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# Science

FINDINGS

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

## PARADOXES IN SCIENCE: A NEW VIEW OF RARITY



*Over 230 species of rare, old-growth forest dependent species, including chanterelles, were originally listed for protection under a federally mandated regional forest conservation program.*

The Northwest Forest Plan is designed to be a new generation forest plan: it looks at the whole forest ecosystem, with the intent of protecting not just a few species such as the spotted owl and the salmon, but all forest creatures great and small. A contentious element of the plan is the "survey and manage" requirement: certain rare species must be surveyed individually prior to ground-disturbing activities so that their location can be considered and protected in the project design.

The logic is sound, but the implementation is mind-boggling. The Northwest Forest Plan considered over 1,000 species associated with old-growth forests west of the Cascade Range in California, Oregon, and Washington. Although only 80 of those require survey prior to ground-disturbing activities, even those numbers are high enough to make survey and manage a controversial undertaking.

"Single-species management of so many species is not inherently wrong, but it's certainly not practical, and effectively forces us to make arbitrary decisions about which species to address and which to ignore," says David Boughton. Boughton conducted research on survey and managed species as a postdoctoral research ecologist with the PNW Research Station. He is now a researcher with the National Marine Fisheries Service. He is trying to squint through the haze of single-species management to detect useful ecological patterns that may not yet have been considered. "If we can find unifying principles among certain species, it may allow us to manage them as a group, a far more practical approach."

But first, we need to examine more thoroughly the very concept of rarity, he says. What if it turned out that rare species had always been a characteristic of the landscape? What if we can engineer our own activities to pose risks no greater than those that occur in the original ecological system?

### IN SUMMARY

*The "survey and manage" requirement of the Northwest Forest Plan is a challenge for land managers strapped for time and funds to implement it and for environmentalists concerned about its implementation. Its single-species management approach raises some interesting questions.*

*What makes these species rare to begin with? And why have they survived? On the one hand, ecological theory predicts that rarity makes a species vulnerable to catastrophes. On the other hand, rare, old-growth-associated species do occur in west-side forests, which have a long history of natural catastrophic disturbances. If we can understand something about how rare species persisted up to the present day, we may learn something about how to manage for their persistence in the future. Understanding mechanisms of rarity is vital to developing multispecies approaches to the survey and manage list.*

## SPECIES ON THE EDGE

What if? is often the question that unveils scientific paradoxes. "The truth is, the scientific community cannot find consensus on why certain species are rare. The only thing we're really confident about, via population theory, is that rare species are especially vulnerable to extinction."

In evolutionary ecology, he explains, we often assume that species are density-dependent, meaning that at high abundance, the population growth slows, and at low abundance, it speeds up. This mechanism acts as a kind of hedge against the population's going extinct.

"But what happens in an environment like the Pacific Northwest, where frequent large-scale disturbances can just overwhelm a species' mechanisms of density dependence?" Boughton asks. "Species on such a landscape can be rare or common purely by chance."

If rare species have been around in the volcano- and flood- and fire- and wind-challenged Pacific Northwest landscape long enough, surely a case could be made

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### KEY FINDINGS

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- There appear to be two syndromes of rarity: habitat-limited species and dispersal-limited species. Habitat-limited species are rare because their habitat is rare; dispersal-limited species are rare because they lag behind the disturbance-forced turnover of their habitat.

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- In simulations of landscape disturbances, habitat-limited species were mostly resilient to disturbance, recolonizing quickly once the landscape recovered.

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- Dispersal-limited species were not very resilient. Their regional persistence and abundance were sensitive to historical accidents. Moreover, dispersal-limited species may be associated with old forest, not because they require its particular structural traits, but simply because it is old and has had longer to accumulate them.

that they had adapted to it? But what if they hadn't?

"On the one hand, ecological theory predicts that rarity makes a species vulnerable to catastrophes. On the other hand, rare, old-growth associated species do occur in west-side forests, which have a long history of natural catastrophic disturbances," he notes. "If we can understand

how rare species persisted up to the present day, we may learn something about how to manage for their persistence in the future."

It may simply be, contrary to prevailing wisdom, that some species are not associated with old-growth forest because they require it as habitat, but simply because it is old and has had longer to accumulate them.



