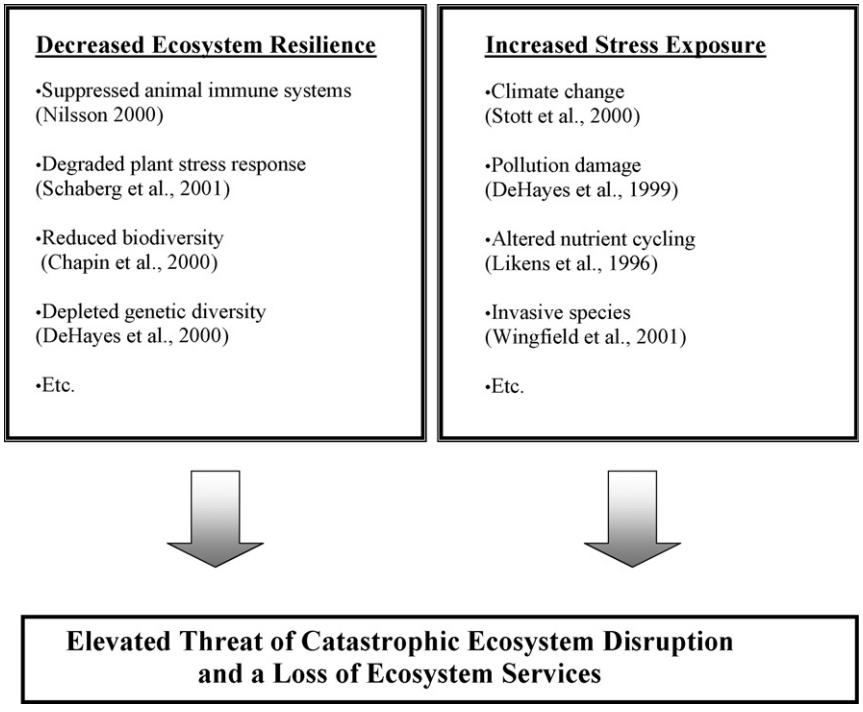

Fig. 1. Conceptual model of the evolving dual threat (decreased ecosystem resilience and increased environmental stress exposure) that may result from unfettered anthropogenic alteration of natural systems. (see refs. Chapin et al., 2000; DeHayes et al., 1999; Likens et al., 1996; Nilsson, 2000; Schaberg et al., 2001; Stott et al., 2000; Wingfield et al., 2001).

relationship between genetic diversity and various fitness measures (e.g., Knowles and Grant, 1981; Mitton et al., 1981; Neale and Adams, 1985; Jelinski, 1993; Li and Wu, 1996; Arcade et al., 1996; Aravanopoulos and Zsuffa, 1998; Li et al., 1998; Mosseler et al., 2003). Considering the potential adaptive benefits of genetic diversity, it is not surprising that natural forces can help maintain or even enhance diversity levels within a population. This pattern was evident in the results of a novel study we conducted to evaluate the influence of natural thinning on the genetic structure of jack pine (*Pinus banksiana*) forests. Rather than conduct repeated evaluations of genetics within one population throughout the course of stand development (a process that would extend over many decades), we compared four distinct, geographically overlapping jack pine populations of different uniform ages at one point in time (Hawley et al., 1989). Five unique attributes of the study site helped foster waves of regeneration that shared a similar genetic base: (1) a large (1600 ha) panmictic population with no obvious internal barriers to gene flow, (2) limited gene migration due to isolation from the species' contiguous range, (3) a uniform environment with constant elevation and soils, (4) four lightning-induced fires that resulted in four adjacent, but distinct, even-aged populations of this uniquely fire-adapted species (22, 30, 47, and 68 years old), and (5) nearly 100% of cones were serotinous, so regeneration following fire incorporated seed from multiple years. Similar gene frequencies (derived from electrophoretic assessments at 25 loci for 36 trees per population) supported our assumptions that all the stands resulted from a common genetic base.

