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WHAT CONSTITUTES A NATURAL FIRE REGIME? INSIGHT FROM THE ECOLOGY AND DISTRIBUTION OF CONIFEROUS FOREST BIRDS IN NORTH AMERICA

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ABSTRACT

Bird species that specialize in the use of burned forest conditions can provide insight into the prehistoric fire regimes associated with the forest types that they have occupied over evolutionary time. The nature of their adaptations reflects the specific post-fire conditions that occurred prior to the unnatural influence of humans after European settlement. Specifically, the post-fire conditions, nest site locations, and social systems of two species (Bachman's sparrow [*Aimophila aestivalis*] and red-cockaded woodpecker [*Picoides borealis*]) suggest that, prehistorically, a frequent, low-severity fire regime characterized the southeastern pine system in which they evolved. In contrast, the patterns of distribution and abundance for several other bird species (black-backed woodpecker [*Picoides arcticus*], buff-breasted flycatcher [*Empidonax fulvifrons*], Lewis' woodpecker [*Melanerpes lewis*], northern hawk owl [*Surnia ulula*], and Kirtland's warbler [*Dendroica kirtlandii*]) suggest that severe fire has been an important component of the fire regimes with which they evolved. Patterns of habitat use by the latter species indicate that severe fires are important components not only of higher-elevation and high-latitude conifer forest types, which are known to be dominated by such fires, but also of mid-elevation and even low-elevation conifer forest types that are not normally assumed to have had high-severity fire as an integral part of their natural fire regimes. Because plant and animal adaptations can serve as reliable sources of information about what constitutes a natural fire regime, it might be wise to supplement traditional historical methods with careful consideration of information related to plant and animal adaptations when attempting to restore what are thought to be natural fire regimes.

Keywords: bird distribution, coniferous forest, historical range of variability, low-severity fire, natural fire regime, post-fire conditions, severe fire

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INTRODUCTION

At a time when there is much discussion about what constitutes a natural fire regime and how to restore systems that are thought to be burning in an unnatural fashion (Arno and Fiedler 2005), data from the wildlife perspective are notably absent, especially for conifer forests of the western United States. This is unfortunate because animal (and plant) species evolve within an environmental context, and many have evolved to depend on particular kinds of fire regimes for the creation of conditions to which they are adapted. Fire specialists, which include those species that are relatively restricted in their distribution to post-fire conditions, can provide insight into what constitutes a natural fire regime (defined as the environmental backdrop against which extant native species evolved) because specialists have evolved adaptations that enable them to do well in a particular subset of burned forest conditions. Thus, we can learn much from fire specialists if we study the patterns of distribution and success of fire-dependent species in relation to the various parameters that characterize a fire regime.

The traditional approach scientists have used to uncover the natural fire regime within a particular area or vegetation type has been to rely primarily on historical evidence of past fires as revealed through stand age-class models or, most frequently, tree-ring studies. However, these and other historical-record approaches have many limitations (Gavin *et al.* 2007, Goforth and Minnich 2007). Tree-ring studies, in particular, are not without potential bias, and have often been suggested

to overestimate fire frequency by some unknown amount (Baker 2006; Kou and Baker 2006a, b; Miller *et al.* 2007). Even if estimates of fire return intervals are unbiased, the time frame from which information can be gathered is relatively limited and often is not far enough removed in time from the relatively recent and heavy human influences on fire regimes to gain insight into the environmental conditions within which extant organisms evolved (Gavin *et al.* 2007). This is an important limitation because during the past several hundred years, humans may have burned the land much more frequently and at lower severities than would have been the case in the absence of a relatively recent and relatively unnatural human influence. Indeed, recent human influences are great enough and widespread enough to have produced fire regimes in many environments that are quite different from the regimes within which extant species evolved (Jurskis 2005, Syphard *et al.* 2007).

A more important issue related to tree-ring studies is that such studies can inform us about recent fire history from within only those forest types that typically experience relatively frequent, low-severity fire. Thus, tree-based studies are necessarily biased toward surface fires that scar, but do not kill, trees (Whitlock 2004). Because a disproportionately large number of historical studies are conducted in forests that support low-severity fire regimes, we may have unwittingly painted a biased broader perspective of what constitutes the dominant fire regime in the majority of conifer forests of North America. In the western United States, for example, the vast majority of forest types lie outside the ponderosa pine

(*Pinus ponderosa*) vegetation type (about 85 % of forested land within the contiguous western United States, according to the LANDFIRE database) and are dominated by mixed- and high-severity fires rather than low-severity fires (see also Agee [1993:Figure 1.4] and Arno and Fiedler [2005:Table 3.1]). This fact is not widely appreciated, and is not the picture of natural fire regimes propagated by the popular press, from which one gets the impression that most western forest types historically burned frequently and only at low severity.

