
Beyond Kyoto: Forest Management in a Time of Rapid Climate Change

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Abstract: Policies to reduce global warming by offering credits for carbon sequestration have neglected the effects of forest management on biodiversity. I review properties of forest ecosystems and management options for enhancing the resistance and resilience of forests to climate change. Although forests, as a class, have proved resilient to past changes in climate, today's fragmented and degraded forests are more vulnerable. Adaptation of species to climate change can occur through phenotypic plasticity, evolution, or migration to suitable sites, with the latter probably the most common response in the past. Among the land-use and management practices likely to maintain forest biodiversity and ecological functions during climate change are (1) representing forest types across environmental gradients in reserves; (2) protecting climatic refugia at multiple scales; (3) protecting primary forests; (4) avoiding fragmentation and providing connectivity, especially parallel to climatic gradients; (5) providing buffer zones for adjustment of reserve boundaries; (6) practicing low-intensity forestry and preventing conversion of natural forests to plantations; (7) maintaining natural fire regimes; (8) maintaining diverse gene pools; and (9) identifying and protecting functional groups and keystone species. Good forest management in a time of rapidly changing climate differs little from good forest management under more static conditions, but there is increased emphasis on protecting climatic refugia and providing connectivity.

Después de Kyoto: Manejo Forestal en Tiempos de Cambio Climático Acelerado

Resumen: Las políticas para reducir el calentamiento global mediante créditos para el secuestro de carbono han pasado por alto los efectos del manejo forestal sobre la biodiversidad. Reviso las propiedades de los ecosistemas forestales y las opciones de manejo para reforzar la resistencia y la elasticidad de los bosques ante el cambio climático. Aunque los bosques han demostrado elasticidad a cambios climáticos en el pasado, los fragmentados y degradados bosques actuales son más vulnerables. La adaptación de especies al cambio climático puede ocurrir por medio de la plasticidad fenotípica, evolución o migración a sitios adecuados, siendo probablemente ésta la respuesta más común en el pasado. Entre las prácticas de uso y manejo de suelo que pueden mantener la biodiversidad y funciones ecológicas de los bosques durante el cambio climático se cuentan 1) representar tipos de bosques en reservas en gradientes ambientales; 2) protección de refugios climáticos en escalas múltiples; 3) protección de bosques primarios; 4) evitar la fragmentación y proporcionar conectividad, especialmente paralela a gradientes climáticos; 5) proporcionar zonas de amortiguamiento para ajustar límites de reservas; 6) prácticas forestales de baja intensidad y evitar la conversión de bosques naturales a plantaciones; 7) mantenimiento de regímenes de fuego natural; 8) mantenimiento de pozas génicas diversificadas; 9) identificación y protección de grupos funcionales y especies clave. El manejo adecuado de bosques en tiempos de cambios climáticos rápidos difiere poco del manejo adecuado de bosques bajo condiciones más estáticas, pero tiene mayor énfasis en la protección de refugios climáticos y en proporcionar conectividad.

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Introduction

Climate change is a major threat to biodiversity over the coming century (Peters & Lovejoy 1992). Therefore, efforts to lessen global warming by reducing emissions of CO₂ and other greenhouse gases or by increasing uptake of carbon by vegetation are of great interest to conservationists. The Kyoto Protocol, an international treaty under prolonged negotiation, offers countries the opportunity to receive credits for reducing emissions or increasing sequestration of carbon (Schulze et al. 2000). Countries can reduce their commitments to emission reductions by afforestation or reforestation. The U.S. government favors such comprehensive carbon accounting and expects to meet about half of its annual commitment under the protocol through land-based carbon sinks (Smaglik 2000). Although the Kyoto Protocol has potential conservation benefits, such as the creation of markets for forest preservation (Bonnie et al. 2000; Kremen et al. 2000), carbon accounting also poses biological risks. Countries could receive credits, for example, by planting trees in natural grasslands. And, because accounting will not begin until the year 2008, a country potentially could accrue credits by logging primary forests now and replacing them with rapidly growing plantations.

Missing from the Kyoto discussions is any consideration of biodiversity. The protocol is silent on forest management issues not directly related to carbon accounting. I explore the basis for a more rational policy for managing forests in the face of climate change. In particular, I ask what inherent properties of forest ecosystems and what kinds of management are likely to enhance the resistance and resilience of forests.

Forests have occupied the earth for nearly 400 million years (Tidwell 1998), experiencing massive upheavals in climate related to shifts in the earth's rotation on its axis, variation in solar radiation, plate tectonics, orogeny, volcanism, glaciation, and occasional collision with asteroids. Forests have persisted through all these events, but not unchanged. Their species composition has varied almost continuously, with the distributions of tree species and forest types shifting, contracting, and expanding over time (Graham 1999). Despite these changes, forests as a class have proved remarkably resilient. Although the present rate of warming is higher than previous rates over the last 10,000 years, forests apparently have weathered even faster changes in the past, albeit the most rapid changes were associated with mass extinctions (Graham 1999).

