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# Natural Disturbance, Patch Dynamics, and Landscape Pattern in Natural Areas

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**ABSTRACT:** Understanding natural disturbances and patch dynamics in natural areas is important for the following reasons: (1) some species and communities depend on periodic natural disturbances, while other species and communities may be threatened by particular natural disturbances; (2) sampling design for monitoring and research must be based on an assessment of the patchiness produced by natural disturbances; (3) preserve design should consider the spatial and temporal characteristics of natural disturbance regimes; and (4) management strategy—whether we allow, promote, resist, or mimic natural disturbance—should consider how species respond to natural processes. In general, species respond individualistically to natural disturbances. Available information about these responses is often inadequate to predict the outcome of particular disturbances on particular species. Scale is important; the size of preserves relative to patch size, number, and dynamics may alter the appropriate stewardship techniques. From general principles it can be argued that the larger the preserve, the less stewardship effort will be required for maintenance of existing species and communities. However, this conclusion may be constrained by several circumstances. Small preserves often have different goals than large preserves (e.g., the protection of a rare species versus the protection of a landscape mosaic of community types), thus reducing the scope of management. Further, large preserve size does not totally mitigate threats to natural area integrity or to rare species populations.

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## INTRODUCTION

The importance of natural disturbance and patch dynamics in natural area stewardship results, in part, from a paradox at the heart of nature preservation: We seek to preserve systems that must change (White and Bratton 1980). Among the sources of change in preserves are natural disturbances like fire, windstorms, and floods. Disturbances may have beneficial effects on protected resources—for example, the dependence of grasslands on fire is well accepted and fire is widely used in stewardship. However, there are other cases where natural disturbances threaten resources (e.g., small populations of rare species may be vulnerable to a particular disturbance). Whether or not effects are beneficial, natural disturbances are likely to be important processes in natural areas.

In this paper I will explore the consequences of natural disturbance and patch dynamics for natural area stewardship. I assume that the goal of this stewardship is the protection of natural communities, the species they contain, and the processes that give rise to these communities. I will

therefore focus on the community level. Because communities vary along spatial gradients and because disturbances overlay these gradients and create a pattern of patchiness in space, the landscape level also is important in this discussion. Natural disturbance and patch dynamics are first defined. The stewardship importance of these topics is then illustrated by describing two examples of insect disturbance from Great Smoky Mountains National Park. Finally, I will discuss several conceptual issues raised by these examples.

## NATURAL DISTURBANCES AND PATCH DYNAMICS

Disturbance is a relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985). This definition stresses disturbance as a physical event and the need for detailed, mechanistic studies of the ways species and communities respond to disturbances.

The most common alternative to this definition is to view disturbance as a change

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The following paper was presented at the Thirteenth Annual Natural Areas Conference, October 23, 1986, in Potosi, Missouri.

in the "normal" processes that control a particular ecosystem. For example, because fire is recurrent in grasslands and is promoted by the plant community itself (e.g., build up of organic fuels), we might conclude that fire is a normal process and that fire suppression is a "disturbance." However, the use of this definition is limited by problems in defining what is normal in natural systems. For example, natural fires were variable in time and space, and extreme events may have been more important than average ones in ecosystem pattern. Further, disturbance regimes vary with changing climates. Such changes occur on time scales varying from decades to hundreds of years, and thus the definition of the "normal" disturbance regime becomes questionable. In any case, when a conservation effort is initiated it is generally not known whether the disturbance regime is stable. Therefore, I believe that the physical rather than the relative definition of disturbance is appropriate.

The importance of natural disturbances in ecosystems has been the subject of a great deal of recent research (Pickett and White 1985), some of it in protected natural areas (e.g., Romme and Knight 1982). Fire has been perhaps the best studied disturbance (Kozlowski and Ahlgren 1974, Heinselman 1981, Mooney et al. 1981) and the use of fire in natural areas stewardship is now widespread in areas such as prairies and coastal plain savannas. Based on the growing disturbance literature, I have listed seven generalizations about the importance of disturbance (adapted from White and Pickett 1985, White, in press). These generalizations are illustrated with brief examples from Great Smoky Mountains National Park.

*Disturbances occur on a variety of temporal and spatial scales.* Disturbances can only be defined relative to the dimensions of the system at hand (i.e., organism size and lifespan). Within Great Smoky Mountains National Park (GRSM) for example, annual disturbance may be occurring in stream-side moss communities, while forest structure is influenced by windstorms occurring on time intervals longer than decades to centuries.

*Disturbances affect many levels of biological organization.* Effects center on the individual but occur at all biological levels from physiological and behavioral to ecosystem-wide. For example, an intense fire in GRSM may remove organic matter from the soil surface, kill dominant trees, influence stream chemistry, and alter the movements of mammals.