Thinning, stimulated by natural competition that was undisturbed by humans, reduced tree densities by nearly 75% between ages 22 and 68. Genetic diversity estimates indicated that gene frequencies and expected heterozygosity (H_E) estimates were not statistically different for the four populations (ANOVA). However, observed heterozygosity (H_O) in the oldest population ($H_O = 0.278$) was significantly higher than the youngest population ($H_O = 0.2203$; Table 1). In the youngest population, H_O was significantly lower than H_E and the population fixation index ($1-(H_O/H_E)$, averaged for all loci) was +0.117, indicating a higher than expected occurrence of homozygous loci, possibly due to mild inbreeding from natural family structuring. In the oldest population, H_O was significantly higher than H_E and the overall population fixation index was −0.090, suggesting a greater concentration of heterozygous loci than expected, presumably as a result of natural selection.

Why would natural selection favor heterozygotes? Two explanations are typically offered to explain heterosis (hybrid vigor). The first involves the concept of *inbreeding depression* or *dominance*, which hypothesizes that individuals with heterozygous loci have a selective advantage over individuals that are homozygous for deleterious recessive alleles. Another possibility involves *overdominance*: the presumed benefit of increased physiological plasticity provided by the ability of heterozygous loci to express more than one form of a gene. Although conflicting data exists (Rieseberg et al., 2000), breeding experiments support dominance as being the primary mechanism for heterosis in crop plants such as maize. Among other lines of evidence, studies consistently show that inbred lines have higher yields than would be expected if overdominance had a strong influence (Crow, 2000; Rieseberg et al., 2000). However, experiments with tree species have often found evidence of overdominance as a significant contributor to heterosis (Ledig et al., 1983; Bush et al., 1987; Li and Wu, 1996; Arcade et al., 1996; Li et al., 1998). Indeed, as suggested by our data for jack pine, dominance and overdominance are not exclusive of one another, and both mechanisms may help shape the genetic structure of forest populations.

Whatever the mechanism(s) involved, numerous other studies support the hypothesis that natural selection favors genetic diversity expressed as heterozygosity. Notably, an association between heterozygosity and growth rate and/or variability has been reported for a range of tree species and their hybrids (e.g., Knowles and Grant, 1981; Mitton et al., 1981; Neale and Adams, 1985; Jelinski, 1993; Li and Wu, 1996; Arcade et al., 1996; Aravanopoulos and Zsuffa, 1998; Li et al., 1998; Mosseler et al., 2003). One interpretation of this association is that cumulative exposure to an array of stressful conditions over time helps eliminate individuals low in heterozygosity and favors heterozygotes that can better adjust growth to accommodate varying environmental pressures. A biochemical mechanism for hybrid growth vigor has also been proposed. Milborrow (1998) hypothesized that the multi-allele expression afforded by heterozygosity might allow for a partial relaxation of endogenous regulations that can constrain growth, and result in enhanced growth potential.

Table 1
Comparison of the density and genetics of four jack pine populations of differing sizes that resulted from periodic fires within a uniform site in north eastern New York, USA

Measured characteristic	Population age			
	22	30	47	68
Reduction in stand density (%) relative to age 22	–	12	63	73
Observed (H_O) heterozygosity	0.203	0.242	0.227	0.278
Expected (H_E) heterozygosity	0.233	0.252	0.234	0.252
Statistical difference between H_O and H_E	*	ns	ns	*
Fixation index	+0.117	−0.007	−0.001	−0.090

Data based on Hawley et al. (1989). *H_O and H_E significantly different ($P < 0.05$) based on *t*-tests. ns: H_O and H_E not significantly different based on *t*-tests.

4. Anthropogenic threats to genetic diversity

Considering the fundamental importance of genetic diversity to the continued adaptability, health, and long-term productivity of tree populations, a loss of genetic diversity (whatever the cause) could be a serious threat to forest ecosystems and the many products and services they provide to all life forms. This generalized threat is particularly serious today as a result of escalating human activity that has not only initiated pervasive and sometimes dramatic changes in the earth's environment, but has also led to measurable declines in the genetic diversity of at least some tree populations.

