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FINDINGS

INSIDE

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"Science affects the way we think together."
Lewis Thomas

SEX AND THE SINGLE SQUIRREL: A GENETIC VIEW OF FOREST MANAGEMENT IN THE PACIFIC NORTHWEST

Photo credit: Wes Colgan III

The northern flying squirrel may be an important indicator of ecosystem productivity in Pacific Northwest forests.

IN SUMMARY

Forest management throughout the world is producing simplified forests. There is growing concern that these forests maintain neither complete vertebrate communities nor conditions favorable to maintenance of genetic diversity of those vertebrate populations that do find habitat in simply-structured stands.

Genetics is increasingly being used as a basis for management recommendations, yet few field data exist to support these recommendations. To test the effectiveness of management alternatives in providing and maintaining healthy, resilient ecosystems, carefully selected species like flying squirrels may be used to index changes that occur in forests under different management strategies.

Understanding how genetic diversity and variability within small populations relate to landscape-level biodiversity is not yet an exact science. However, research on flying squirrels—selected for their complex food web relationships that indicate overall ecosystem productivity—is helping formulate questions that will help us understand how forest management activities affect genetic building blocks.

"A squirrel leaping from bough and making the wood but one wide tree for his pleasure . . ."

Ralph Waldo Emerson, 1803-1882

Strong sexual drive and promiscuity may be among the saving graces of the northern flying squirrel, a nocturnal tree-dwelling rodent common in Pacific Northwest forests. Combine these life-history attributes with landscapes that don't impede their movement, and the ability of flying squirrels to recover after management disturbance is possibly quite robust. The question is, how robust, and under which specific management conditions?

The effect of timber harvest on genetic diversity (biodiversity) of wildlife is a major issue of contemporary forest management. Can populations of species remain healthy through commercial thinnings, clearcuts, forest fragmentation? Can multiple societal goals—ranging from timber production to wildlife habitat—be met simultaneously across the same landscape?

"Forest management over the last 150 years has simplified and fragmented many forests, and produced conditions unfavorable for maintaining genetic diversity in vertebrate populations," says Todd Wilson, a wildlife biologist with the Ecological Foundations of Biodiversity team at the Pacific Northwest Research Station in

Olympia, Washington. "Because the ecological health of forests is coming under closer scrutiny, managers must now choose among strategies that vary in intensity and amount of timber harvest, and therefore in intensity of disturbance to forest organisms."

Within the continuum of forest management practices, ranging from short-rotation monocultures to long rotations without intermediate intervention, lie alternatives that can produce opposing effects. Management strategies may promote landscape function, enhance biodiversity, and maintain genetic diversity, or they may lead to unpredictable and chaotic conditions, fragmented populations, and accelerated loss of genetic diversity, according to Wilson.

"Our current understanding of the effects of either historical or new forest management on the genetic diversity of vertebrate populations is primarily limited to theory—few field studies have been conducted," he says. Recent advances in DNA analysis techniques have improved approaches for analyzing population structure in wildlife, and Wilson took the methodology into the field with flying squirrels.

KEY FINDINGS

- Flying squirrels residing in a highly fragmented forest had markedly lower genetic variation, a reduced gene pool, and less variety in genetic form than did populations within relatively continuous forests with few physical barriers to squirrel movement. Restriction of gene flow owing to past and current forest management could account for much of the variation.
- Sharp population declines in experimental forests after variable density thinning reduced gene diversity by more than one third; diversity returned to initial levels within 3 years.
- Flying squirrel mating behavior (promiscuity by both sexes and long-distance mate-seeking by males) as well as high landscape permeability (lack of impediments to movement) produced rapid gene flow and quick recovery after management disturbance.