*Disturbance regimes vary, both regionally and within one landscape.* The role of fire varies across North America; within GRSM the importance of fire varies considerably over small distances (Harmon et al. 1983). Frequency and predictability of disturbances are often inversely related to magnitude. Fires in GRSM are most frequently of low intensity (Harmon 1981).

*Disturbances overlay environmental gradients, both influencing and influenced by those gradients.* Some disturbances may be influenced by environmental gradients. For example, fires in GRSM burn with greater intensity when they move across dry ridges than when they move across adjacent moister slopes. Some disturbances reinforce compositional and structural change along physical gradients, while some may be independent of environmental gradients (Harmon et al. 1983). Most disturbances are patchy and thus produce patterns that are not strictly parallel to underlying environmental gradients.

*Disturbances interact.* Some disturbances promote others. For example, in GRSM southern pine beetle outbreaks increase available fuels, which increase the severity of subsequent fire; drought years may stress trees, thus promoting beetle outbreaks. One disturbance can also decrease the likelihood of another. For example, because of its low stature, a young, postfire stand may not be affected by a windstorm that disturbs a neighboring, older stand.

*Disturbances may result from feedback between community state (e.g., successional age) and disturbance vulnerability.* Vulnerability to disturbance often in-

creases with individual age and successional time. Thus, biotic feedback controls the occurrence of many disturbances that are, at first glance, initiated by factors external to the community. The understanding of biotic feedback is important and influences perceptions of whether vegetation change is caused by endogenous (from within the community) or exogenous (from outside the community) factors. For example, as trees in GRSM's cove hardwood forests age, they become more susceptible to the effects of a windstorm of a given intensity.

*Disturbances produce variability in communities.* Even for a single ecosystem and type of disturbance, effects vary spatially. This may decrease the predictability of community patterns from site factors if stand history is unknown; even if stand history is known, postdisturbance composition may not be entirely predictable. For example, the effects of a given windstorm or fire in GRSM produces patchy and variable effects (some areas with many dead trees and other areas in which only parts of tree crowns have been killed).

Disturbances periodically remove dominant organisms, set succession back to early stages, or alter the physical substrate such as in dune systems and avalanches. Such processes also may create new patches within the original community or landscape. Because organisms take up space and use resources, the removal of a single dominant individual often creates a patch of space and resources. Because dominant individuals generally reduce the survival and establishment of younger individuals, disturbance to the dominant individuals often enhances regeneration. Thus, disturbances often have long-lasting effects on community structure and composition; these effects are disproportionate to the relatively brief occurrence of the disturbance. Natural patchiness consists of landscape heterogeneity in the age and structure of ecosystems. This patchiness ranges in size from a few dominant organisms to patches consisting of hundreds or thousands of dominant individuals.

After a given disturbance, some species increase in importance, some decrease, and others remain unchanged, showing that species responses to disturbances are generally individualistic. Some species depend on a given disturbance for regeneration, while the regeneration of others is prevented. Even a single species may differ in response to a given disturbance depending on a variety of stochastic factors such as the timing of the disturbance relative to seed set. Knowledge is generally limited. We often do not know the autecology of species well enough to predict response to a given disturbance. This is particularly a problem with rare species, since an entire small population should not be manipulated in a single unreplicated experiment. The problem magnifies if several rare species occur in the same community and respond differently to disturbance. Clearly, understanding species response to disturbance (whether natural or stewardship techniques) is an important area of basic research in natural areas.

#### PATCH DYNAMICS

When mechanisms of change within patches are studied, we may be able to understand the patch dynamics within a particular study area. The phrase "patch dynamics" (Pickett and White 1985, White, in press) emphasizes the study of individual patches within communities and the successional trajectory and interactions of those patches. As noted above, the patchiness of natural systems occurs on a spatial scale set by the size of the dominant organisms.

A concept similar to this one is the "shifting mosaic" (Heinselman and Wright 1973). This concept suggests that an overall balance of patch births and deaths can produce a dynamic equilibrium—there is local change, but the overall processes and frequency distribution of patch states are stable, at least on the appropriate spatial and temporal scales. This is an attractive concept for natural area preservation, suggesting that some landscapes are in overall stasis despite local change. However, in most field situations we do

not initially know whether such an equilibrium applies. A minimum condition for equilibrium includes large preserve size relative to patch size. If we could show that a given landscape was in equilibrium with a stable disturbance regime, then the protection of such a landscape would be relatively simple; the natural disturbance regime would maintain the dynamic equilibrium. Whether this is likely will be the subject of discussion in the final section of this paper.

The patch dynamics of terrestrial vegetation has consequences for aquatic systems and wildlife populations as well. For example, Romme and Knight (1982) suggested that natural fire resulted in decade-to century-long changes in bird and fish populations in a Yellowstone National Park watershed. The magnitude of these changes was a function of the size of the area burned relative to total watershed area.