*The forests of the Pacific Northwest are well known for their rich diversity of macrofungi, such as these mycena. Issues relating to conservation and management of forest fungi in the Pacific Northwest must be placed in the context of public land resources and federal laws regulating forest management.*

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### *Purpose of PNW Science Findings*

To provide scientific information to people who make and influence decisions about managing land.

*PNW Science Findings* is published monthly by:

Pacific Northwest Research Station  
USDA Forest Service  
P.O. Box 3890  
Portland, Oregon 97208  
(503) 808-2137

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United States  
Department of  
Agriculture



Forest Service

## “LIFE-HISTORY SPACE” AND OLD-GROWTH FOREST

To investigate the history of rarity, Boughton ran an existing landscape change model developed by his colleague Michael Wimberly, a forest ecologist at the PNW Research Station. The model is based on natural fire rotation (estimated from paleo-data), on known aspects of community dynamics among trees, and on fire behavior—all in the Oregon Coast Range. Existing data from the model suggest that fires have caused old-growth forest to act like a shifting mosaic, and to vary in amount from 25 to 80 percent of the landscape.

Currently, Boughton says, the Coast Range landscape is outside its historic 25- to 80-percent old-growth range. Because of logging and fire in the 20th century, it now carries only about 5 percent old growth. Nonetheless, a diverse flora and fauna persists in the old-growth stands, including some of the 404 rare, poorly known species granted federal protection under the survey and manage program (Some of these species are so poorly known that a better understanding may reveal they are less rare than originally thought.)

“The species—mostly lichens, fungi, mollusks, and bryophytes—reflect a typical conservation problem: protecting each species individually is expensive and impractical,” says Boughton. “Protecting them en masse via coarse-filter approaches requires assumptions that are difficult to assess.”

To address the question of how rare species might survive the kind of historical variability imposed on the Coast Range, Boughton and colleagues developed a new method in which they examined the “life-history space” of the prehistoric landscape.

“The approach we took involved what I think of as reverse engineering of the biota,” Boughton says. “The life history of an animal or plant tells us how it allocates time and energy to maximize its fitness for a certain set of environmental conditions. Turning this on its head, we wanted to analyze the properties of the landscape to find out what life-history strategies would allow for an animal or plant’s survival.

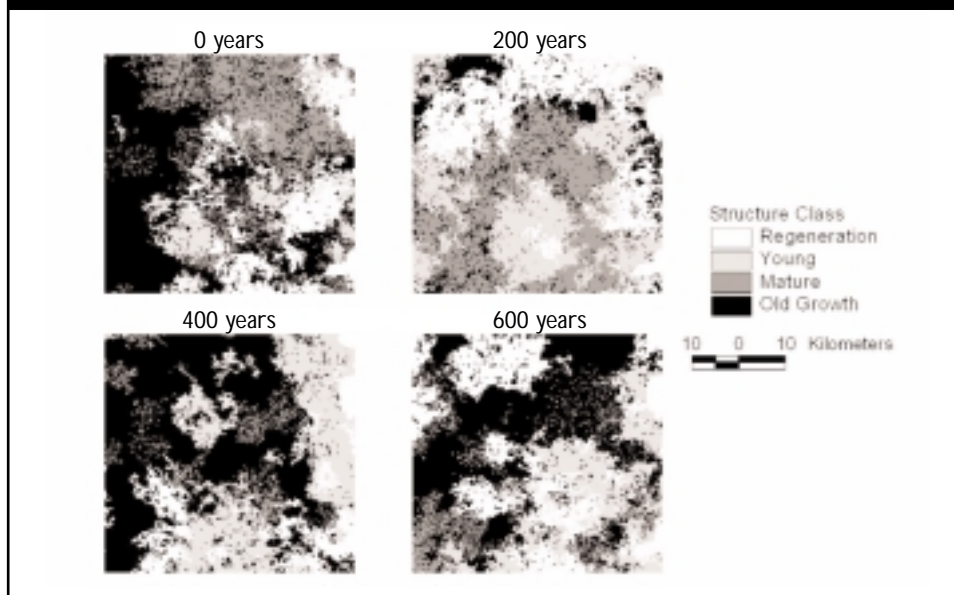


### LAND MANAGEMENT IMPLICATIONS



- The simulations suggest that structure-based management may be an effective conservation strategy if species are habitat-limited. But dispersal-limited species may take too long to colonize the new habitat, so a more effective conservation strategy might be to protect existing habitat in which the species already occurs.
- It is plausible that dispersal-limited species’ sensitivity to historical accident could be used to advantage in long-term management. It may be possible to design managed disturbance regimes that enhance species persistence.
- The “life-history space” concept suggests an alternative to trying to manage species we know nothing about: manage the life-history space of the entire landscape. Or, use it as a first-cut risk assessment that is cheaper and faster than field studies.