Whereas elevated genetic diversity may help a population persist and prosper despite moderate selective pressure, extreme and/or novel selective pressure can overwhelm the capacity of a species to adapt. Tree species declines following the introduction of exotic pathogens provide vivid examples of this. For example, chestnut blight (caused by the fungus *Cryphonectria parasitica*) was the first introduced pathogen to measurably alter the viability of an indigenous tree species in North America. First detected at the New York Zoological Park in 1904, the disease virtually eliminated the American chestnut (*Castanea dentata*) throughout its range within 50 years (Tainter and Baker, 1996). Dutch elm disease (caused by the fungus *Ophiostoma ulmi*) provides another vivid example: through one outbreak in North America and two in Europe, the majority of elms (e.g., *Ulmus americana* and *Ulmus glabra*) were killed within only a few decades following the accidental introduction of this pathogen native to Asia (Tainter and Baker, 1996). Examples of the impact of exotic species on forest health are not limited to historical accounts of introduced pathogens; contemporary introductions of the hemlock wooly adelgid (*Adelges tsugae*) and the Asian longhorn beetle (*Anoplophora glabripennis*) to

North America may yet result in the functional removal of other keystone forest species. Yet, even for the dramatic cases of chestnut blight and Dutch elm disease where population (and presumably gene) losses have been extreme, rare alleles may form the basis of species survival. Rare genotypes resistant to both chestnut blight and Dutch elm disease have been identified and are critical to species recovery efforts (Cheng et al., 1997; Griffin, 2000). However, remnant individuals from heavily depleted populations are unlikely to contain the breadth of genetic resources favorable for competitive success across a species' historical range, and may be particularly inadequate for populations simultaneously burdened by an increasing number and intensity of anthropogenic stresses.

Although the legacies of chestnut blight and Dutch elm disease provide prominent examples of the potential consequences of dramatic population declines, the intensity of selection may not have to be this overwhelming to alter the long-term health and survival of trees. Some evidence suggests that simply by narrowing gene pools, moderate anthropogenic selection may diminish the potential of a species to adapt to further environmental change. The response of native plants to air pollution exemplifies this possible effect.

Similar to the influence of natural competition, evidence from an assortment of tree species indicates that selection associated with prolonged pollutant exposure often favors heterozygotes (Müller-Starck, 1985, 1989; Oleksyn et al., 1994; Bergmann and Hosius, 1996; Prus-Glowacki et al., 1999). Pollution tolerant individuals can also harbor unique gene forms that may contribute to their resilience as well as the adaptive potential of the population (Müller-Starck, 1985; Mejnartowicz and Palowski, 1989). Findings such as these support the proposition that genetic diversity can help populations adapt to and survive environmental stress. However, pollution-induced mortality or genetic drift (random changes in gene frequencies most pronounced in small isolated populations) within restricted areas exposed to high pollutant loads may also result in gene loss (Agrawal and Agrawal, 2000). Several studies have documented that pollution-sensitive individuals can harbor rare alleles not generally found elsewhere (Müller-Starck, 1989; Bergmann and Scholz, 1987; Longauer et al., 2001). Consequently, although pollution sensitivity may partially reflect the deleterious effect of rare alleles under conditions of air pollution exposure (Longauer et al., 2001), pollution-induced mortality can also result in the loss of certain gene forms, and contribute to the depletion of a stand's genetic base (Müller-Starck, 1989; Bergmann and Scholz, 1987; Longauer et al., 2001). Among other measures, this loss of genetic potential has been detected as an impoverishment of genes and genotypes among the progeny of stands growing under high pollutant stress (Mejnartowicz, 1983, 1986).

5. Silvicultural selection and genetic structure

Although many human influences may work to reduce the genetic diversity within forest stands, another factor that could alter the gene pools of woodland ecosystems is forest management. For example, artificial regeneration with reproductive material of unknown origin can change genetic structures in unpredictable ways (Finkeldey and Ziehe, 2004). Furthermore, intensive or selective silvicultural harvesting can reduce population densities or population sizes, thereby reducing gene exchange, increasing inbreeding, and potentially elevating the possibility of genetic drift (Finkeldey and Ziehe, 2004). However, by some accounts, selective logging systems with short harvest cycles pose the greatest threat to genetic variation patterns at gene loci coding for economic and adaptive traits (Finkeldey and Ziehe, 2004).