A final reason for the study of patch dynamics concerns the need to address human impacts in natural areas (Harmon et al. 1983), such as those caused by atmospheric pollution and climatic warming. These human threats affect ecosystems that possess great spatial variation in their expected (nonimpacted) growth rates, mortality rates, and compositional trajectories as a function of past disturbance. If we are to document a departure from the expected values of these characteristics, we must carry out studies with explicit reference to this natural patchiness.

#### NATURAL DISTURBANCE, PATCH DYNAMICS, AND LANDSCAPE PATTERN: TWO EXAMPLES FROM GREAT SMOKY MOUNTAINS NATIONAL PARK

Two contrasting insect infestations in Great Smoky Mountains National Park (GRSM) illustrate the importance of understanding disturbance and patch dynamics in preserves. The southern pine beetle (*Dendroctonus frontalis*), a native

insect, periodically infests pine stands and may be essential to the successful regeneration of these stands. The balsam woolly adelgid (*Adelges piceae*), an exotic insect, has recently negatively impacted populations of Fraser fir (*Abies fraseri*), a southern Appalachian endemic tree.

#### Great Smoky Mountains National Park

Great Smoky Mountains National Park is a 208,000 ha preserve in the Unaka Range of the southern Blue Ridge physiographic province of North Carolina and Tennessee (35° 37' N). Elevation ranges from 260 to 2,021 m (853 to 6,630 feet). At the time of park establishment (1934), 20 percent of the park was free from major human disturbance (if the influence of chestnut blight, which began in the 1920's, is excluded), and an additional 8 percent of the park had been minimally disturbed (Pyle 1985). The rest of the park had been farmed (predominantly at lower elevations) and logged. Since park establishment, several other kinds of disturbances have occurred and constitute major stewardship problems. Among the most important have been three exotic species invasions (chestnut blight, balsam woolly adelgid, and the wild hog) and atmospheric pollution (White and Bratton 1980, Harmon et al. 1983).

The vegetation of the Great Smoky Mountains is a complex mix of evergreen, needle-leaved, and deciduous broad-leaved forest, with two major types of nonforest vegetation (heath and grassy balds) (Whittaker 1956). Elevation and soil moisture class are the two dominant environmental gradients controlling old-growth vegetation distribution (Whittaker 1956, Golden 1974). Although these factors explain much of the variance in vegetation distribution, other factors modify the vegetation pattern. Disturbance forms an overlay to the general environmental control of vegetation (Harmon et al. 1983, Pyle 1985). The sources of heterogeneity in the Great Smoky Mountains have produced a vegetative landscape pattern that is among the

most complex in North America (Whittaker 1956).

Pronounced successional change is occurring in certain vegetation types. For example, xeric pine stands are succeeding to oak-dominated stands due to a decreased fire frequency (Harmon 1981) and the periodic outbreaks of the southern pine beetle (Kuykendall 1978). Grassy balds, which are high elevation open areas that were created by clearing and grazing in the early to mid-1800's (Lindsay and Bratton 1979), are being invaded by trees and shrubs. Heterogeneity in the GRSM landscape consists of a diversity of vegetation types and a diversity of successional ages imposed by past disturbance.

### Southern Pine Beetle Infestation

An example of patch dynamics in the GRSM landscape is supplied by pine-dominated vegetation. This vegetation type is found on dry slopes (convex topography, upper slope and ridge positions, and warm slope aspects) at low to middle elevations. Thus, pine stands are found in repeated elongated stands on ridges, with intervening coves, valleys, and slopes dominated by hardwoods and hemlock. Sometimes these stands interconnect where ridges join; sometimes the stands are isolated from one another. Pine stands, as well as patches within pine stands, often consist of discrete age classes of trees because of fire history. The pines in the GRSM landscape are shade intolerant; thus the understories of these stands are dominated by hardwoods.

The pine stands are not stable. Periodic outbreaks of the southern pine beetle, a native insect, kills overstory pines and releases understory oaks (Kuykendall 1978), thus hastening succession to deciduous trees. Similarly, fires that are not hot enough to expose mineral soil also aid deciduous trees in the post-disturbance stand because some overstory trees (predominantly pines) are killed, while understory hardwood stems are able to sprout back after top kill (Harmon 1981). Fire frequency has decreased in the last fifty years because of fire suppression. Pine

dominance is slowly being lost at a rate determined by overstory pine mortality, whether this mortality is caused by insects, fire, or other factors.

The pattern of loss can be determined from remote sensing; we have already identified successional states of the pine ecosystem using remote sensing data. Using comparisons with past aerial photographs, we may be able to assess the rate of this loss as well. Decreases in the aerial extent of this ecosystem type causes the losses of populations of a southern endemic pine (table mountain pine, *Pinus pungens*) and probably threatens other associated plant and animal species. All of the yellow pines of GRSM are shade intolerant and require exposed mineral soil for regeneration. Although there is some variation, table mountain pine usually produces serotinous cones that require exposure to fire for seed release.