### FOREST PATTERNS PRODUCED BY MODEL OF FIRE REGIMES



▲ The reconstruction of the fire history in Oregon’s Coast Range over the past 3,000 years has shown dynamic variation, with the range of old-growth cover from 25 to 80 percent of the landscape. Old-growth cover is currently about 5 percent.

The life-history space of a landscape is the array of life histories that can persist in it. To keep it simple in this initial phase of research, we gave the space only four dimensions, he explains: colonization ability, expected extinction rate, habitat breadth, and dispersal range. A point in this created space represents a hypothetical species with a particular combination of the four

traits. At the end of a simulation of 3,000 years of a natural fire regime, species were common, rare, or extinct, depending on their position in life-history space.

Boughton then reviewed what landscape traits a species required to persist, and yet remain rare, at below 5 percent incidence in old-growth forest.

### WRITER’S PROFILE

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## ORIGINS OF RARITY

What the researchers found not only has implications for management of rare species but also for the hazy interface between two scientific schools of thought.

“Our simulations produced an interesting series of hypotheses,” Boughton says. “First, there were two syndromes of rarity: habitat-limited species, which were rare because their habitat was rare; and dispersal-limited species, which were rare because they lagged behind the fire-driven turnover of old growth. We believe many lichens, bryophytes, and fungi may be dispersal-limited.”

Habitat-limited species mostly were resilient to disturbance, the researchers found, recovering quickly once the landscape recovered. Because their habitat is rare, they must be efficient at colonizing it if they are to persist over the long term. This trait means they would be effectively

protected by structure-based management, he points out. Dispersal-limited species, however, were not resilient, and would not respond to old-growth structure unless it was actually old and had therefore allowed them plenty of time to colonize.

“Their regional persistence and abundance were contingent on the particulars of fire history,” says Boughton. “In other words, in the literature about rarity, you find a lot of discussion of mechanistic cause and effect in the current environment. But our model suggests that rarity could occur by ‘accident,’ by a series of events that occurred prehistorically, but that were not inevitable.” You have to pull back into the philosophical realm, he notes, and see that such events, like fire, are not repeatable and deterministic in the classic scientific sense. One particular prehistory occurred, but it could just as easily have been a different prehistory.

“What this thinking does is challenge our

notions of how a system is ‘supposed to be.’ We’re balancing on a line between two fields of science: system dynamics and population demography,” Boughton says. Ecosystem ecologists tend to emphasize the dynamics of the overall system and ignore the demographic constraints of individual species. Population ecologists focus on demographics but tend to simplify the external dynamics of the overall system.

“We believe that the two ways of thinking do not need to be exclusive, that the general principles about what each species needs to persist can usefully be injected into ecosystem thinking,” Boughton observes. “In fact, acknowledging both the system dynamics and demographic constraints was what led to the idea of dispersal-limited species.”

At the intersection of these two disciplines is the idea of habitat, created by the system and used by the organism.

## PATCH DYNAMICS: BIRTH, DEATH, AND ABUNDANCE

Ecologists have examined the impact of randomness of birth-death processes, both for individual organisms and for entire populations, and have described the consequences for extinction risk. Boughton wanted to apply the same questions to habitat via patch dynamics, which often encapsulate the birth and death processes of populations small and large.

“What if we assume habitat patches to have births and deaths of their own that arise from the interplay of disturbance and succession?” he asked. “If risk can be managed via the overall disturbance regime, it may be possible to protect large numbers of species even when they individually lack demographic data.” Think survey and manage.