If climate change were the only factor menacing forests today, and if the landscape were still pristine, there arguably would be little cause for worry. The fossil record shows numerous examples of species migrating and persisting through past changes. By and large, climatic change may have been as great a force for specia-

tion as for extinction (Sepkoski 1998; Hewitt 2000). Even with the rapidity of change predicted for the next few decades, in the absence of other threats most species could be expected to adjust to these changes as they have in the past. This knowledge might lead some to suppose that the current warming of the atmosphere caused by emissions of greenhouse gases is of little concern. Today, however, climate change is being played out on a very different court—one in which direct destruction, fragmentation, and degradation of ecosystems by humans, accompanied by vast invasions of alien species, are proceeding at a breakneck pace worldwide. It is in combination with these threats that global warming becomes so insidious (Peters & Darling 1985; Dudley 1998; Sala et al. 2000). More optimistically, by learning how forests adjust to climate change and other stresses under natural conditions, we might be able to maintain, restore, or mimic these processes of adjustment.

Resistance, Resilience, and Change in Forest Ecosystems

Many reviews of the potential effects of climate change on forests are available (e.g., Ciesla 1995; Beniston & Innes 1998; Brown 1998; Dudley 1998; Jarvis & Aitken 1998; Sedjo & Sohngen 1998; Winnett 1998). The Intergovernmental Panel on Climate Change (IPCC 1996a, 1996b) concluded that forests are highly sensitive to modern climate change. Although the details of expected change in forests on a regional scale are unclear, the scenarios of general circulation models (GCMs) predict major shifts in the area occupied by forest biomes (Neilson et al. 1994; Hadley Center for Climate Prediction and Research 1998). For example, globally, the area occupied by tropical and temperate forests is projected to expand by up to 20%, whereas boreal forests may decline by 50% (Krankina & Dixon 1993), if other causes of change are ignored. Moreover, the rate of climate change over the next century may be faster than most historic changes, suggesting that adjustments forests have made to changes in the past may be more difficult today.

Beyond the crude biome-scale projections of GCMs, prediction of how forests will respond to climate change or other perturbations requires some understanding of their composition, structure, and function (Franklin et al. 1981). These three classes of ecosystem components are interdependent, so change in function—for example, a climate-induced increase in fire frequency or windstorms—produces corresponding changes in the species composition and physiognomy (structure) of the forest. Over an intermediate length of time, say thousands of years, the species in a given forest represent those that have evolved under a definable range of conditions, often called a “natural” or “historic” range of variability

(Landres et al. 1999; Swetnam et al. 1999). Many ecologists consider this range the appropriate set of "reference conditions" for comparison with human-altered conditions and as a guide to management (Stephenson 1999).

The time period selected to represent reference conditions is subjective, but the logic behind the use of historic variability to guide management is compelling. Changes that occur at a faster rate, greater intensity, different pattern, or broader spatial scale than historically are likely to fall outside the limits of adaptability for some species. If this departure affects critical life-history functions, extinction (at least locally) is likely. As changes become progressively faster, more intense, or broader in extent, a global mass extinction becomes probable. The challenge for conservationists is not to prevent change. It is to keep rates, scales, and intensities of change in ecosystems within the historic range of variability for those systems—or, at least, to come close. Conservationists must also develop strategies to mitigate the effects of inevitable changes that fall outside the historic range of variability.

Resistance and Resilience

Stability has been defined in many ways, representing three general concepts: (1) the ability to maintain a relatively constant state in the face of disturbance and stress; (2) the ability to recover quickly after a disturbance; and (3) a combination of these two abilities. The first concept is often referred to as resistance. The second concept is usually referred to as resilience (Pimm 1984, 1991), although other meanings of resilience can be found in the literature (Table 1).

Some theory and empirical evidence suggest that resis-

tance is inversely related to resilience (Fisher et al. 1998). Specifically, resistance may decrease and resilience increase as the supply of limiting nutrients increases (DeAngelis et al. 1989). Herbert et al. (1999) tested this hypothesis in an Hawaiian forest previously studied with respect to nutrient limitation to productivity and then damaged by a hurricane. As predicted, with phosphorus treatments the severity of damage to trees increased, indicating lower resistance, but rates of recovery of prehurricane stem growth and net primary productivity also increased, indicating higher resilience.

Nevertheless, resisting and recovering from disturbance may be positively associated at other spatiotemporal scales or under other ecological conditions. A forest that, on the scale of a biome, resists change to a fundamentally different condition is one that continually recovers from disturbances at finer spatial scales. Whitford et al. (1999) found that both the resistance and resilience of vegetation to drought are reduced in intensely stressed ecosystems (in this case, desert grasslands grazed by domestic livestock) compared with lightly stressed ecosystems.