Beetle kills are rarely complete, thus imposing a degree of patchiness on the pine stands. In particular, stressed trees (e.g., old trees and trees previously injured by fire) are most susceptible to the beetle. Further, beetle outbreaks increase fuel loads (Nicholas and White 1984). Those few fires in the last several decades that have been hot enough to regenerate pine have occurred on heavy fuel accumulations. Fuel moisture also influences potential fire intensity. For example, fire intensity is highest on dry ridges for fires that burn across several site types, even where fuels are higher on moist sites (fuels peak in GRSM on moist sites because organic productivity is higher on these sites). Droughts stress trees (causing a greater probability of beetle infestation) and produce low fuel moisture (causing a greater probability of intense fire). Hence, periodic beetle outbreaks, droughts, and fire may interact in the

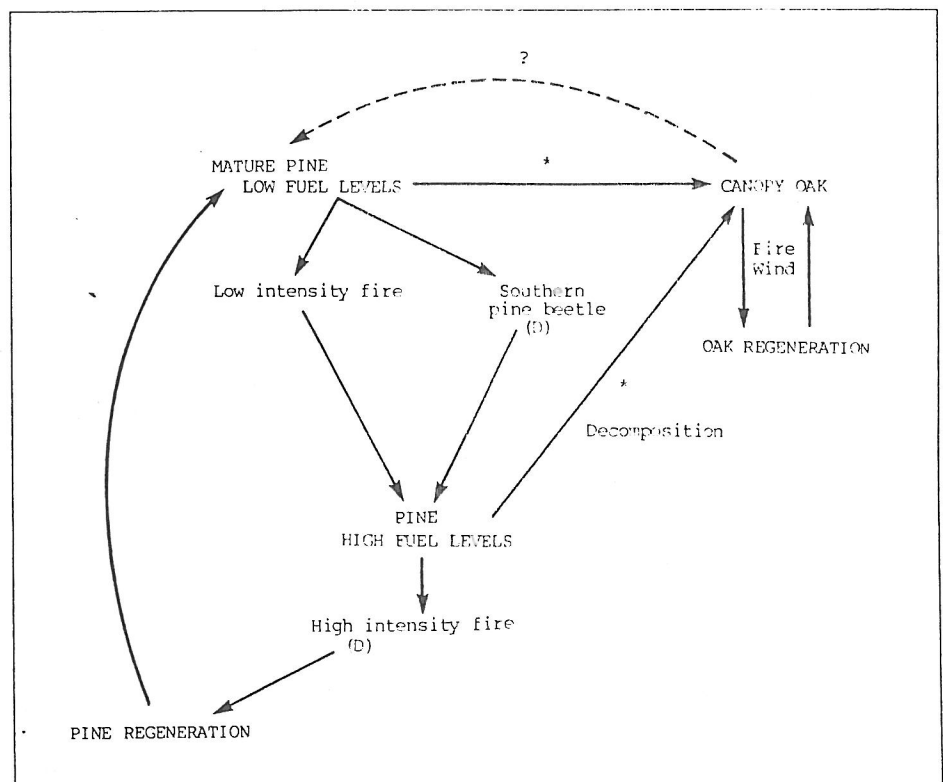


FIGURE 1. Interactions between succession and disturbance in the xeric pine ecosystems of Great Smoky Mountains National Park. "D" is indicated where drought interacts with fire (by lowering fuel moisture, thus promoting high intensity fire) and southern pine beetle (by stressing trees, thus promoting beetle outbreak). "\*" indicates successional processes that are dominant in the current landscape. "?" indicates that we are uncertain whether there are any natural mechanisms for converting oak to pine dominance once succession has allowed hardwoods to enter fire-resistant size classes.

landscape to control the amount of pine regeneration (Figure 1). Such interactions are probabilistic and are likely to produce a heterogeneous and patchy distribution of various pine forest successional states. In one scenario, severe droughts for several years following years of heavy pine mortality, whether from beetles or low intensity fire or both (beetles are drawn to trees stressed by factors such as fire), would result in intense fires and subsequent pine regeneration. Such events may occur several times during the 100-year lifespans of the overstory trees. Decomposition is fast in this humid landscape; there is a ten-to-twenty year period during which the post-disturbance fuel accumulations are available for the initiation of intense fires.

The modeling of this landscape problem, including assessing the rate of pine forest loss, is an example of the importance of understanding patch dynamics in a spatial context. We know the outlines of this patch dynamics problem, but we have not yet quantified rates for the processes indicated in Figure 1. We do not know the rate of loss of pine or the conditions of fuel quantity and moisture that are needed for pine regeneration.