Silvicultural selection represents an anthropogenic selective force in which sometimes large numbers of trees (and the genes they contain) are removed from a natural system within a relatively short period of time. Certainly, tree harvests are critical to supply human resource needs. Indeed, an important premise of silvicultural selection is that the prudent removal of select trees can foster favorable commercial attributes (e.g., fast growth, good form, etc.) in both residual trees (through an improvement of current growing conditions) and their progeny (through a manipulation of the gene pool), while simultaneously safeguarding environmental quality. Still, the long-term impact of tree removals to the genetic base and ecological resilience of forests remains largely unknown.

Can timber harvesting alter forest gene pools and, as a result, the long-term health and productivity of forest communities? Do various types or intensities of harvest differentially impact the gene pool? How might these potential impacts differ among species? Studies that have examined these questions within temperate forests have produced mixed evidence of the influence of timber harvesting on genetic resources. For example, Neale (1985) found that shelterwood harvesting had little impact on the genetic structure of Douglas fir (*Pseudotsuga menziesii*) forests. El-Kassaby et al. (2003) reported that silvicultural treatment caused no significant differences in measured genetic parameters for amabilis fir (*Abies amabilis*), but that a shelterwood treatment resulted in lower H_O and H_E in western hemlock (*Tsuga heterophylla*). In contrast, Cheliak et al. (1988) reported that phenotypically selected white spruce (*Picea glauca*) trees possessed on average only 75% of the genes found among randomly selected trees from the same population, indicating that phenotypic selection resulted in gene loss. Buchert et al. (1997) found that when eastern white pine (*Pinus strobus*) received a 75% density reduction harvest that preferentially retained trees with old-growth characteristics (e.g., large size), the total number of alleles was reduced by 25% and the percent polymorphic loci decreased by 33%. Importantly, this phenotypically directed harvest resulted in an 80% reduction in rare alleles and a 40% reduction in low frequency alleles. This preferential loss of rare alleles was also found when microsatellite DNA analysis was used to evaluate the genetic effects of harvesting for this species (Rajora et al., 2000). For coastal Douglas-fir, Adams et al. (1998) found that, although various regeneration methods appeared compatible with gene conservation, removal of the smallest trees to form shelterwoods of large trees resulted in a reduction of rare alleles relative to uncut control stands.

Our recent work has also highlighted the potential for harvest-induced alterations of genetic resources. For one study, we evaluated the influence of long-term silvicultural treatment on the genetic structure of an eastern hemlock (*Tsuga canadensis*) forest in the Penobscot Experimental Forest in eastern Maine, USA (Hawley et al., 2005). We compared genetic diversity parameters of an unmanaged control stand with those of stands that had undergone either selection cuts (smaller trees and ones with poor form preferentially removed) or fixed diameter limit cuts (largest trees in each diameter class preferentially removed) through a series of harvests over the past 40 years. Starch-gel electrophoresis of megagametophyte tissue was used to examine 27 gene loci representing 19 enzyme systems for 106 individual trees. Results of these analyses revealed that both silvicultural treatments appeared to contain fewer rare alleles relative to the control (Table 2). For the selection cut, the repeated removal of small, poor-formed trees was associated with fewer rare alleles (5 alleles no longer detected compared to the control), and a reduction in the estimated number of the genotypes that could arise from the stand given random mating (i.e., genetic multiplicity). For the diameter

Table 2
Measures of genetic diversity for mature eastern hemlock trees in an unmanaged control stand and residual trees in two adjacent silvicultural treatment stands in east-central Maine, USA

Stand parameter	Treatments		
	Control	Diameter limit cut	Selection cut
Number of trees	35	31	40
Mean observed heterozygosity (Ho)	0.087	0.112	0.083
Total # of rare alleles	9	5	4
Total # of low frequency alleles	2	8	4
Percent trees with alleles that were rare in the control	29	68	34
Percent trees homozygous for alleles that were rare in control	0	42	5
Lost alleles relative to control	–	2	5
Genetic multiplicity[a] (millions)	1.26	11.34	0.1

Data based on Hawley et al. (2005).
[a] An estimate of the potential number of different genotypes possible within the stand given measured genetic information and assuming random mating (Bergmann et al., 1990).