What properties of a forest ecosystem contribute to resistance and resilience? Some studies have demonstrated increased tolerance to environmental extremes and greater temporal stability and recovery potential as species richness increases (McNaughton 1993; Tilman & Downing 1994; Tilman 1996, 1999). The most compelling explanation for how species richness enhances stability is the redundancy provided by multispecies membership in critical functional groups (Walker 1992, 1995; Peterson et al. 1998). A species that is the only member of its functional group in a community is a keystone species: if it disappears, many other species will also disappear or at least decline. In western Australia, for exam-

Table 1. Some definitions of ecological stability, in terms of resistance and resilience.

<i>Resistance</i>	<i>Resilience</i>
Measurement of the consequences on other variables of permanently changing a given variable; if the consequent changes are small, the system is relatively resistant (Pimm 1984, 1991)	magnitude of disturbance that can be absorbed or accommodated by an ecosystem before its structure is fundamentally changed to a different state (Holling 1973, 1986)
System undergoes less change in a state or flux variable as a result of disturbance (DeAngelis et al. 1989; Grimm et al. 1992; Herbert et al. 1999)	variable that has been displaced from equilibrium returns quickly to it (Pimm 1984, 1991)
System stays essentially unchanged (constancy) (Grimm & Wissel 1997)	rate of return to the reference state following disturbance (DeAngelis et al. 1989; Grimm et al. 1992; Herbert et al. 1999)
Ability of a community to maintain its composition and biomass in response to environmental stress (Grime et al. 2000)	capacity to recover from a disturbance in species composition (Walker 1995)
	system returns to the reference state (or dynamic) after a temporary disturbance (Grimm & Wissel 1997)

ple, a single plant species, *Banksia prionotes*, is the only source of nectar for a guild of honeyeaters during a critical time of the year (Lambeck 1992). Figs (*Ficus*) of various species assume a similar role in many tropical forests (Terborgh 1986). A functional group with more diverse membership can maintain its role in the ecosystem despite fluctuations in the member species (Walker 1995).

Diversity of functional groups, in addition to diversity of species within groups, appears to encourage ecological resistance. Experiments with microcosms subjected to warming show that changes in the distribution of organisms among trophically defined functional groups lead to differences in ecological processes beyond those expected from temperature-dependent physiological rates, but diverse communities retain more species than depauperate communities (Petchey et al. 1999). A test of the effects of functional group richness on the invasibility of grasslands showed that invasion success was negatively related to functional group richness (Symstad 2000). Three lessons emerge from these findings: (1) a diversity of functional groups should be maintained; (2) species richness and redundancy should be maintained within functional groups; and (3) keystone species must be identified and kept in ecologically optimal, not just minimally viable, populations. The current body of research is insufficient to identify thresholds in richness within or among functional groups at which resistance or resilience break down.

Adaptation

Minimizing extinction during climate change requires that species be given opportunities to adapt. Adaptation of species to climate change can take place through phenotypic plasticity (acclimatization), adaptive evolution, or migration to suitable sites (Markham 1996; Bawa & Dayanandan 1998). The only other alternative is decline and ultimately extinction.

Migration appears to have been the primary way species responded to past climate changes. Few beetles, for example, showed morphological change over the Quaternary (Pleistocene and Holocene), whereas species shifted markedly in distribution over this period (Coope 1979). Similarly, only 3 out of 177 mammals examined by Prothero and Heaton (1996) showed continual morphological change during the Eocene and lower Oligocene (37–30 million years ago), but again there were major changes in distributions. Although evolution can take place in the absence of morphological change, through physiological responses for example (Nowak et al. 1994; Hoffman & Hercus 2000), it seems clear that most species respond to changing climate by tracking suitable habitats geographically.

The speed at which species can migrate to track changing climate is of considerable interest, especially if

the current climate change is, as predicted, faster than most previous changes during the Quaternary. Migration rates of trees recolonizing regions after glaciation have been estimated from paleoecological data as ranging from 50 m/year for American beech (*Fagus grandifolia*) (Davis 1983) to 2000 m/year for spruce (*Picea* sp.) (Dennis 1993). The slower rates are thought insufficient for response to the current pace of climate change, especially given dispersal barriers such as intensive agriculture and cities (Peters & Darling 1985). Recently, however, paleontological evidence of rapid, long-distance migration of many tree species has arisen (Clark 1998; Clark et al. 1998), providing hope that at least some trees may be able to track a rapidly changing climate. In northern Europe, rapid migration of trees following ice recession 8500–8000 BP was relatively unconstrained by physical barriers such as mountain ranges, seas, and large lakes (Kullman 1998). Haphazard, long-distance establishment events may explain the evidence of rapid migration (Clark et al. 1998). Incorporating such rare dispersal events into models is difficult, which is why empirical rates of plant migration are often substantially higher than modeled rates (Higgins & Richardson 1999).