Against this background of potential limitations associated with the more commonly employed methods of reconstructing fire histories, there is a clear need "...to conduct more comprehensive assessments of existing disturbance regimes, and to determine whether natural disturbances are occurring at rates and scales compatible with the maintenance of biodiversity" (Odion and Hanson 2006:1177). Here, we attempt to show how a consideration of biological information, specifically information related to bird distribution and reproductive success in relation to environmental conditions, can provide insight into what constitutes a natural fire regime for any given system.

METHODS

To be meaningful, we must narrow the focus of our attention toward adaptations of true fire specialists. Fire specialists are defined here as species that are relatively restricted to burned-forest conditions, or to conditions that were created exclusively by fire during their evolution. A focus on fire specialists is important because the only way a species could possibly be restricted to a narrow set of conditions created by fire is if those particular conditions had been created repeatedly on the landscape for millennia. The specific burned forest conditions to which a specialist is restricted must have been the primary

environmental backdrop against which that species evolved. In contrast, we cannot learn what constitutes a natural fire regime in burned forests occupied by a broadly distributed species such as the American robin (*Turdus migratorius*). This is because these generalist species occur across such a broad range of both burned and unburned forest conditions that it is impossible to know which conditions occurred naturally in the distant past and were occupied prehistorically, and which conditions might be relatively recent and are now occupied only opportunistically.

For the purposes of this paper, we distinguish among low-, moderate-, and high-severity fire regimes by whether the fires burn predominantly as understory, mixed-severity, or stand-replacement fires, as defined by Brown (2000). We selected several fire-dependent bird species to illustrate the usefulness of considering the biology of organisms when evaluating what constitutes a natural fire regime. We determined whether a given bird species was fire-dependent by looking directly at its distribution across as complete a range of environmental conditions as possible. Bird monitoring programs that couple local vegetation conditions (including the age and severity of past fires) at and surrounding survey locations with the presence of bird species are fruitful sources for this kind of distribution information. Species that seldom occur outside recently burned forests can be confidently classified as fire specialists, with extreme fire specialists being those species that are entirely restricted to forest conditions created by fire. An important point to recognize is that the mere presence of an organism in burned-forest conditions does not automatically mean that the organism depends on fire to construct these forest conditions (La Puma *et al.* 2007); it is a relative restriction to, or a relatively high reproductive or survival success in, such conditions that is required to demonstrate a dependence on fire.

As forest succession proceeds, it becomes more and more difficult to argue that a particular forest age or condition (and any specialist species restricted to that forest age or condition) exists only because of a previous fire event. Nonetheless, it is certainly possible for a particular plant or animal species to appear only during a window of time from, for example, 25 yr to 50 yr after fire, and only in response to fire as the agent of change. If so, it could be considered a fire-dependent species. The time period after fire during which conditions become suitable to a fire specialist varies with the species in question. Some fire-dependent species colonize during the first year after fire and persist as migrants or residents for a decade or so after fire (e.g., most woodpeckers). Others (e.g., Florida scrub-jay [*Aphelocoma coerulescens*]) do not even colonize until a decade or two following fire, and then persist for another decade or two. In this paper, we provide examples of forest bird species that respond relatively rapidly to, or are relatively restricted to, the recent conditions created by fire events. We acknowledge, however, that some fire specialists do not colonize burned areas immediately after a fire. For example, a species like the Kirtland's warbler (*Dendroica kirtlandii*), which is relatively restricted to 20-year- to 30-year-old forest conditions, would still be considered a fire specialist because it fails to find suitable conditions outside a narrow temporal window of early succession conditions historically created by fire. Thus, defining what constitutes a fire specialist can be somewhat ambiguous, but the key is that a specialist was prehistorically restricted to conditions created by, and within a specified time window after, fire.

RESULTS

Although the designation of fire specialist is somewhat arbitrary because no organism is

entirely restricted to a particular environmental condition (we regularly observe plants and animals outside their preferred set of environmental conditions), the following bird species are at least on the extreme end in terms of the degree to which they are restricted to post-fire forest conditions. Each species is very probably specialized in a number of ways to live successfully in a subset of post-fire conditions—those created by a specific type of fire regime.