In this example, there is a feedback between community state and disturbance vulnerability. As trees age, they become more vulnerable to beetle infestation and more likely to be stressed or to die from any cause (Figure 2). Droughts will have more influence on canopy pine trees (in terms of increasing vulnerability to beetles) than on younger trees. Further, if no stand regenerating disturbance occurs, succession leads to oak trees that cannot be affected by the beetle. Thus, vulnerability to disturbance declines (Figure 2). The effect of a fire of a given intensity also varies through successional time. As hardwoods age, they grow into fire-resistant size classes (Harmon 1984). The park may be passing through a "window" during which fire can be successfully used to regenerate pine but after that it will be very difficult to achieve this stewardship goal with the same level of effort.

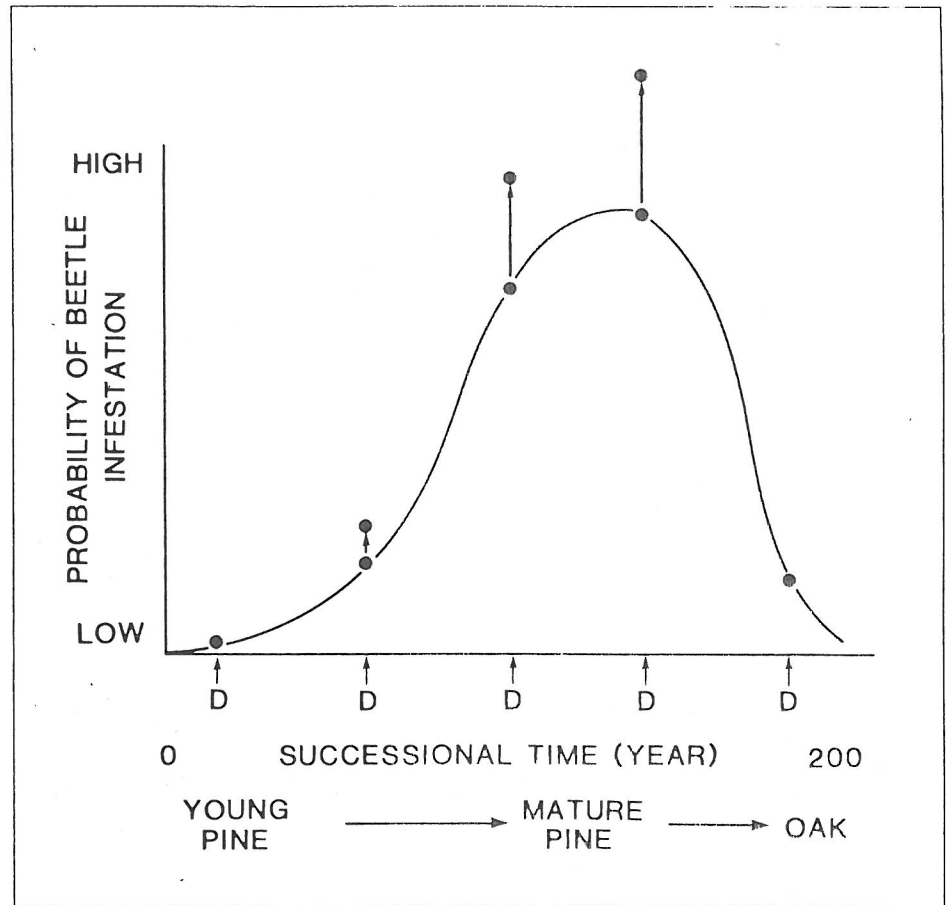


FIGURE 2. Vulnerability to southern pine beetle infestation as a function of successional time in xeric pine ecosystems of Great Smoky Mountains National Park. "D" signifies four drought years (droughts affect vulnerability to disturbance only when mature canopy pine are present).

There are other reasons for understanding the patch dynamics of this situation. Some pines are susceptible to air pollution and assessing the effects of air pollution requires understanding the patch structure of these stands and the influence of other stresses, like beetles and drought. In fact, air pollution is likely to interact with these other factors and may alter the patch dynamics of this system.

Before leaving this example, I will point out one other complication of fire management in GRSM. There is a philosophical dilemma underlying the question of pine stewardship. That dilemma concerns the question: What is natural? (Bratton et al. 1981). Fires set by European settlers were prevalent for more than 100 years before the park was established; Indian-set fires probably occurred for many hundreds of years. Thus, the

amount of pine currently in the GRSM landscape could be an artifact of that human disturbance regime. However, such frequent fires have obscured the natural disturbance regime—it is difficult now to assess what that natural disturbance regime was. Further, if vulnerability to hot fire and beetles increases with successional age in pine stands, we could conclude that human-set fires generally replaced or even prevented natural fires that would have occurred. It is also possible that changing climates (such as the end of the Little Ice Age in about 1850) have altered the fire regime historically.