Consider a grasshopper that lives on riparian gravel bars. Its habitat is periodically eliminated by floods or willow invasion, but the floods also create new patches elsewhere along the river. The sporadic nature of floods—3 to 10 per century—tends to create even-aged “cohorts” of gravel bars, Boughton explains.

“The grasshopper is exposed to two distinct risks: first, the river may go so long without a



▲ *Rare and endangered species have been rarer on the landscape than previously understood, simply as a result of natural disturbance history.*

flood that all habitat is lost to willow invasion. Second, the river may flood several times in rapid succession, such that grasshopper populations in old patches are eliminated before they can colonize any new patches,” he says. “Either way, the grasshopper would be driven to regional extinction by its patch dynamics. What seems to matter is not just the overall flood rate but the way the floods are distributed in time.”

This case study from central Europe illustrates how the dynamics of a habitat patch system can determine extinction risk of a particular species in a particular habitat type. “Are there risks that cut across all species in all habitat patches?” Boughton asks. “Answers to this question could form the basis for multispecies conservation strategies applied at a regional scale.”

## PATCHING THE LANDSCAPE

To address this question, he used a model of habitat patches. A habitat patch is considered to be a geographic area required by a species at some characteristic time during succession. The patch is therefore measured in two dimensions: lifetime measured in years, and carrying capacity or size measured in number of organisms.

The model allowed for different patch sizes and lifetimes and also for the randomness of patch occurrence. Different landscapes could be compared under different conditions.

The results of simulations suggest that the strongest effects on species arise from a fluctuating patch birthrate, Boughton explains. "In this form of variability, risk is

increased three ways: the overall abundance of species is lower, the fluctuations in abundance are greater, and the habitat itself is more likely to fluctuate to zero.

"In short," says Boughton, "we found that species attrition might be prevented by manipulating the dynamics of patch births. Can we therefore figure which kinds of management are better or worse in terms of how patches move around the landscape?"

Some areas, such as Oregon's Coast Range, already see such manipulations going on at several scales. The Coast Range is made up of about 5.6 million acres whose ownership is mixed amongst federal and state agencies, large corporate timber companies, and small private holdings. The property lines

between ownerships delineate the management type and thus the prevailing disturbance regime: rotational timber harvest on private lands, structure-based management on state lands, and fire suppression on federal lands.

"Each of these represents a different compromise between conflicting environmental and economic worldviews," Boughton says. "We need to lay the groundwork now for a way of thinking that makes species conservation consistent with economic activity. If we count too much on a reserve-based system, our efforts are likely to be foiled by accelerating climate change." What might be some alternative coarse-filter approaches?

## MULTISPECIES MANAGEMENT SOLUTIONS

The two modeling projects cut usefully across this question, in different ways.

"The life-history space concept addresses a knotty problem in species conservation: how to manage species you know nothing about. The alternative provided by the life-history space approach is to manage the life-history space of the entire landscape. Or simply use the life-history space as a first-cut risk assessment that is cheaper and faster than field studies, and helps you target your field studies to most important questions" Boughton says.

In the life-history space model, the dispersal-limited species were sensitive to historical contingency. He believes it is plausible that this could be used to advantage for long-term management strategies. "In particular, the sequence of disturbances that actually occurred in prehistory was not necessarily the most benign for a given species—quite the opposite. So it may be possible to design disturbance regimes that enhance species persistence."

Furthermore, such designed regimes might be engineered to be compatible with other goals, such as fiber production, fuels management, and so forth, but he emphasizes that this research is only in its early

stages. The patch dynamics model, on the other hand, raises additional questions relating to climate change. If the frequency of extreme events such as droughts, floods and wildfires increases, so will pulses of disturbance, thus increasing threats to persistence of rare species, Boughton explains.

"However, the model also suggests that manipulations could reduce the level of risk. In particular, if disturbances are more evenly distributed in time, attrition of the regional biota might be prevented."

The implications of this work for conservation measures such as survey and manage are profound, and Boughton believes it is important to bring the new perspective on rarity with us into the 21st century. The issues promise only to become more complex.

*"Suddenly, as rare things will,  
it vanished."*

Robert Browning 1812-1889

## FOR FURTHER READING

Boughton, D.A. [and others.] [In press]. *Can disturbance regimes keep species rare without driving them extinct?: Analyzing the life-history space of landscapes*. Ecological Applications.

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