Rapid range shifts in response to warming trends over the last few decades have been documented for a number of species of vertebrates and invertebrates (Wuethrich 2000). For example, in a sample of 35 nonmigratory European butterflies, 63% have shifted their ranges to the north by 35–240 km during this century, whereas only 3% have shifted south (Parmesan et al. 1999). Nevertheless, migration to track a rapidly changing climate may be difficult for species with poor dispersal abilities, such as small forest vertebrates and flightless invertebrates, especially in relatively homogeneous landscapes with few opportunities for short-distance moves into suitable microhabitats. Barriers to movement may be formidable in fragmented landscapes (Noss & Csuti 1997).

Some species may adapt to climate change by in situ evolution. The modern Great Basin (U.S.) flora, for example, appears to consist of a mix of species that migrated northward from Pleistocene refugia in the southern portions of the region, and species that changed little in distribution during the Pleistocene and coped with climate change by genetic adaptation (Nowak et al. 1994). Tree species show genetic and phenological gradients associated with the environmental gradients over which they occur (Campbell 1986). Adaptive evolution ultimately depends on adequate levels of genetic variation within and among populations, although this variation can be expected to decline in response to the directional selection imposed by changing climate.

Many of the documented phenological responses of plants and animals to global warming may represent rapid microevolution (Hughes 2000). In Spain, populations of *Drosophila subobscura* have evolved in response to the warming of temperatures since the mid-1970s (Rod-

riguez-Trelles & Rodriguez 1998). On a broader temporal scale, pulses of speciation recorded in the fossil record are sometimes associated with climate change (Sepkoski 1998). Mitochondrial DNA analyses of birds suggest that divergence of populations during the glacial cycles of the Pleistocene led to formation of new species or completed speciation events that were initiated earlier (Avice & Walker 1998; Klicka & Zink 1999).

Land Use and Management Guidelines

Forest management has the potential either to exacerbate or reduce the effects of climate change (Franklin et al. 1991; Dudley 1998). Climate change is not currently the greatest threat to forests but adds another layer of stress to species and ecosystems already suffering from poor land-use practices. To protect forests from the harmful effects of climate change, we must first mitigate the proximate threats of habitat destruction, fragmentation, and degradation. Markham (1996) pointed out that "the potential impacts of climate change will be an academic question in relation to ecosystems that we are unable to save from current and immediate threats." Furthermore, human management appears to affect forest productivity and carbon storage much more than the effects of climate change or CO₂ enrichment (Caspersen et al. 2000; Schimel et al. 2000).

Following are some recommendations for land use and management that have a reasonable chance of enhancing the resistance and resilience of forests to climate change.

Represent Forest Types across Environmental Gradients in Nature Reserves

One of the oldest conservation strategies is to represent all ecosystem types in reserves (Pressey et al. 1993; Noss & Cooperrider 1994). Representative areas have been selected for scientific study, as ecological benchmarks to compare with disturbed areas, and as a way to conserve taxa too difficult to inventory and manage individually. Representation is also a sensible strategy in times of changing climate. Because we do not know precisely which forest types will be most sensitive, maintaining a full spectrum of types in protected areas will help assure that some resistant and resilient types persist.

Representation often is assessed by remote sensing of vegetation. For example, the Gap Analysis Program in the United States produces maps of vegetation in each state from LANDSAT imagery and determines how well each type is represented in reserves (Scott et al. 1993). The resolution of this imagery usually is sufficient only to map overstory vegetation, however. Beta diversity (the turnover of species along environmental gradients) generally increases from trees to shrubs to herbs (Whittaker

1960; Zobel et al. 1976). Hence, mapping only overstory vegetation is likely to miss significant patterns in plant species diversity and associated patterns in faunal diversity and ecological processes. A combined approach of mapping abiotic and biotic features may provide the best basis for a representation assessment (Hunter et al. 1988; Kirkpatrick & Brown 1994). We are applying this approach in the western United States (e.g., Noss et al. 1999), testing the hypothesis that representing vegetation along environmental gradients (capturing as much soil and microclimatic heterogeneity as possible) will result in the protection of more species and higher genetic diversity within species, in turn providing for adjustment to changing climate. Ideally, reserves will span uninterrupted environmental gradients and allow dispersal of organisms to favorable microsites.

Protect Climatic Refugia at Multiple Scales

Biogeographers have long been interested in the refugia that harbored plants and animals during times of unfavorable climate (Haffer 1969; Prance 1982; Colinvaux et al. 1996). Recent research suggests that full-glacial refugia had more influence on biodiversity in temperate than in tropical regions (Willis & Whittaker 2000), whereas in Amazonia the warm stages of the Quaternary and late Tertiary, which raised sea levels up to 100 m, may have isolated habitats as islands and archipelagos, fostering the speciation that occurred during these times (Nores 1999). A similar process apparently unfolded in Florida, where speciation occurred on sandy ridges, which formed an archipelago during interglacial phases of the Pleistocene (James 1961; Myers 1990).