SELECTING THE INDICATORS

Great care must be taken in selecting species to be used to index changes occurring under different management strategies, he says. In the Pacific Northwest, the northern flying squirrel occupies a central place in complex food webs: it feeds on nuts and fruits of Northwest plants as well as the fruiting bodies of various fungi, and it is prey to larger species such as owls and weasels. Flying squirrels occupy a wide range of forested habitats, and their populations vary widely in abundance, depending on local habitat conditions. They are thus well-positioned to indicate the overall productivity of their native ecosystems.

"Flying squirrels are totally dependent on trees for major travel and dispersal, thus nonforested patches are virtually impermeable to them," Wilson explains. "They can use stands of small trees such as those found at high elevations or latitudes, but large clearcuts in Pacific Northwest forests produce barriers to flying squirrel dispersal for at least 20 to 35 years following harvest."

To complicate matters further for the flying squirrel, the current landscape of the Pacific Northwest, once covered by significant areas of large, old-growth forests, is now dominated by a checkerboard of clearcuts and dense stands of second-growth Douglas-fir forests. "The juxtaposition, shape, and age of stands may limit the ability of flying squirrels to mate widely and disperse as colonizers—processes important for genetic exchange and maintenance of genetic diversity. Thus they may be more sensitive to the effect of human disturbances on genetic diversity at management-unit levels than other species," he notes.

Wilson established a study designed to examine whether flying squirrel "microsatellite DNA" could be used to evaluate genetic diversity in managed forests. Microsatellite DNA is a special class of DNA that is well-suited for statistical analysis because it passes randomly from both parents to offspring; it does not code for physical traits that might be selected for or against in the wild, such as hair color or tail length; and it can be highly variable, which can help uniquely identify both individuals and populations.

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The study's objectives included developing genetic "libraries" to find and catalog segments of flying squirrel microsatellite DNA suitable for analysis; genetically describing flying squirrel populations that have been subjected to both natural and anthropogenic disturbances; exploring forest-level flying squirrel populations subjected to different disturbances and management strategies during the last 70 years; evaluating effects of variable-density thinnings on small, stand-level populations of flying squirrels; and contrasting populations in a highly fragmented forest to those in forests with relatively unbroken canopies. Ultimately, the study could help build a base of information for choosing among various management alternatives.

LAND MANAGEMENT IMPLICATIONS

- Landscape permeability is key to maintaining genetic diversity in managed forests. Squirrel populations in continuous-canopy forests demonstrated resiliency to management activities that produced noncatastrophic disturbances and maintained connectivity over large forested landscapes.
- Landscape barriers, both anthropogenic and geographic, can lead to rapid divergence of the genetic composition of squirrel populations. Narrow corridors in fragmented landscapes may not provide adequate permeability for movement-restricted species like flying squirrels.
- A focus on landscape-unit turnover (stand age, rotation age, juxtaposition) and rate of stand development may be more effective than a focus on corridors in producing both variety and volume of wood products, as well as highly permeable landscapes for wildlife.

SCALE, QUALITY, AND CONNECTIVITY

"The spatial scale at which populations are evaluated is important in the interpretation of vertebrate genetics for forest management," Wilson notes, "because effective conservation cannot take place without looking at multiple scales, including both the stand or patch scale where management directly influences individuals and local populations, and the broader patchy landscape." At the landscape scale, degree of permeability for gene flow is crucial; in other words, how successfully can individuals travel across patches to mate, disperse, or immigrate?

Other key factors in conserving genetic diversity include habitat quality and connectivity. The quality of habitat available in patches across the landscape significantly influences genetic diversity by controlling the population dynamics of the species using that landscape; such factors as reproductive success and population density, for example, are central to the persistence and survival of a species, particularly after habitat disturbance.

Because conservation requires that mating, dispersal, and immigration processes continue unimpeded, barriers created by open space back flying squirrels up against the wall: their promiscuity and sexual drive certainly help, but cannot succeed without support. Connectivity can help provide that support by regulating gene flow. Corridors, closeness of patches of a particular type across the landscape, and overall landscape permeability are the elements of greatest importance.