In summary, understanding the patch dynamics of the pine ecosystem will allow us to assess the rate of loss of an ecosystem type in the GRSM landscape and to choose a stewardship strategy. Patch dynamics probably involve a syner-

gistic effect between several disturbances. Vulnerability to disturbance is in some measure controlled by ecosystem state (successional age). Despite its short-term, negative effect on pine dominance, the pine beetle may play a role in the eventual regeneration of pine stands (Figure 1). The southern pine beetle is a native insect and should be considered a protected resource in GRSM, independent of its effects. The effect of preserve size is also evident; GRSM is a large preserve and contains a great deal of heterogeneity in pine ecosystem state. No single fire or beetle infestation will be catastrophic and stewardship can be carried out without affecting all of the protected resource.

### Balsam Woolly Adelgid Infestation

The recent infestation of the southern Appalachians by the balsam woolly adelgid contrasts with the situation just described for the southern pine beetle. This insect is an exotic species that invaded the southern Appalachians in the late 1950's (Eagar 1984). It is severely threatening a southern Appalachian endemic tree (Fraser fir) and has already drastically altered the last undisturbed remnants of the southern Appalachian spruce-fir. GRSM holds the largest block of virgin southern Appalachian spruce-fir (White 1984).

The balsam woolly adelgid is a parthenogenically reproducing species that is dispersed passively on wind currents (Eagar 1984). Infestations begin at lower elevations within the range of fir and then spread up the elevational gradient. It has been hypothesized that the insect is deposited at lower elevations by wind eddies. In any case, mortality typically develops from low to high elevations on a given slope. Infested mature fir trees die within seven years. There appears to be no genetic resistance to the adelgid in GRSM and mortality of mature trees after infestation appears to be complete. Young fir are less affected, evidently because the adelgid requires bark fissures for feeding. The first heavy mortality occurred in GRSM in the 1960's in the eastern region of the park. Heavy mortal-

ity occurred in the western region of the spruce-fir zone in the late 1970's to mid-1980's.

The most important questions from a conservation point of view concern the future of Fraser fir: Will this species become extinct? Can we quantitatively determine the extinction risk for this species? At what rate is it being lost? Although we have good data on the adelgid's effects on fir and on the nature of post-infestation succession, we cannot yet answer broader scale questions because they involve landscape level patch dynamics processes that have not been studied. These questions include the following: (1) as mature trees die, do adelgid populations become locally extinct (i.e., what are the patch specific dynamics of adelgid populations)? (2) if the adelgids become locally extinct, will understory seedlings and saplings be able to reach reproductive size and age before they are reinvaded by the adelgid? and (3) as the patches of mature trees become rarer, will the rate of adelgid dispersal be sufficient to eliminate all patches? There is also the possibility that plot specific studies have missed heterogeneity in mortality and that

some fir possess a measure of resistance to the adelgid (this may be true for one population outside GRSM). Despite their obvious critical nature, the answers to these questions are not yet known. The research that has been carried out has lacked the patch dynamics perspective at the appropriate landscape scale.

We have a good idea about the processes active at one point in time and space, but we cannot yet produce a prediction of the outcome of these processes over longer times and broader spatial scales (Figure 3). With a better understanding at these broader spatial scales, we could better predict the extinction risk of Fraser fir over the next several decades and, if the extinction risk is high enough, we could prioritize stewardship strategies with greater confidence. For example, genetic diversity still present in these populations could be assessed and protected by seed storage and long-term tissue culture. At present, the park is spraying two small populations of Fraser fir with an insecticidal soap (relatively benign to other organisms and not persistent), however, this is an expensive operation and can only be carried out in small areas.