It makes abundant sense to identify past climatic refugia wherever possible and protect these areas so that they can again function as refugia during present and future climate change (Eeley et al. 1999). Refugia occur at a variety of spatial scales. In North America, postulated regional refugia include the southern Appalachians, valleys of major rivers in the southeastern coastal plain (Delcourt & Delcourt 1984), and the Klamath-Siskiyou region of California and Oregon. The latter region is known for its heterogeneity of landforms, geological strata, soils, and microclimates, which have promoted diversity and endemism (Whittaker 1960; Noss et al. 1999). Major refugia in Europe include Iberia, Italy, the Balkans, and the Caucasus (Hewitt 2000). In Central America, many lowland species appear to have been limited to riparian habitats during the late Pleistocene (Aide 1998). Across continents, topographically diverse areas have allowed habitats and lineages to persist through elevational shifts and, in many cases, to diverge during periods of climate change (Hewitt 2000).

Climatic refugia at much smaller scales also can be important for maintaining species assemblages vastly different from those adapted to the dominant regional climate.

Algific slopes in Iowa (U.S.) occur in a deciduous forest matrix on steep, usually north-facing carbonate talus slopes, where cold air flows out of ice-filled caves that developed late in the Pleistocene. These slopes support over 60 species of vascular plants disjunct in Iowa from northern or western boreal forests and at least eight land-snail taxa thought to have become extinct at the end of the Wisconsin glacialiation (Nekola 1999). Such slopes, which also occur in other regions, may well continue to support species characteristic of colder climates during the current period of global warming. At a still smaller scale, sandstone and limestone outcrops in Near Eastern deserts support hundreds of relict and endemic Mediterranean-climate plants that have survived from periods of moister climate (Danin 1999). Again, these microrefugia, if protected, are likely to continue to support many species. If climatic refugia at all spatial scales can be identified and protected, persisting populations may be able to recolonize the surrounding landscape when conditions favorable for their survival and reproduction return.

Protect Primary Forests

A community of long-lived organisms is seldom, if ever, in equilibrium with the prevailing climate (Perry et al. 1991). Rather, vegetational change lags behind climate change, such that the vegetation at any point in time is a legacy of climatic conditions decades or centuries in the past (Sprugel 1991; Millar & Woelfenden 1999). Old-growth forests are predicted to possess considerable inertia in the face of climate change (Franklin et al. 1991). Mature trees can survive long periods of unfavorable climate, remaining "several centuries after climatic deterioration makes local conditions unsuitable for seedling establishment" (Brubaker 1986). This inertia could be a significant mechanism for ecological resistance.

A simulation of tree species distributions in Sweden under global warming scenarios predicted the long-term persistence of old-growth *Picea* stands protected from disturbance (Sykes & Prentice 1996). In forest types where the dominant trees live for hundreds or thousands of years, stands protected from catastrophic disturbance might persist through a few centuries of unfavorable climate, to reproduce again when favorable conditions return. Despite this inertia, however, slow shifts in composition along environmental gradients are expected even in mature, established forests (Franklin et al. 1991). Because the intensity and rate of change will be buffered in forest interiors, maintaining large patches of old-growth forest is a sensible strategy for maintaining biodiversity during rapid climate change.

Avoid Fragmentation and Provide Connectivity

The negative effects of fragmentation are abundantly documented worldwide (Harris 1984; Noss & Csuti 1997).

Fragmentation may threaten biodiversity during climate change through several mechanisms, most notably edge effects and isolation of habitat patches. Intact forests maintain a microclimate that is often appreciably different from that in large openings. When a forest is fragmented by logging or other disturbance, sunlight and wind penetrate from forest edges and create strong microclimatic gradients up to several hundred meters wide, although they may vary in severity and depth among regions and forest types (Ranney et al. 1981; Franklin & Forman 1987; Chen & Franklin 1990; Laurance 1991, 2000; Chen et al. 1992; Baker & Dillon 2000). With progressive fragmentation of a landscape, the ratio of edge to interior habitat increases, until the inertia characteristic of mature forests is broken. Fragmented forests will likely demonstrate less resistance and resilience to climate change than intact forests.

Another potentially serious impact of fragmentation is its likely effect on species migration. By increasing the isolation of habitats, fragmentation is expected to interfere with the ability of species to track shifting climatic conditions over space and time. Weedy species, including many exotics, with high dispersal capacities may prosper under such conditions, whereas species with poor mobility or sensitive to dispersal barriers will fare poorly. Many models of species migration during climate change have included the convenient but often unrealistic assumption of a homogeneous environment. Collingham and Huntley (2000) used a spatially explicit model to investigate the effects of different landscape patterns on the ability of a wind-dispersed tree (*Tilia cordata*) to migrate in response to changing climate. Simulated dispersal rates slowed dramatically when habitat availability fell below 25% of landscape area. Landscapes with a "blocky" (coarse-grained) pattern had the strongest negative effect on migration, suggesting that multiple small reserves might be preferable to fewer large reserves. Other species, more dependent on large habitat blocks and requiring intact habitat corridors to migrate, would probably favor a different landscape pattern (Collingham & Huntley 2000).

