Integrating Ecological Restoration and Conservation Biology:
a case study from Southwestern Ponderosa Pine forests

NORTHERN ARIZONA UNIVERSITY
Ecological Restoration Institute

The Ecological Restoration Institute at Northern Arizona University is a pioneer in researching, implementing, and monitoring ecological restoration of southwestern ponderosa pine forests. These forests have been significantly altered over the last century, with decreased ecological and recreational values, near-elimination of natural low-intensity fire regimes, and greatly increased risk of large-scale fires. The ERI is working with public agencies and other partners to restore these forests to a more ecologically healthy condition and trajectory—in the process helping to significantly reduce the threat of catastrophic wildfire and its effects on human, animal, and plant communities.

Cover photo (WARGRA): Grace's warbler is only one of many plant and animal species dependent upon southwestern ponderosa pine forests. Photo: Mike Danzenbaker

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INTRODUCTION

Among the many challenges land managers face in implementing restoration projects, one of the greatest is the difficulty of integrating restoration with other management imperatives. One of the most significant of those is the need to manage natural areas for the conservation of native animal and plant species. Some species are popular for hunting and wildlife watching; many serve vital ecological roles; many are rare and under special legal protection. It is not always clear if their habitat needs are compatible with restoring ecological integrity across the landscape. Yet there is evidence that ecological restoration can overlap to a large degree with the priorities of conservation biology.

In 2004 the Ecological Restoration Institute sponsored two workshops aimed at exploring this issue. In presenting some of the results of those workshops, this publication examines how the two fields are related in a single ecosystem type—southwestern ponderosa pine forests—and suggests steps managers might take to better integrate the two.

Efforts to conserve populations of the threatened Mexican spotted owl have underlined differences—and common ground—between ecological restoration and conservation biology. Photo by Amanda Moors.

BACKGROUND

Ecological restoration and conservation biology have different yet overlapping roots and aims.[1] Ecological restoration grew out of a perceived need to restore damaged sites at a small scale (such as strip-mined areas) and habitats that had been damaged on a larger scale (such as tallgrass prairies that had been heavily altered by agriculture).[2] In the southwestern United States restoration of ponderosa pine forests has grown out of a recognition that such nineteenth- and twentieth-century practices as logging, livestock grazing, and exclusion of natural fire dramatically changed ecological structures and processes.[3] These changes, in turn, have led to damaging and unnatural high-severity fires well outside this ecosystem's natural range of variability, as well as damaging insect outbreaks, large-scale mortality exacerbated by drought, declines in herbaceous vegetation, and other declines in ecological health. Ecological restoration activities are intended to address the root causes of these declines, not just the symptoms, by returning forests to a condition similar to that which prevailed before extensive human-caused changes. Within southwestern forests restoration activities run a gamut from "hands-off" actions, such as allowing lightning-caused fires to burn, to intensively "hands-on" activities, such as large-scale thinning to reduce unnaturally high tree densities.

Conservation biology is rooted in concerns about the present-day extinction crisis and the widespread destruction of ecosystems by human activity.[4] Though it recognizes the importance of ecological processes such as fire in maintaining ecosystem health, it has focused heavily on the ecological needs and genetic integrity of individual rare species and with the identification and protection of "hot spots" where biological values and risks are concentrated.[5] Like restorationists, its practitioners engage in a wide range of management actions, from avoidance (e.g. declaring tracts around Mexican spotted owl nest sites off-limits to most human activities) to direct intervention (e.g. reintroducing Mexican wolves to wildlands through captive breeding, feeding, and intensive management).

Both ecological restoration and conservation biology are problem-solving disciplines. Their practitioners are mission-oriented and emphasize particular values in land management. In the case of restoration, the primary values revolve around returning natural processes to the landscape so that ecosystems can function within their natural range of variability.[6] In the case of conservation biology, the primary values revolve around retaining a full range of biological diversity—in ecosystems, in species, and in gene pools within species.[7]

More so than many ecosystems, southwestern ponderosa pine forests present a promising, yet urgent, opportunity to link these two disciplines and management approaches. These forests, though often in need of management attention, are still large and extensive enough to allow a wide array of management goals and activities to be put into place. Furthermore, restoration of southwestern ponderosa pine forests can help reduce the likelihood of dangerous high-severity fires; it is more closely linked to human needs and desires than is restoration within many other ecosystems.[8] For that reason, widespread public support and political will exists for restoration within this particular landscape. Restoration of these forests, if successful, would result in sustainable conditions across much of the region similar to those that prevailed before Euro-American settlers disrupted the region's ecology. Those conditions will closely replicate the evolutionary environment in which native plant and animal species evolved. For that reason, it ought to be easier to achieve conditions that provide habitat for native species in this ecosystem than in many others.