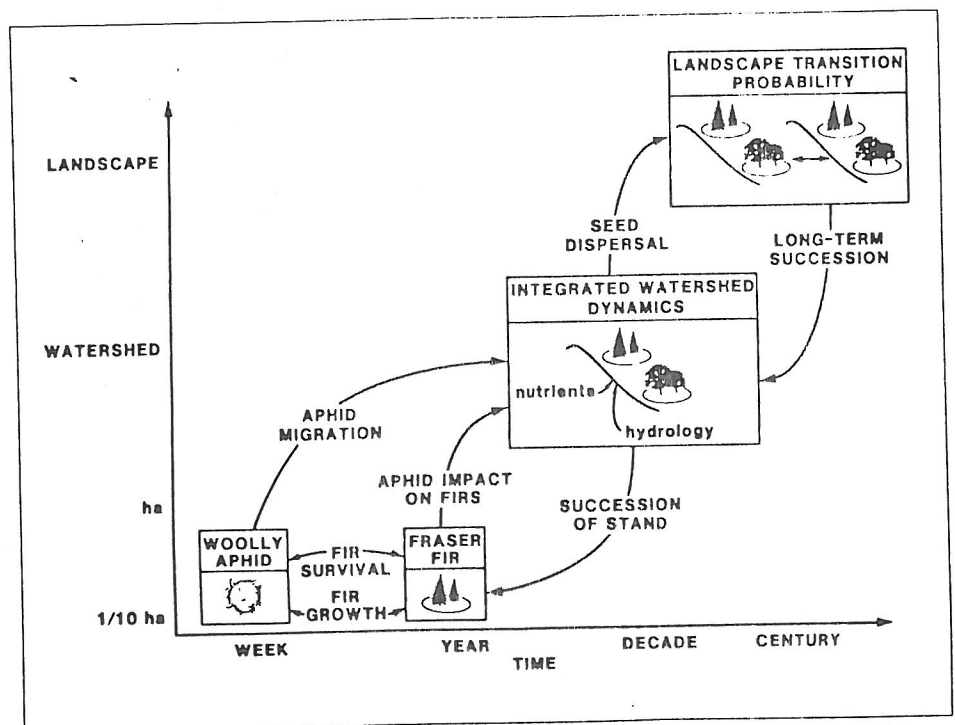


FIGURE 3. Key interactions between the balsam woolly adelgid and Fraser fir at a range of temporal and spatial scales (from Dale et al., in review).

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## Summary

The two examples described above point out the limitations of plot specific studies if these plots are not set in a larger landscape and patch dynamics perspective. For both southern pine beetle and balsam woolly adelgid, researchers have tended to focus on successional change within specific patches (the most affected areas); there has been no analysis of how much of the landscape is in particular patch states or how this changes over time. There has been little research on spatial patterns (number, shape, and isolation of patches and interactions of patterns and mechanisms with topography) or landscape-level processes like the dispersal rates of the insects. This is understandable due to the complexity and long-term nature of these problems. However, the result is that we lack a quantitative understanding of the rate of loss of the resources in question and we therefore lack stewardship direction in these programs.

## CONSEQUENCES OF PATCH DYNAMICS FOR PRESERVE DESIGN AND MANAGEMENT

The most important conceptual issue that emerges from a consideration of patch dynamics in natural areas concerns preserve size and whether preserve size itself determines the level of stewardship effort required for natural area protection. In one of the first papers on patch dynamics and nature preservation Pickett and Thompson (1978) criticized early applications of island biogeographic theory to preserve design. They pointed out that the critical minimum area for a preserve had to be large enough to include all successional states for the vegetation types present to allow the disturbance regime to continue to control natural dynamics. If the "shifting mosaic" was entirely contained, both early and late successional species would persist in the preserve. This would guarantee the persistence of higher species diversity than would be present if the preserve contained only some elements of the mosaic. Further, if preserves contained a subset of the patch dynamic states, the elements contained

might be unstable in the long-run (for example, if the requisite species for response to disturbance were absent). Thus, it was concluded that the maintenance of diversity within a preserve depends on inclusion of enough area to contain the natural processes and patch states. This view is further underscored by the frequent conclusion that disturbance maintains higher diversity in landscapes than would be present if disturbance was absent (White 1979, Denslow 1985).

If preserved systems are in equilibrium, then we can surmise that natural processes will maintain the communities and species present (at least if we ignore evolutionary time scales and changing climates). Theoretically, stewardship should consist of preventing human interference with these processes. Optimum preserve design then consists of finding preserve configurations that protect or promote the natural processes in question. This is an attractive concept in part because it suggests that nature can take care of itself. The protection of the balance of nature is an emotional motivation that has probably inspired many conservation efforts. Further, if natural processes are extant, stewardship can be relatively unobtrusive and we can avoid the second paradox of nature preservation, namely that deliberate human manipulation must be used to restore naturalness and protect natural areas from further human influences (White and Bratton 1980).

Although the concept of dynamic equilibrium in preserves is attractive, we must carefully assess its usefulness. For example, due to lack of historic or baseline data, we often do not have quantitative information on whether protected resources are in a dynamic equilibrium or are changing.

Under what circumstances are we likely to have a patch dynamic equilibrium—a shifting mosaic steady state? One necessary condition is a stable disturbance regime. Two other factors are also important: (1) the size of patches and the frequency of disturbances relative to preserve size (Romme and Knight 1982,

Shugart 1984) and (2) biotic feedback (the correlation of disturbance probability with community state, as when disturbance vulnerability increases through successional time). The likelihood of a dynamic equilibrium of patches increases if patch size is small relative to preserve size and if the probability that a disturbance will occur increases through successional time.