Connectivity is the antithesis of fragmentation. Maintaining habitat linkages parallel to climatic gradients and minimizing artificial barriers is a prudent strategy under any climate-change scenario (Hobbs & Hopkins 1991; Noss 1993). Biogeographic corridors, such as the Mississippi Valley and other major river valleys that trend north-south, allowed dispersal during past climate changes (Delcourt & Delcourt 1984). Hunter et al. (1988) suggest that a corridor of natural habitat bordering the Appalachian Trail from Georgia to Maine might facilitate range shifts. Whether or not such latitudinal corridors will be functional under the rapid pace of change now forecast is an open question. Elevational corridors, which span a broader climatic gradient over a shorter distance, may better promote migration in mountainous terrain (Noss 1993; Bennett 1999). Connec-

tivity also may help sustain genetically diverse populations that span environmental gradients within the present range of species (Bennett 1999).

In designing linkages, several considerations should be kept in mind: (1) A full range of geological substrates and soil types should be included in linkages because some plant species are exacting in their requirements. (2) Many species have mutualistic or other dependencies on other species, such that migration of assemblages of co-adapted species will be required (Bennett 1999). (3) Because movement routes probably will vary among species, protecting broad linkages rather than narrow corridors is advised. (4) As suggested by Collingham and Huntley (2000), a mixed strategy of corridors and small stepping-stone habitats is desirable to address the distinct dispersal characteristics of different species.

Roads are major agents of fragmentation (Noss & Cooperrider 1994; Baker & Knight 2000). In the context of climate change, roads pose two problems: they restrict the dispersal of less mobile species while they encourage the dispersal of invasive exotics. Roads function as barriers to the movements of many species (Noss 1993; Noss & Csuti 1997; deMaynadier & Hunter 2000; Trombulak & Frissell 2000). Particularly vulnerable are small, nonvolant forest vertebrates and invertebrates that do not usually venture into openings as wide as a road clearing (e.g., rodents, Oxley et al. 1974; Adams & Geis 1983; beetles, Mader 1984). Even large animals such as bears may refuse to cross roads with heavy traffic (Brody & Pelton 1989), and many others are killed on roads. Hence, roads may impede the movement of many species in response to climate change. Closing unnecessary roads and providing wildlife crossings on roads with heavy traffic might mitigate some of these effects (Noss 1993; Clevenger & Waltho 2000).

On the other hand, roads are common avenues of invasion by exotic pests (Schowalter 1988; Tyser & Worley 1992; Lonsdale & Lane 1994; Parendes & Jones 2000), which many ecologists believe will increase in abundance with climate change. Disturbed roadsides with high light levels harbor many weeds that disperse along the route of the road and often invade adjacent habitats. Vehicles transport seeds and spores long distances (Wilson et al. 1992). To reduce this risk we must understand how alien species invade natural ecosystems and identify ecosystems that are especially prone to invasion (Hobbs & Huenneke 1992; Simberloff 1997; Lonsdale 1999). We also must identify the anthropogenic changes in landscapes that promote invasions and develop a strategy for mitigating those changes.

Provide Buffer Zones

The fixed boundaries of reserves are poorly suited to a dynamic environment unless individual areas are extremely large (Peters & Darling 1985; Noss & Cooper-

rider 1994). With changing climate, buffer zones have the potential to provide for shifting populations as conditions inside reserves become unsuitable. For this strategy to work, buffer zones must be large, managers of reserves and surrounding lands must demonstrate the flexibility to adjust their land-management activities across the landscape, and adequate data must be available from monitoring to determine where populations are shifting. That none of these conditions is met, even on public land, suggests that the buffer-zone strategy will be difficult to implement. Nevertheless, if incentives can be provided to managers outside reserves to manage their lands sensitively, species will have a better chance of shifting distributions in response to climate change than if land-use adjacent to reserves is intense.

Practice Low-Intensity Forestry and Prevent Conversion to Plantations

Forestry that minimizes soil disturbance (hence reducing invasion of exotic pests, loss of carbon from soil, and potential loss of mycorrhizae; Perry 1994), size of canopy openings (Whitmore 1998), and removal of biomass will do more to promote the resistance and resilience of forests to climate change than intensive logging. (Of course, the historic range of variability must be taken into account in such considerations.) Although some studies have shown rapid recovery of biotic control of ecosystem processes after intensive logging (Bormann et al. 1974; Boring et al. 1981), others have shown profound losses of productivity and processes. In many parts of the world, regeneration of trees has failed after clearcutting (Perry 1994). Rapid recovery of host plants after logging appears essential for maintaining obligate mycorrhizal fungi and other soil microbes. Herbicide treatments and other intensive "vegetation management" can destroy this linkage (Perry et al. 1990; Perry 1994; Amaranthus 1998).