"We think of permeable landscapes as those with a dominance of patches whose boundaries are of low contrast, such as undisturbed forest next to lightly thinned forest. Landscapes with high permeability help the movement of individuals among patches, and help maintain gene flow between populations," Wilson explains. "In landscapes where permeability is inhibited or disrupted by poor-quality habitat or nonhabitat, genetic dispersal of a species like the flying squirrel can be essentially eliminated."

The concept of landscape permeability for key wildlife species has yet to be applied globally to the decisionmaking process in both stand- and landscape-scale forest management, he adds, emphasizing that the potential benefits of permeability are great.

FLYING SQUIRRELS AND FOREST HISTORY

The purpose of Wilson's preliminary study was to develop hypotheses for future testing. In this study, squirrel populations were evaluated at both the patch (small, stand-scale effects) and forest scale. Three forests were selected in western Washington; 17 populations of squirrels on 32-acre patches were the focus of genetic studies.

Each of the three forests developed after widespread clearcutting in the early 20th century. This management eliminated significant portions of habitat for flying squirrel populations for several decades, and required recolonization subject to local conditions.

Two of the forests studied are owned by the U.S. Army and are surrounded by the heavily urbanized south Puget Sound. But apart from some recent clearcuttings and land conversion, according to Wilson, the surrounding area has since remained relatively free of any major disturbance.

"Thus, a relatively continuous canopy connected much of the area between and around these two forests, broken occasionally by a mosaic of small prairies and an extensive network of small, unpaved roads which we know do not unduly inhibit flying squirrel movement."

Of these two forests, one (Legacy) was clearcut 60 years ago and has not subsequently been disturbed by management activity. Forest cover was 99 percent Douglas-fir, with sparse understory of mosses and shrubs, and widely scattered old-growth legacies. The other forest (Timber) was clearcut 70 years ago and subsequently disturbed by two light commercial thinnings. Douglas-fir cover was 95 percent; understory was heavy with salal and ferns. No old-growth legacies remained.

In addition to these management histories, variable-density thinnings were implemented on half the patches (four of eight) in each forest to evaluate the short-term response of flying squirrels to intermediate-scale disturbance.

For comparison, Wilson chose a third (Isolated) forest that was more intensively disturbed than the two Puget Sound locations; most of the Isolated stands were subject to regular clearcuts, leaving a highly fragmented forest in their wake. Although less than 25 miles distant, this forest was separated from the other two by the I-5 corridor, the cities and suburbs of Lacey, Olympia, and Tumwater, and many rural roads, agricultural fields, prairies, and grasslands. This was a mixed hardwood-conifer forest, with a dense understory of ferns and salmonberry. The study site was surrounded by stands less than 10 to 25 years old, but connected to other second-growth forests of similar age by narrow strips of trees about 80 yards wide.

While immediate history—of the past 70 years—is one factor affecting current populations, the nature of their gene pool has been developing over a far longer period.

GLACIERS, GENES, AND FIRES

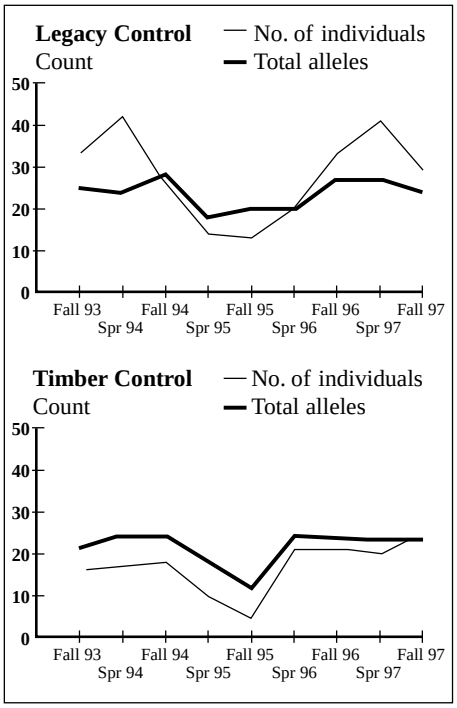
"There are never true 'controls' in evaluating the genetics of any wild population because each population arises from a unique combination of geological and ecological events," Wilson explains. "Thus an understanding of the known history of a population can be important for providing critical insight into observed genetic patterns."