Assuming these conditions, what preserve size is adequate for dynamic equilibrium? Based on work with simulation models, Shugart (1984) predicted minimum equilibrium areas as a function of disturbance size for a variety of landscapes. For Appalachian forests subject only to tree-fall disturbances, minimum area was 100 to 10,000 ha (250 to 25,000 acres); for Appalachian forests subject to wildfires, minimum area was about 100,000 ha (250,000 acres); and for Australian forests, where fire size is large, minimum area was 1 million to 1 billion ha (2.5 million to 2.5 billion acres). Romme and Knight (1982) investigated the fire regime of a watershed in Yellowstone National Park and suggested that patch dynamic equilibrium was likely to apply to only very large areas because of large fire size, that equilibrium was absent from a study watershed of 10,000 ha, and that equilibrium was probably barely obtained in the park as a whole.

Based on Shugart's (1984) models, Great Smoky Mountains National Park, at 200,000 ha (494,000 acres), would be large enough for equilibrium in terms of tree-fall disturbance and possibly for wildfire. However, we must note the caveats: as discussed above, fire regime has changed in GRSM. Thus, despite this prediction of equilibrium, we have already noted that the pine forests of GRSM are succeeding to hardwood dominance. Further, big tree stands of old-growth forest are not homogeneous. For example, stands of hemlock-hardwoods, with the largest tree sizes in the park, are found in stream valleys, separated from one another by intervening ridges. The minimum area available for equilibrium dynamics is less than the area of the park.

Particular big tree stands may be out of equilibrium even if this forest type as a whole is in equilibrium (data are currently lacking to allow a conclusion on this patch dynamics question as well). Finally, such threats as chestnut blight invasion have caused widespread changes in tree-fall dynamics despite relatively large preserve size.

Our experience in large national parks suggests that direct and indirect human threats to resources are not eliminated by large preserve size. Examples include water level fluctuations in Everglades National Park caused by manipulation outside the park; exotic species invasions (chestnut blight, balsam woolly adelgid, and the European wild hog) and air pollution in Great Smoky Mountains National Park; and changing fire regimes in Sequoia-Kings Canyon National Park. All of these are large (>200,000 ha) preserves. These examples show that large park size does not, by itself, remove the threat of irretrievable loss of resources and that there must be monitoring and stewardship programs in even our largest preserves. Even where preserves are large relative to the dynamic processes of interest, active stewardship is important.

A final reason to be cautious in accepting park size alone as a predictor of conservation success has to do with the large seasonal movements of some species. Mammals with seasonal migrations are not entirely protected even in our largest national parks (e.g., Yellowstone). Migratory birds pose the same problem; their survival depends on processes that cannot be contained within even the largest preserves.

There are, of course, several independent reasons that argue for large preserves. For example, the stewardship problems just described are often a function of preserve size; the smaller the preserve, the more communities and species require active stewardship and monitoring. Also, small preserves may be internally homogeneous and lack the full mosaic of community types that maintain high diversity for a given landscape or biogeographic

region. Such homogeneous areas may not support all of the species needed to respond to a natural disturbance and the whole preserve may be vulnerable to a single disturbance. Small preserves may contain only one or a few samples of key resources; larger preserves may have some redundancy in the form of multiple samples of these resources. Constraining the conclusion that stewardship intensity is inversely related to preserve size is the fact that many small preserves are established for narrow goals, such as the maintenance of a single rare species. Thus, the overall scope of stewardship is not comparable to that of larger preserves.

### CONCLUSIONS

Ideally, preserves should be large enough to encompass the natural dynamics of protected ecosystems. Where preserve size is large relative to the scale of internal dynamics, species and community diversity for the preserve as a whole may be stable. However, this conclusion depends on several assumptions that are frequently violated, the most important of which is that the disturbance regime is stable. We ought to be suspicious of this assumption because of climatic fluctuation, if for no other reason. Because of the lack of historic data, we often do not know whether disturbance regimes are stable. Further, all preserves are too small to contain some of the processes that maintain resources (most clearly seen in the case of mammals and birds that migrate seasonally and certainly if climatic warming becomes a reality). The development of cooperative stewardship schemes to protect migratory species in larger spatial settings will be required.

Because the need for stewardship may increase as preserve size decreases, small preserves are likely to require relatively intense stewardship. However, this is true only as long as the goals of large and small reserves are equivalent. For example, small preserves are often established to protect a single rare species population, rather than to protect an entire ecosystem type or landscape array of

ecosystems. Under these circumstances, stewardship effort, while still critical, is not disproportionately larger on a system of small preserves compared to larger ones.

Our experience in national parks suggests that some human threats are not mitigated by large park size. These examples show that monitoring and stewardship must be active programs in even the largest preserves. Further, we will almost always be dealing with several sources of change within protected areas. The interpretation of permanent plot data will be influenced by how the plots are established relative to the spatial distribution of community states. Only by understanding how study plots are situated relative to the spatial pattern will we be able to use these plots to determine overall landscape change.

In general, we lack the ability to predict the response of particular species to given natural disturbances. Since species responses are probably individualistic and are also influenced by stochastic factors, the response of species to disturbance is an important area for research.

### LITERATURE CITED

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