Intensification of forestry activities is often promoted on the basis that young, actively growing trees will sequester carbon more rapidly than old-growth forests in which respiration may equal or even exceed photosynthesis (Birdsey 1992). Replacement of old forests with plantations is a "perverse incentive" of the Kyoto Protocol (Brown 1998; Dudley 1998). Simplistic carbon accounting, encouraged by the protocol, ignores the tremendous releases of carbon that occur when forests are disturbed by logging and related activities such as site preparation and vegetation management (Perry 1994; Schulze et al. 2000). It ignores the fate of woody debris and soil organic carbon during forest conversion (Cooper 1983; German Advisory Council on Global Change 1998). Typically, respiration from the decomposition of dead biomass in logged forests exceeds net primary production of the regrowth (Schulze et al. 2000). Considerable time is required—often hundreds of years—for

regenerating forests to accumulate the carbon stocks characteristic of primary forests (Harmon et al. 1990). Over several rotations of growth and harvest, the mean carbon pool of intensively managed forests is only about 30% that of primary forests (Cooper 1983).

From the standpoint of maintaining biodiversity during climate change, conversion of natural forests to plantations cannot be justified. Tree plantations around the world, especially exotic monocultures, have less biodiversity than natural forests in the same regions (Hunter 1990; Noss & Cooperrider 1994; Perry 1994). Plantations are often markedly less resistant to disturbances such as fire and more subject to pest outbreaks than natural forests (Schowalter 1989; Perry 1994). Pest outbreaks could increase in severity or change in distribution with changing climate (Williams & Liebhold 1995), amplifying the vulnerability of plantations. On the other hand, tree plantations on marginal agricultural land and natural succession on these lands could play a useful role in carbon sequestration. North America is currently a carbon sink, largely because of agricultural abandonment and regrowth of forests harvested before 1980 (Fan et al. 1998; Caspersen et al. 2000; Schimel et al. 2000).

Plantation management, where it is appropriate, should emphasize mixed-species forestry and native species, which would allow migrating species to be incorporated into the mix (Ravindranath & Sukumar 1998). Although shortened rotations would enable quicker response to forest dieback or other symptoms of changing climatic conditions, the risk of depleting critical soil nutrients and facilitating species invasions would also be higher.

Maintain Natural Fire Regimes

How fire should be managed in response to climate change is a complex issue. Fire regimes are known from paleoecological evidence to change through time in response to changing climate. Hotter, drier conditions tend to increase fire frequency, which generally shifts vegetation toward more fire-tolerant species (Clark 1990; Swetnam 1993; Veblen et al. 1999). Many forest types and other plant communities depend on fire for their persistence (Mutch 1970; Platt et al. 1988). Reviews of endangered ecosystems in North America show that many of the most imperiled plant communities have declined largely because of fire suppression (Noss & Peters 1995; Noss et al. 1995). On the other hand, fires set by humans are a leading threat to other forests, especially in the tropics (Trapnell 1959; Dudley 1998). Permanent conversions from one vegetation type to another in response to fire have been documented—for example, boreal forest changing to tundra in Canada (Sirois & Payette 1991) and dry tropical forest changing to shrubland in Zambia (Trapnell 1959). In tropical forests, the extent of fire depends on moisture levels, which decline

with logging disturbance. A 50% reduction in canopy cover has the potential to increase average temperatures in the forest by 10° C and to decrease relative humidity by 35% (Kauffman & Uhl 1990). Such differences indicate that fire policies should be based on what is known of the fire ecology of each region and forest type.

Discussions of climate-change policy often include suggestions that fires be suppressed to help reduce emissions. There is little question that, in the short term, fire suppression enhances carbon storage (Tilman et al. 2000), but the threat to biodiversity from lack of fire in many forest types outweighs the potential advantages of fire suppression. Although the increased frequency and spatial extent of fires predicted by some models—for example, for forests of the Sierra Nevada in California (Miller & Urban 1999)—are cause for concern, the appropriate policy response is not straightforward. Should managers step back and allow fires to occur in the hope of facilitating vegetation adjustment to the new climate? Or should they actively suppress fires that appear to exceed, in intensity or frequency, the historic range of variability? Perhaps this is a moot point. Experience in trying to suppress large, intense fires such as the Yellowstone burns of 1988 has shown that such attempts are usually futile. Curiously, a 300-year fire history in the boreal forest of Quebec shows a significant decrease in the number and extent of fires, in the absence of fire suppression, beginning with a warming period 100 years ago (Bergeron & Flannigan 1995), suggesting that the predicted increase in fire with climate change is by no means universal. In any case, efforts to protect forests from intense fires through regular, prescribed burning and/or understory thinning have been much more successful than efforts to suppress intense fires (Moore et al. 1999; Stephenson 1999). A mixed strategy, in which managers let many natural fires burn, protect (to the extent possible) old growth from stand-replacing fires, and manage other stands by prescribed burning and understory thinning to reduce the risk of high-intensity fire, may be the optimal approach.