All three forests, he says, developed under the influence of the most recent glaciation to affect western Washington, about 14,000 years ago. The Legacy and Timber Forests were covered by thick sheets of ice; the Isolated Forest was not under such deep cover, but habitat conditions would have been harsh and likely inhospitable to flying squirrels.

Although the postglacial landscape between the Puget Sound forests and the Isolated Forest did contain barriers, Wilson points out that they were relatively ephemeral, and large forests to the south could have provided a large gene pool for squirrel repopulation in all three forests once glaciers receded. Contiguous forests throughout the region after glaciers receded also would have helped gene flow.

"But the mosaic nature of the landscape has had a dynamic history too," he says. "Gene flow was likely sporadic and circuitous owing to the dynamic forest-prairie mosaic maintained by fires set by Native Americans, which would have periodically changed the isolation-by-distance effects between the areas."

But then over the last 150 years, forest contiguity would have increased as settlers from the Eastern United States suppressed fires. And then, in turn, conversion of forests to farming homes and towns would have turned the tables again. Thus flying squirrel gene pools have developed, struggled, and returned through a variety of both natural and anthropogenic disturbances.



Variation in numbers of individual squirrels and total numbers of alleles (pooled over four DNA segments) in a subset of populations from two forests over 5 years—one forest with higher quality habitat (Legacy) and one with lower quality habitat (Timber). A drop in squirrel population levels occurred in both forests owing to variable-density thinnings in 1993 and subsequent predation. However, both populations recovered to initial levels 3 to 4 years after thinnings, suggesting the potential for resiliency after certain management activities.

ADAPTING TO DISTURBANCE

"It should be emphasized that our approach was to describe patterns of genetic variation in forests with different management histories—cause and effect cannot be shown," Wilson says. "Our discussion of these results should only be viewed as generating hypotheses—an important, yet cautious first step for describing the genetics of this selected species."

Patch populations within and between the Legacy and Timber Forests were genetically similar even though they had passed through notably different management regimes that had different effects on population size and density, including reductions owing to previous commercial thinnings in the Timber Forest. The Legacy Forest had slightly higher genetic variation because it had a larger population size, presumably because of higher quality squirrel habitat compared to the Timber Forest. In contrast, Wilson says, the Isolated Forest differed from the other two in both variety and composition.

"Restricted gene flow owing to current and historical forest management, along with recent geologic events could account for much of the difference we observed," he concludes. "Landscapes of varying permeability arose out of disruptions of canopy connectivity, and this difference between the two locations suggests that landscape-level barriers could lead to rapid divergence of the genetic composition of local squirrel populations."

In the two Puget Sound forests, similarities were observed among 16 subpopulations, even though they had different management histories, and both were disturbed by the variable-density experimental thinnings. Sharp population declines caused by the variable-density thinnings and subsequent heavy predation reduced genetic variation by more than one third, but diversity returned to initial levels in all stands within 3 years.

WRITER'S PROFILE

Sally Duncan is a science communications analyst and writer specializing in natural resource issues. She is currently a Ph.D. candidate in Environmental Sciences at Oregon State University in Corvallis.

"It appears from our findings that squirrel populations in continuous forest demonstrated resiliency to management activities that produce noncatastrophic disturbances and maintain connectivity over large forested landscapes," Wilson says. Key to this was the availability of nondisturbed adjacent forest for recolonization to occur.

NEW GENES OR LOST GENES?

Analysis of the genetic composition in the heavily managed Isolated Forest suggested that the present flying squirrel population was mating randomly, but evidence of high inbreeding and lowered genetic variety indicated a recent genetic bottleneck had occurred.