INTEGRATING THE TWO DISCIPLINES: A HOW-TO GUIDE

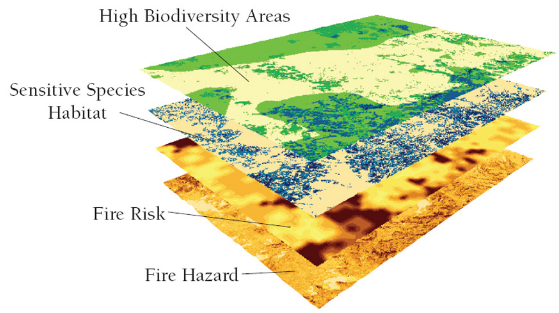
There will likely never be full agreement between the priorities of ecological restoration and conservation biology. The need to preserve a particular tract of rare-plant habitat from soil disturbance and invasion by nonnative species, for example, may override—at least in the short term—the need to return its tree density to that which prevailed before modern human-caused ecological disturbance. But there are numerous steps that can be taken to integrate the two.

SET GOALS

Both ecological restoration and conservation biology use the past as a guideline for the future. Restoration uses "reference conditions," which document such variables as tree density, as a guideline to indicate what a particular tract of land looked like, and how it functioned, within its natural and sustainable range of variability.[9] Conservation biology uses an ecosystem's native suite of species as a guideline in setting protection and management goals and advocates protection of representative examples of native ecosystems, in part for their value as reference sites that allow comparison with more intensively used areas.[10] Both disciplines use the concept of the "evolutionary environment," or the suite of environmental conditions in which native species evolved, as a key in determining what is natural and sustainable.[11] Both ask how human intervention has altered natural systems, and seek to use further well-guided intervention to alter them in the future. Both place a premium on setting goals wisely and on working, realistically, to accomplish them.

Within southwestern ponderosa pine forests, a primary goal of most restoration work has been reducing the likelihood of dangerous, high-severity fire, which according to multiple lines of evidence was uncommon in this ecosystem prior to Euro-American settlement.[12] Such restoration activities as thinning of small trees and prescribed fire reduce fire risk, but they also produce corollary benefits. They reduce the likelihood of large-scale insect outbreaks and can promote the growth of a diverse herbaceous understory.[13] Well implemented, they will also allow low-severity fire (whether ignited by lightning or by people) to safely shape the landscape in the future. Indeed, the reinstitution of a regime of frequent, low-severity fires that maintains healthy forest conditions is a worthwhile end goal for forest restoration work in the region.

Conservation biology has as a primary goal the perpetuation of species and evolving lineages. Increasingly, ecologists take a landscape-level view of conservation priorities and tactics, recognizing that even large protected areas are by themselves too small for viable populations of such animals as wide-ranging predators.[14] This recognition underlines the importance of maintaining areas outside designated parks and reserves as healthy habitat for native plants and animals. In the upland Southwest a matrix of relatively unprotected forested land—much of it within national forests or on tribal or private land—connects scattered wilderness areas and other core wildlands. A successful conservation biology strategy must incorporate those lands as parts of an overall reserve network. That the health of those lands is closely tied to their dependence on a natural fire regime provides a close link between the goals of conservation biology and ecological restoration.