limit cut, the apparent loss of rare alleles was driven by an increase in the frequency of some alleles that were rare (occurred in <5% of individuals) in the control, but now occurred at a higher frequency (i.e., were low frequency alleles that occurred in up to 25% of individuals) in the treated stand (Table 2). Even though a fewer total number of alleles were considered rare, the percent of trees with alleles that were rare in the control stand was about double for the diameter limit cut relative to the control. In fact, 42% of trees in the diameter limit stand were homozygous for some allele that was rare in the control, compared to 0% in the control stand itself. This concentration of unusual gene forms (rare or low frequency alleles, often in a homozygous form) resulted in a 10-fold increase in the estimated number of genotypes potentially generated by the diameter limit stand compared to the control. Probably because of an association between rare alleles and the negative phenotypes (small size, poor form, etc.) preferentially retained, the diameter limit treatment resulted in a residual stand with greater genetic diversity. However, any potential benefits in long-term adaptive flexibility afforded by this were likely accompanied by a meaningful tradeoff: a reduction in stand fitness and productivity under existing environmental conditions. By repeatedly removing larger competitors, gene forms that were rare (presumably because they imparted reduced fitness) following natural selection in the control plot, were allowed to proliferate in the diameter limit stand. This concentration of marginally fit individuals was associated with reduced woody biomass accumulation relative to the selection treatment (Hawley et al., 2005). This concentration could also jeopardize the production of other ecosystem services that utilize competition and natural selection to promote the biological and ecological efficiencies that help optimize ecosystem function. For example, the preferential retention of smaller, slower growing trees could reduce rates of nutrient uptake and recycling, decrease the competitive capacity of native trees to protect against invasive species establishment and proliferation, or alter other ecological functions within the stand.

Although natural selection tends to remove phenotypes that are functionally inferior under current selective conditions, the interplay of environmental heterogeneity and stochastic events also allows some gene forms to persist at low frequencies despite minor contemporary fitness costs. An accumulation of these genetic variants contributes to the genetic load within forest species, and native tree populations are usually heterozygous for a large number of deleterious recessive alleles (Wright, 1976). However, rare alleles are also a reservoir of adaptive potential (Palumbi, 2001). Evidence from a range of organisms including bacteria (Abramson and Sexton, 1999), insects (Georghiou, 1991), herbaceous plants (Heap, 1997), and trees (Berrang et al., 1989; Cheng et al., 1997) have shown that rare alleles provide the basis of survival despite strong selection pressure. Indeed, Yanchuk and Wheeler (2008) identified at least 20 breeding programs that have used naturally occurring rare alleles to develop trees with improved resistance to targeted insect pests or pathogens. In general, natural selection supports the productive capacity of ecosystems in the short-term through the preferential reproductive success of gene forms best fit under current environmental conditions. However, because it is variable and incomplete, natural selection also accommodates long-term flexibility through the accumulation of gene variants that are the starting point for ongoing adaptation. Considering this, one of the great risks of anthropogenic selection might be its ability to overwhelm natural selection and disrupt the balance between fitness and flexibility that sustains ecosystem health across time scales.

As another approach to examine the possible influence of silvicultural selection on genetic structure, we established a computer-based genetically mapped model forest (Nijensohn et al., 2005). Our model was built using data from an approximately 10 ha stand dominated by mature eastern white pine in central Vermont. Data collected included information on tree size, age, growth, vigor, crown class, and spatial location of the over 220 white pine trees comprising this stand. Genetic information was obtained for all trees using starch-gel electrophoresis to examine 46 gene loci (26 which exhibited polymorphisms) from 19 enzyme systems. Within this framework, we were able to assess patterns of genetic structure relative to the various data layers in the model (e.g., tree age, location, etc.). We then conducted simulated harvests that employed the virtual removal of trees from the database to examine how different harvest scenarios influenced genetic structuring relative to the original stand and compared to random harvests of equal sampling intensity.