Maintain Diverse Gene Pools

Genetic adaptation to climate change depends on genetic variation. Diverse gene pools should be maintained within and among populations of commercially important trees and other forest species (Dudley 1998). Reforestation, rather than relying on local seed sources (which under relatively stable climatic conditions would be an appropriate strategy), should incorporate individuals from a wide range of localities, but should emphasize sources at lower elevations or latitudes (Bawa & Dayanandan 1998; Ravindranath & Sukumar 1998). Breeding programs to promote faster growth or other commercially desired qualities of trees at the expense of genetic varia-

tion should be discouraged because they are likely to leave tree species less resilient to climate change.

Protect the Most Acutely Threatened Species Ex Situ

For some ecosystems, climate change is already the dominant threat, such that mitigation of other factors such as land use will do little good. The cloud forests of tropical mountains, which typically harbor large numbers of endemic species, appear to be such an ecosystem. Simulations of changes in temperature and moisture under doubled CO₂ show an upward shift in the cloud layer of hundreds of meters during the winter dry season, coupled with increased evapotranspiration (Still et al. 1999). Cloud forests have nowhere to shift and are expected to be lost, along with their endemic species. The disappearance of 20 species of anurans (frogs and toads), including the endemic golden toad (*Bufo periglens*), from highland forest in Costa Rica has been linked to a warming trend since the 1970s and to a severe reduction in dry-season mists; meanwhile, species from lower elevations have invaded these forests (Pounds et al. 1999). In situations such as these, ex situ preservation of species in zoos and botanical gardens until global warming is reversed may be the only way to avoid extinction. Ex situ collections should include sufficient genetic diversity to allow adaptation to uncertain conditions in reintroduction sites.

Identify and Protect Functional Groups and Keystone Species

Keystone species and functional groups are essential to the resistance and resilience of forests to climate change and other stresses. The identification of these species and groups has been haphazard, however. For some forests, such as longleaf pine (*Pinus palustris*) in the southeastern coastal plain of North America, scientists have identified several ecologically pivotal species and processes (Platt et al. 1988; Noss 1991; Simberloff 1998). For many other forests, one can only guess which species (e.g., top predators) might be of unusually high ecological importance. Efforts should be made to identify such species, functional groups, and processes for all forest types and other ecosystems; then, management must be aimed at maintaining these components in natural patterns of abundance and distribution.

Research Needs

The management actions I suggest represent a reasonable guess of what is prudent in the face of abundant uncertainty about the responses of forests to climate change. To refine these recommendations, and perhaps turn some of them on their heads, several lines of research must be pursued:

- More precise determination of the biomes, vegetation types, species, and sites that are most vulnerable to adverse effects of climate change. This will require rigorous monitoring, observations, and, where possible, experiments.
- Studies of population responses to climate change that focus on reproductive processes, demography, genetics, and species interactions and that involve species with contrasting life-history traits (Bawa & Dayanandan 1998).
- Higher-resolution models of the direction, magnitude, rate, and effects of climate change within regions, including such critical components as the seasonal distribution of rainfall (Herbst & Hörmann 1998).
- Increased combinations of modeling approaches, such as the linkage of ecosystem process models with spatial landscape models, as done by He et al. (1999) to predict forest landscape responses to climate warming.
- Empirical research on the details and mechanisms of biotic change in response to climate change at the edges of species' ranges (Coley 1998) and along ecotones between vegetation types (Allen & Breshears 1998), where rapid responses to climatic variation are most likely.
- Long-term monitoring with an experimental design adequate, at least, to determine correlations and, ideally, to determine causality between changes in climate parameters and responses of biodiversity at several levels of organization.
- Identification of ecological indicators (species and otherwise) that will provide an early warning of biological problems related to climate change. Epiphytes, for example, may play this role in tropical forests because of their extreme sensitivity to climatic conditions (Benzing 1998).

Conclusion

Society's response to climate change is determined through the political process. If educated to understand the multiple benefits of sustaining diverse, healthy, resilient forests, people will place value on protecting these forests. From this point of view, certain policies, such as conversion of primary forests to rapidly growing plantations in an attempt to sequester as much carbon from the atmosphere as possible, will do more harm than good. The literature I have reviewed suggests that a well-managed native forest has a reasonable chance of surviving or adapting to climate change. It appears that good forest management during a time of changing climate differs little from good forest management under more static conditions. Increased emphasis must be placed, however, on actions such as protecting climatic refugia and providing habitat connectivity parallel to environmental gradients.

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