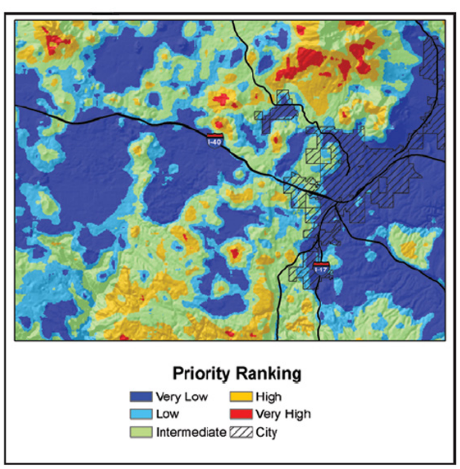


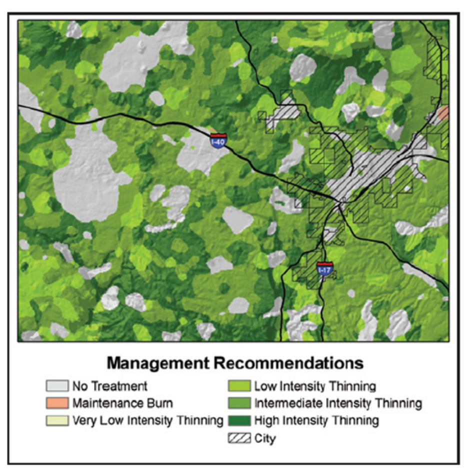
WILDLIFE LAYERS

(above: Wildlife layers; below: Priority Ranking) Landscape assessment tools, such as ForestERA, offer a means of integrating conservation biology needs with other management objectives in order to prioritize treatments across a broad landscape. Illustrations courtesy of NAU ForestERA.

THINK BIG

There will always be conflicting goals in land management, yet resolving them becomes easier as the scale of the region in question increases. It may be impossible to manage a forest area of only a few acres to protect a rare plant species and to meet large-scale ecosystem restoration objectives: managing only patches on the scale of a few acres may leave those areas and the larger landscape threatened by severe disturbances, such as wildfires, that occur over a much larger spatial extent.[15] On the scale of many southwestern ponderosa pine forest areas, though, it is possible to balance both. For example, it is quite possible, and indeed advisable, for managers to reduce fire risk in ponderosa pine forest areas around many Mexican spotted owl territories, whether or not any thinning or prescribed burning takes place within the territories.[16] Many Mexican spotted owl pairs live within forest stands that are denser, for reasons of





topography, climate, or chance, than surrounding pine forest areas.[17] Buffering those stands from high-intensity wildfire is likely to benefit both the owls (by making it less likely that nest and roost stands will burn) and the surrounding landscape matrix (by reducing the overall connectivity of trees and other fuels that could feed a large-scale blaze). Over time, well-planned and -implemented treatments to reduce fuel loads are likely to benefit the species more than a hands-off strategy.[18]

Thinking big is also critical in preserving or reestablishing healthy populations of the wide-ranging species, notably large carnivores, that play a key role in maintaining ecological functioning. The size and the natural variability of the southwestern landscape ought to ensure that conservation goals can be met at multiple scales while restoration work proceeds at a scale large enough to affect the landscape as a whole. Such landscape-level assessments as the ForestERA project provide planning tools and data with which managers can set priorities that meet both sets of goals.[19]

WORK WITHIN THE NATURAL RANGE OF VARIABILITY

Ecosystems are dynamic, yet they tend to operate within a certain range of variability that matches the evolutionary experience of the majority of species within them. It is when they depart from this natural range that the viability of species within them is threatened. Many southwestern ponderosa pine forests appear to have reached a condition well outside their natural range of variability, with the result that they are threatened with long-term changes in species composition and function.[20] For example, some areas once forested with ponderosa pine remain shrubfields or grasslands decades after unnaturally severe crown fires.[21] At a landscape scale, such changes could be harmful to species that rely on forest conditions. Our knowledge of the landscape's natural range of variability, then, can help set targets for restoration.

It also provides a cautionary note. Both ecological restoration and conservation biology need to be case-specific; it is unwise to extrapolate from one forest area to another, or from one threatened species to another. Ponderosa pine forests in the southwestern United States are unlike some of those in other parts of western North America. Even within the Southwest they exhibit a great natural diversity, as has been documented on the Kaibab Plateau and in the San Juan Mountains.[23] Prior to disturbance by Euro-American settlers the region's ponderosa pine forests supported both Mexican spotted owls and pronghorn, which have dramatically different habitat needs. There is simply no "one size fits all" restoration strategy or tactic that will return all southwestern ponderosa pine forests to conditions of ecological health; there is ample room, instead, for differing tactics that work with, rather than against, the landscape's natural heterogeneity.[24]