Results of these analyses revealed significant genetic structuring within the stand (Nijensohn et al., 2005). For example, when the stand was divided into five equal-sized age classes, it became evident that these classes differed in both observed heterozygosity and number of rare alleles (Table 3). Similar patterns were detected for tree location and crown class (Nijensohn et al., 2005). Considering these patterns, although most simulated harvests did not significantly after genetic parameters of the residual stand, harvests that targeted parameters associated with detected structuring did alter stand genetics. For example, when the oldest merchantable trees were preferentially removed, mean Ho significantly decreased relative to the random removal of an equal number of trees (e.g., $P \leq 0.05$ for a 43% intensity cut, and $P \leq 0.01$ for a 68% harvest, based on Monte Carlo simulations). These simulated harvests also significantly reduced the number of rare alleles in the residual stand relative to random harvests (e.g., $P \leq 0.03$ for a 43% cut, and $P \leq 0.06$ for a 68% harvest).

Table 3
Differences (*P*-values) in observed heterozygosity (H_O) and the number of rare alleles among five equal-sized age classes of mature eastern white pine trees within a genetically mapped forest in central Vermont, USA

Genetic diversity parameter	Age class (years)					
	60–67	68–71	72–77	78–86	87–118	P^a
Average H_O	0.095	0.103	0.116	0.117	0.102	0.02
Average # rare alleles	0.864	0.659	1.204	1.341	0.795	0.03

Data based on Nijensohn et al. (2005).
[a] Probabilities of statistical differences among age classes determined using analyses of variance.

It should be emphasized that not all harvest scenarios had a neutral or negative impact on genetic diversity measures. When harvesting criteria preferentially retained portions of the stand that concentrated unusual gene forms or combinations, genetic diversity was often enhanced. For instance, when the youngest 25% or 50% of trees were removed from the stand, observed heterozygosity significantly increased ($P \leq 0.05$) relative to the original stand (Nijensohn et al., 2005). In addition, similar to our results for eastern hemlock, when suppressed trees were preferentially retained, the residual forest had a higher frequency of trees with rare alleles (Nijensohn et al., 2005). The reappearance of this association between rare alleles and low competitive performance further highlights the possibility that a proliferation of uncommon gene forms could result in a forest that is ill-equipped for optimal productivity and ecosystem function under current conditions.

Similar to studies within temperate ecosystems, recent research in tropical forests underscores the potential influence of harvesting on the genetics of tree populations. For example, André et al. (2008) found a significant reduction in the number of alleles, H_O, and distinct multilocus genotypes in a mahogany (*Swietenia macrophylla*) population post-harvest as compared to pre-harvest. In a *Hymenaea courbaril* population, Lacerda et al. (2008) noted that a 61% harvest of the reproductive trees caused a loss of 37 low frequency and rare alleles from the mature population (although 24 of these "lost" alleles remained in younger age classes). Similarly, Silva et al. (2008) reported that three alleles no longer detected among older trees following harvest were retained by younger cohorts. In contrast, Obayashi et al. (2002) found that selective logging did not significantly alter the mean heterozygosity or the effective number of alleles of mature trees, but did significantly reduce the average number of alleles derived from pollen donors, raising the possibility of a loss in genetic variation for future generations. Other research with a eucalyptus (*Eucalyptus consideniana*) detected significant reductions of allelic richness, effective number of alleles, and H_E in regeneration following one silvicultural treatment (a seed tree system), but not another (a clear felling system followed by aerial seeding) (Glaubitz et al., 2003). Studies employing computer-based simulated harvests also indicate that tropical forests are at risk of allelic loss following harvests (Degen et al., 2006; Sebbenn et al., 2008), although these apparent losses are predicted to be transient in populations with overlapping generations (Degen et al., 2006).

Evaluations of actual and simulated harvests in both temperate and tropical forests highlight that, for at least some tree species and management regimes, silvicultural selection can alter the frequency and existence of alleles within local populations. While rare alleles are more vulnerable to rapid depletion than more common ones, extended bottlenecks persisting over generations are predicted to cause more wide-spread and severe depletions of genetic diversity (Lande, 1988). Simulation of the influence of habitat degradation for neotropical trees supports the possibility that broader genetic depletions occur over longer periods, especially when gene flow is limited (Lowe et al., 2005).