"Breeding success, predation, and environmental factors are all critical in shaping small populations—even a single bottleneck can result in a serious loss of genetic variation, especially if recolonization opportunities are restricted, as by continuous clearcut harvests." The highly fragmented landscape may have restricted opportunities for interbreeding outside the patch, thus reducing gene flow, keeping patch population small, and increasing inbreeding.

"There's always the possibility that small, isolated populations may give rise to a new gene variation that enhances survival in fragmented forests," Wilson notes. "But the more important point in this whole story is that mutations are extremely rare (only show up about once every 10,000 generations for microsatellite DNA), whereas we can lose genes many many times faster than that."

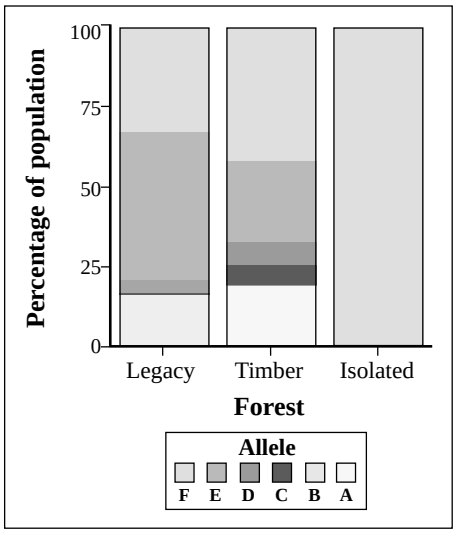
Life-history adaptations contribute to resiliency of the flying squirrel populations. Not only do both sexes seek multiple mates, but males will travel great lengths to find willing females, and thus genetic contributions to each litter are often made from more than two parents. These mating behaviors can promote high gene flow even for low-density populations, Wilson says. "This suggests to us that environment may have a greater influence on gene flow and genetic structure of populations than behavior or physiology."

It appears to researchers that had the Legacy and Timber Forest squirrel populations been cut off from other forested areas, such as by clearcuts, the loss of genetic diversity would have been as high as one third. Thus, they concluded that 540-acre patches of forested habitat appear too small for low-density populations to prevent genetic loss if the area is not connected to undisturbed surrounding forest for several years after thinning takes place.

So what are the preliminary management implications?

"First of all, we suggest caution in proposing any single approach to resolve issues surrounding the conservation of genetic diversity in forest ecosystems," Wilson says. "We know that connectivity is important, but extremely narrow strips may not provide suitable connectivity for species like flying squirrels, and could lead to restricted gene flow, or even predator traps."

A workable alternative might be management of landscape-unit turnover—that is, more consideration of permeability through patch age, rotation age, harvest pattern, and rate of patch development—to ensure adequate gene flow for flying squirrels and organisms with similarly restricted mobility.



An example of the genetic variation present in flying squirrel populations that resided in forests with different management histories. Each bar represents the proportion of the total population within each forest that carries alleles (alternative forms of a gene) for a specific segment of DNA evaluated during the study. For this segment, the Isolated Forest had only one allele present in the population, evidence of a genetic bottleneck in the recent past; the Legacy and Timber Forests had more diversity, with up to six alleles present within their populations.

Longer rotations with retention of biological legacies and biocomplexity also appear to produce landscapes with few impermeable edges.

Research into the complexities of genetic structure will continue to help clarify the relationships between genetic diversity and conservation efforts. Key questions still require intensive field testing: What are the differences in genetic diversity between extensive and isolated old-growth forests? Do highly fragmented, repeatedly harvested forests provide the same genetic diversity as extensive contiguous second-growth forests?

Further development of microsatellite DNA libraries, while extremely time-consuming, appear to offer strong promise for addressing such questions, and also may allow researchers to pursue information on kinship relationships among populations.

"We suggest caution in proposing any single approach to resolve issues surrounding the conservation of genetic diversity in forest ecosystems."

Todd Wilson

FOR FURTHER READING

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