For the same reason, restoration prescriptions that place a blanket cap on the cutting of trees above a certain size are likely to hamstring managers who desire flexibility, for example in creating grassy openings within forests. However, in some places socio-political realities dictate that a diameter limit be put into place. Implementing treatments with a diameter cap may bring the landscape closer to its natural range of variability without engaging in political conflict that could result in further limits on restoration activities. It may ensure that more large trees remain, and these trees have particular importance for many wildlife species both while they are alive and later as snags or downed logs. However, conducting treatments with a diameter cap can prevent managers from re-creating the grassy openings that were a key element of presettlement ponderosa pine forests, thereby resulting in a forest structure unlike what once existed—and one that offers less habitat for some species. The scale of the southwestern ponderosa pine landscape suggests that a variety of restoration approaches should be tried in case a single approach results in unanticipated harmful effects sometime in the future.

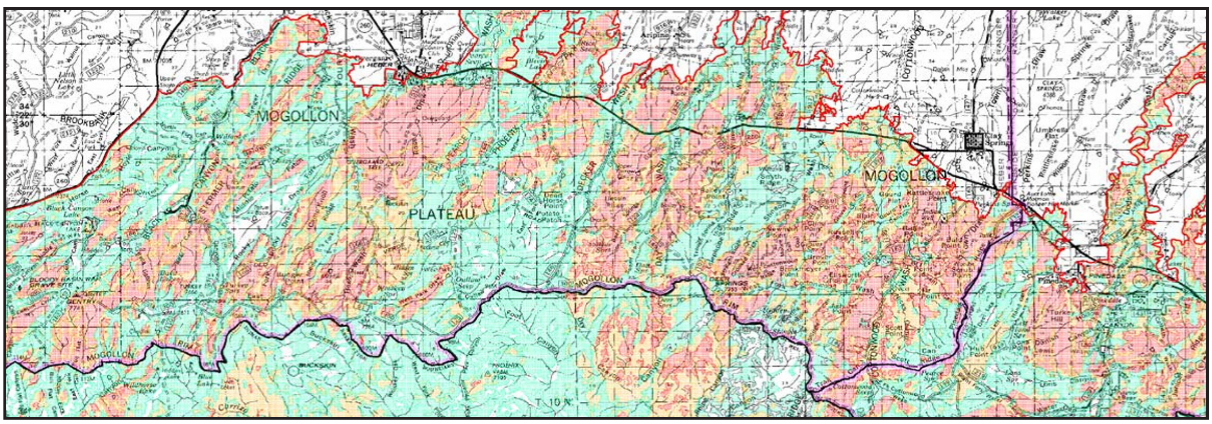
FOCUS BOTH ON PROCESSES AND ON SPECIES

There is a close relationship between species and their habitats. Species such as bunchgrasses fundamentally shape southwestern ponderosa pine forests because their flammability and ability to resprout allow frequent low-intensity fires to sculpt forest structures. But ecological processes such as fire also shape the landscape and the species that live within it. Ecological restoration recognizes this relationship: if the ecological structures and processes within a forest are restored so that they fall within the natural range of variability, then the species that lived within that natural range ought to be able to live there. Nevertheless, conservation biology recognizes that some imperiled species require individual attention until they recover to the point where they can take care of themselves within a restored ecosystem.

Yet shaping the landscape for restoration and conservation biology must be approached from both ends—in other words, at multiple scales at the same time. Over large parts of the landscape it may make sense to allow natural processes to shape forest structure. At a smaller scale, though, it may be necessary to shield some areas from those natural processes. The habitat of a rare plant, or of a Mexican spotted owl, may need to be buffered from both restoration thinning and from fire even if it remains much denser than it may once have been. An early awareness of such tradeoffs, while projects are in a conceptual phase, will do much to ensure that eventual conflicts are minimized. So will a recognition that multiple ecological processes are important. Many so-called restoration projects focus solely on reducing woody fuels through thinning. Without the reintroduction of fire and an emphasis on restoring a healthy understory, these projects are unlikely to result in true restoration of ecological processes or in habitat that is beneficial for the widest possible array of native species. True restoration is holistic.[25]

It is fortunate that southwestern ponderosa pine forests are in many cases extensive enough to allow both management tactics that focus on processes and those that emphasize the needs of particular species. Planning for restoration on a regional scale protects the overall landscape from severe disturbance and allows local areas—such as spotted owl nesting areas—to be maintained in a certain condition without increasing overall fire risk.