6. Understanding and managing genetic diversity

Although it appears that genetic resources within forests are vulnerable to manipulation, study is needed to assess the extent of the threat posed to forest ecosystem health as a result of anthropogenic genetic alteration. For example, it is often assumed that high outcrossing rates associated with pollen and seed dispersal from surrounding uncut stands could maintain genetic richness within populations under silvicultural management (Hamrick, 2004). However, patterns of genetic structuring within forests have shown that the effective bounds of gene flow may be quite limited—often less than 35 m for wind pollinated pines (Epperson and Chung, 2001; Rajora et al., 2002; Robledo-Arnuncio et al., 2004; Nijensohn et al., 2005). Results of recent models of pollen flow on a landscape scale also indicate that pollen movement is more restricted than previously suspected (Smouse et al., 2001; Sork et al., 2002; Irwin et al., 2003). However, dispersal distances for insect-pollinated species can be much further (e.g., from 75 to 1500 m depending on the tree species and insect pollinator; Nason and Hamrick, 1997; Dick et al., 2003; Cloutier et al., 2007; Silva et al., 2008). Furthermore, although some studies have found little influence of harvesting on pollen flow (Cloutier et al., 2007), others have found significant reductions in pollen dispersal with cutting (Dick et al., 2003), whereas others have noted an increase in dispersion following harvest (Sork et al., 2005). Apparent conflicts in the literature regarding the influences of harvests on stand genetics and pollen flow likely reflect, in part, the ecological and life history differences among the species studied. However, these differences also spotlight many nuances and uncertainties that one confronts when assessing human influences on genetic resources.

Many fundamental questions must be addressed in order to assess likely levels of ecological risk or gain associated with anthropogenic manipulation of genetic resources within forest stands. Which human activities most deplete genetic reserves? What species and/or populations are most vulnerable to alteration? Which management options most limit genetic losses or increase levels of diversity and gene flow? Issues that warrant specific attention include:

(1) the impacts of varied, complex, and rapid environmental change (including multi-pollutant exposures) on genetic resources,
(2) the effect of silvicultural selection criteria and harvest intensity on the genetic structure and mating systems of various tree species and forest types,
(3) the influence of genetic diversity on competition, selection, and survival following invasive species introductions,
(4) the possible combined or interactive effects of anthropogenic and natural forces on genetic resources,
(5) the use of integrated pest management to diversify control strategies and reduce the intensity of pest-related selection pressures,
(6) the potential role of federal and state lands (e.g., National Forests), and other areas of limited development (e.g., ski areas), as genetic reserves or sites for the possible establishment of managed refuge plantings, and
(7) the influence of land use planning on the establishment and preservation of forest corridors that reduce forest fragmentation, assist gene flow, and help maintain genetic diversity and adaptation potential.

Clearly, many gaps exist in our current understanding. Yet the fundamental knowledge that genetic richness is both critical to long-term population health and is also susceptible to anthropogenic manipulation underscores the necessity of considering gene conservation when managing forest ecosystems. Ideally, forest landscapes should not only be managed to optimize current fitness and commodity flow, but also to preserve forests as dynamic evolutionary systems (evosystems: Gordon et al., 1992) where the adaptive potential of populations is safeguarded into the future. Specific methodologies for this "adaptability management" (management that preserves genetic richness and adaptive potential of forest systems) will require time and concentrated effort to develop. Essential to this broadened management approach is the shift in perspective that follows the realization that forests harbor patterns of genetic structuring that are vulnerable to modification through silvicultural selection.

7. Conclusions

Ecosystem resilience is an important component of ecosystem health that is vulnerable to anthropogenic degradation, but also shows the potential for enhancement through enlightened management. Within-species genetic diversity, perhaps especially the presence of rare alleles, is a component of ecosystem resilience that exemplifies this convergence of risk and potential benefit. Rare alleles provide a basis for population adaptation and survival following environmental change. However, the distribution of rare alleles can also coincide with phenotypic characteristics used as silvicultural selection criteria. Because of this, some silvicultural prescriptions can decrease the frequency of rare alleles within residual stands whereas others can increase rare allele frequencies relative to baseline levels established through natural selection. Management-associated shifts in gene frequencies may alter the balance between current fitness and long-term adaptive potential that sustains forest health, productivity, and the perpetuation of vital ecosystem services across time scales. Yet, the association of rare gene forms with phenotypic selection criteria also raises the possibility that silvicultural management could be used as a tool to help conserve genetic variation within forest stands.

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