DON'T WRITE OFF BURNED AREAS



Severely burned areas can act as firebreaks that allow the implementation of cost-effective restoration treatments, such as prescribed fire, in adjacent, less severely burned areas. Illustration courtesy of Apache-Sitgreaves National Forests.

Rehabilitation of severely burned areas is not the same thing as restoration before fire occurs. Yet it is important. Reseeding of grasses and herbaceous plants may help prevent severe soil erosion in burned areas, especially on steep slopes. Where necessary, reseeding to combat erosion should be done with local seed of native species, or at a minimum with seed of sterile annual plants such as cereal grains.[26]

Post-fire (salvage) logging is often promoted as a means of reducing future fire danger in severely burned areas. However, some forest scientists suggest that salvage logging is more likely to increase reburn potential than reduce it, since the large, less flammable boles are removed and the more flammable logging slash is left behind.[27] Although available evidence suggests that salvage logging can rarely be justified ecologically,[28] there has been remarkably little peer-reviewed research on the effects of salvage logging,[29] and virtually none in dry ponderosa pine forests. In certain locations salvage logging is needed for public safety, such as along roads and in campgrounds. Also, in some cases salvage logging may facilitate restoration in ponderosa pine stands that, as a consequence of fire suppression and increased tree density, experienced unnatural high-severity fire that left overly abundant dead wood on site.[30]

Many observers write off badly burned tracts of ponderosa pine forests because they have lost important ecological attributes such as large trees and even soils. Yet such areas still function as wildlands that provide wildlife habitat and watershed values. They should not be neglected. Severely burned areas can form the building blocks of future forests, and research shows that even severely burned forests have remarkable recovery potential.[31] Specifically, the mosaic pattern typical of most large fires in ponderosa pine forests can help to create a future patchwork of forest conditions. Severely burned areas can serve as de facto firebreaks between lightly burned areas where denser stands of trees remain. They may allow restoration work to proceed more easily within those denser stands. An "island" of dense ponderosa pine forest surrounded by burned areas may be a prime candidate for restoration with prescribed fire alone, for example, because the surrounding areas function as large firebreaks. Using such features will allow restoration to proceed more quickly, and at lower cost.

MANAGE ROADS WISELY

Roads cause significant ecological harm in southwestern forests and other ecosystems.[32] Roads facilitate the spread of invasive plant species,[33] contribute to off-road-vehicle use and soil compaction,[34] and provide an avenue for human-caused fire starts.[35] Road density is in general inversely proportional to habitat suitability for species sensitive to human contact, such as large carnivores.[36] Areas without roads often have high conservation value and serve as core reserve areas for such wildlife.

Forest roads serve a valuable function in some restoration projects by providing access for logging equipment and functioning as firebreaks, but new roads typically cause ecological harm. Much restoration work can be conducted without constructing new roads.[37] In some cases this can be done by using fire, appropriately timed and scaled, to restore natural forest structures and fire regimes.[38] Programs of this sort exist in the Gila National Forest and Grand Canyon National Park.

In other areas, where thinning before prescribed burning is necessary to avoid overly severe fires, thinning should be done without the development of new roads to the extent possible. Some modern logging equipment with wide tires or treads allows access to forest areas without building roads and without significant soil compaction. Logging slash can be disposed of on site.[39] Where roads are used in implementing restoration work, they can be closed and rehabilitated after the completion of thinning and/or prescribed burning.[40]

In roadless areas managers should also take full advantage of topographic features that affect how fire moves across the landscape. Rocky hillsides or canyons may serve as natural firebreaks that reduce the need for mechanical thinning in downwind areas. By assessing a forest landscape as a whole, managers can limit the need to conduct intensive restoration thinning in many roadless areas.

RECOGNIZE THAT PROTECTED AREAS MAY REQUIRE ACTIVE MANAGEMENT

Though protected areas such as national parks and designated wilderness areas provide important core habitats for many species,[41] it is widely recognized that they are by themselves not large enough to provide for their perpetuation and fail to represent many species and habitats entirely.[42] Nor does their protected designation ensure their ecological health. Many protected areas have been subjected to the same factors—fire exclusion, livestock grazing, recreational pressures, invasions by noxious species—as unprotected areas. It is unrealistic to expect that changes caused by these factors can be reversed in all cases without active, hands-on management. In many cases deliberate intervention, such as mechanical thinning, the deliberate introduction of fire, or the eradication of invasive species, may be necessary to avert further ecological declines in parks or wilderness areas.[43] For example, it may prove necessary to manually thin dense stands of ponderosa pine within a national park if they threaten to fuel unnaturally intense fires that could damage some of the park's natural values.

Such interventions, though, must be well considered, and should be conducted with extreme care.[44] Regardless what sorts of treatments are implemented, managers need to remain aware of the great value many members of the public place on protected areas. To the extent possible, treatments should consist of the minimum intervention required to reverse ecological damage. In many reserves fire alone, whether kindled by lightning or with a drip torch, may serve as a restoration tool, albeit one with often unpredictable results.[45] Wildland Fire Use policies in the Gila National Forest, Grand Canyon National Park, and Saguaro National Park serve as good models that show how managers have been able to reestablish somewhat natural fire regimes within protected yet altered forest landscapes. In other situations managers may be able to buffer wilderness areas without treating them directly by focusing on reducing fire danger in strategically located areas upwind of or topographically below them.[46]

Because of the important role many parks and reserves play as reference areas, park managers should also ensure that some areas remain untouched even if they are suffering ecological damage. It is vital to retain some "control" areas with which treated areas, whether inside or outside a park, may be compared. Such control areas are more likely to persist inside rather than outside reserves. Researchers in the future will be able to learn much, including the answers to questions yet unasked, by comparing treated with untreated areas.

FOCUS ON BOTH THE WUI AND ON BACKCOUNTRY WILDLANDS

Much forest restoration work has focused on areas in the "wildland-urban interface" (WUI), or areas immediately adjacent to human communities and resources.[47] Given the high fire danger present in many southwestern forests, this is perfectly reasonable. Yet integrating conservation biology with restoration requires that the conservation and restoration of backcountry wildland areas be emphasized as well.

WUI and backcountry wildland areas are linked by an array of ecological phenomena. Fires pass unhindered from one to another; so do watercourses. Animals range between interface areas and remote wildlands, as do the seeds of plants, including invasive species. Many of the species of greatest conservation concern live primarily in backcountry areas whose future health is as much at risk from high-severity fire as is the health of human communities. A conservation biology approach requires that questions of forest restoration be posed across the entire landscape, not just in scattered "islands" within the landscape.

From the perspective of conservation biology many backcountry wildland areas are far more irreplaceable than WUI areas. It is tragic to lose houses or other elements of human infrastructure to wildland fire, but they are generally much more easily replaced than many backcountry attributes that can be lost during high-severity fires. It may take hundreds of years to replace a burned old-growth forest that supported Mexican spotted owls, and perhaps a thousand or more to rebuild soils degraded by high-severity fire and subsequent erosion. At a time when the human population of the Southwest is rapidly increasing,[48] healthy wildlands represent an important and diminishing resource that should be protected from all threats, including unnaturally severe wildfire.

The planning of fuel and restoration treatments in WUI areas often focuses on buffering towns and cities from fires that begin in wildlands. Yet forest managers should also consider how ecological processes move in the other direction. Human-caused fires begin on the outskirts of town and move into wildlands; so do invasions by noxious weeds. By in effect "zoning" forest areas on the edges of towns and cities for different degrees of access and different types of recreational use, managers can minimize harmful ecological effects in neighboring wildlands.[49]

USE ADAPTIVE MANAGEMENT

Both ecological restoration and conservation biology are young, and rapidly evolving, disciplines. It is likely that within only a few years new discoveries will undermine some of what their practitioners believe today. Yet forest managers, policy makers, and members of the public often demand a certitude in decision making that scientists are unable to endorse. For these reasons, it is essential to design restoration and conservation work to incorporate and respond to uncertainty.

The best framework within which to do so is that of adaptive management, which calls for managers to design management actions as experiments whose results can be carefully tested.[50] Adaptive management requires more than simple observation of treatment results; it requires tailoring treatments so that the effects of different management tactics can be measured and assessed experimentally according to variables that are decided upon in advance. It also requires a stepwise approach, so that a treatment implemented this year yields lessons that inform a treatment being planned for next year. To be effective, adaptive management requires patience, the commitment of dollars and other resources to regular monitoring, and a clear-eyed assessment of results.

CONCLUSION

Ecological restoration of fire-adapted southwestern forests, like conservation biology, is an exercise in risk assessment. Not conducting restoration treatments in these forests exposes them to continued risk of high-severity fire and many other forms of ecological degradation. Yet the implementation of treatments itself carries with it risks of ecological damage or loss of biodiversity. Managers must balance the risks that exist in the presence or absence of restoration work with the reality of what is fiscally, logistically, and politically possible. Conservation biologists must assess how much the continued viability of native plants and animals is at risk from both direct human impacts—including those caused by restoration projects—and from the indirect impacts that result from long-term changes in land uses. Considerable uncertainty exists today, and will no doubt remain, in both restoration and conservation work. In both disciplines it is prudent to use a precautionary approach that minimizes the risks of action; yet it is also critical to avoid inaction, since inaction has the potential to result in severe and large-scale ecological changes across the landscape.

Balancing caution with the need for action can be done with the help of the best available science, including new landscape planning tools. In a landscape as large as the ponderosa pine forests of the Southwest, it should be possible to integrate an array of restoration treatments with an array of conservation work, and to do so in a way that is acceptable to members of the public. These forests, in fact, offer managers a chance to demonstrate that ecological restoration can succeed on a truly large scale, across an entire landscape, and that a complete array of native species can survive within that landscape.

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NOTES

[1] Young 2000; Noss et al. 2006a.
[2] Jordan 2003.
[3] Covington and Moore 1994; Allen et al. 2002; Covington 2003.
[4] Soulé and Wilcox 1980; Soulé 1985.
[5] Myers et al. 2000.
[6] Landres et al. 1999.
[7] Wilson 1992.
[8] Schoennagel et al. 2004.
[9] Egan and Howell 2001; SER 2004.
[10] Noss and Cooperrider 1994.
[11] Noss et al. 2006a.
[12] Covington et al. 1997; Moore et al. 1999.
[13] Abella and Covington 2004; Huffman and Moore 2004.
[14] Noss et al. 1996; Soulé and Terborgh 1999.
[15] Sisk et al. 2005.
[16] See Working Paper 14: Integrating Forest Restoration Treatments with Mexican Spotted Owl Habitat Needs.
[17] Beier and Maschinski 2003.
[18] Lee and Irwin 2005; Prather et al. in review.
[19] www.forestera.nau.edu; Sisk et al. in press.
[20] Covington 2003.
[21] Savage and Mast 2005.
[22] Brown et al. 2004.
[23] Fulé et al. 2003b; Romme et al. 2003.
[24] Allen et al. 2002.
[25] See Working Paper 4: Fuels Treatments and Forest Restoration: An Analysis of Benefits.
[26] Sieg et al. 2003.
[27] Society for Conservation Biology Scientific Panel on Fire in Western U.S. Forests 2006.
[28] Beschta et al. 2004; Lindenmayer et al. 2004; Donato et al. 2006.
[29] Lindenmayer and Noss in press.
[30] Noss et al. 2006b.
[31] Turner et al. 2003.
[32] Trombulak and Frissell 2000; Forman et al. 2003.
[33] Gelbard and Belnap 2003.
[34] Trombulak and Frissell 2000.
[35] Chou et al. 1993.
[36] Noss et al. 1996.

[37] DellaSala and Frost 2001.

[38] Fulé et al. 2003a.

[39] See Working Paper 13: Treating Slash after Restoration Thinning.

[40] See Working Paper 12: Restoring Forest Roads.

[41] Noss et al. 1999.

[42] Scott et al. 2001; Lindenmayer and Franklin 2002.

[43] Sydoriak et al. 2000; Noss et al. 2006a.

[44] Allen et al. 2002.

[45] Fulé et al. 2003a.

[46] Finney 2001.

[47] Radeloff et al. 2005.

[48] Dombeck et al. 2004

[49] Marzluff and Bradley 2003.

[50] Murray and Marmorek 2003.

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