Black-backed Woodpecker (*Picoides arcticus*)

The black-backed woodpecker occurs in the boreal conifer forests of Canada and the western United States, where it is relatively confined to burned forest conditions (Dixon and Saab 2000). In burned forests, the woodpecker feeds on wood-boring beetle larvae (Dixon and Saab 2000), which become abundant after the adult beetles (which are specialized to detect trees killed by fire) lay their eggs on the abundant, recently killed trees that characterize a severely burned forest. The degree to which the black-backed woodpecker is restricted to burned forest conditions in the intermountain west is truly remarkable. Although this species has been detected outside burned forest conditions, particularly in unburned, beetle-killed forests, the numbers therein are small, and nest success therein is substantially lower than in burned forests (Saab *et al.* 2005). Neither Powell (2000) nor Morrissey *et al.* (2008), for example, found any black-backed woodpeckers in surveys of mountain pine beetle-infested mixed-conifer forests even though they located northern flickers and three-toed, hairy, downy, and pileated woodpeckers. Similarly, a region-wide bird survey across a series of unburned, beetle-infested conifer forests within the Forest Service Northern Region (Cilimburg *et al.* 2006) yielded only two black-backed

woodpecker detections (0.46 % of 433 point counts). This is less than one-tenth of the frequency of detection in forests burned <10 yr before (Hutto 2008). No other forest bird species appears to be as restricted to a single kind of forest type or condition as the black-backed woodpecker is to burned conifer forests (Hutto and Young 1999).

In addition, two lines of evidence suggest that it is the more severe fires that are needed to create conditions most suitable for this fire specialist: (1) not only is the black-backed woodpecker restricted to burned forests, but its distribution within burned forests is also relatively restricted to the more severely burned conditions (Kotliar *et al.* 2002, Smucker *et al.* 2005, Russell *et al.* 2007, Hutto 2008); (2) black-backed woodpecker nest sites occur in locations that harbor significantly larger and more numerous trees than occur around randomly selected sites within a burn (Saab and Dudley 1998, Kotliar *et al.* 2002, Russell *et al.* 2007). Such nesting locations would be difficult to find in forests maintained as low-density, open, park-like stands due to frequent, low-severity fire.

How could a species evolve to depend on a condition that occurs only infrequently? The answer lies with the distribution and abundance of such fires across space and time. The return interval for severe fire in one location may be several hundred years, but black-backed woodpecker populations persist in a particular fire for >6 yr (Saab *et al.* 2007), so the probability of a severe fire occurring somewhere within an entire watershed in any given 6-year window is very high. Thus, when viewed on a landscape scale, it becomes easy to imagine that a sufficiently mobile plant or animal species (e.g., fire morel [*Morchella angusticeps*]; jewel beetle, Buprestidae; black-backed woodpecker) could become specialized to use a burned forest condition that is ephemeral on a local scale but always present somewhere in the larger landscape. How the

specialized black-backed woodpecker finds a newly burned forest every half decade or so is unknown, but the story of how fire beetles use infrared detection to do so (Evans 1964, 1966) is legendary.

Buff-breasted Flycatcher (*Empidonax fulvifrons*)

Buff-breasted flycatchers breed in pine (*Pinus* spp.), pine-oak (*Quercus* spp.), and mixed-conifer forests of the southwestern US and northern Mexico, and their breeding range in the US has been reduced by >90 % over the past 100 years (Conway and Kirkpatrick 2007). Because of these declines, the US Fish and Wildlife Service (FWS) formerly listed the buff-breasted flycatchers as a candidate species under the Endangered Species Act (Federal Register 1994, 1996). Numbers of breeding flycatchers have continued to decline over the past 20 years (Conway and Kirkpatrick 2007). Declines have repeatedly been attributed to suppression of forest fires (Phillips *et al.* 1964; Arizona Game and Fish Department 1988, 1996; Bowers and Dunning 1994; Bowers *et al.* 1996; Martin and Morrison 1999). The buff-breasted flycatcher could be considered a fire specialist because they are twice as common in areas with evidence of recent high-severity fires compared to areas with evidence of recent low-severity fires or no recent fires (Figure 1). Moreover, two of the three mountain ranges in southern Arizona that still have breeding flycatchers had evidence of high-severity fire at >10 % of the points sampled, whereas the six mountain ranges that had no flycatchers had evidence of high-severity fire at <10 % of the points sampled (Conway and Kirkpatrick 2007). Buff-breasted flycatchers have recently recolonized one mountain range (Rincon Mountains) in southern Arizona (Kirkpatrick *et al.* 2007) where they had not been detected since 1911. This mountain range has experienced more

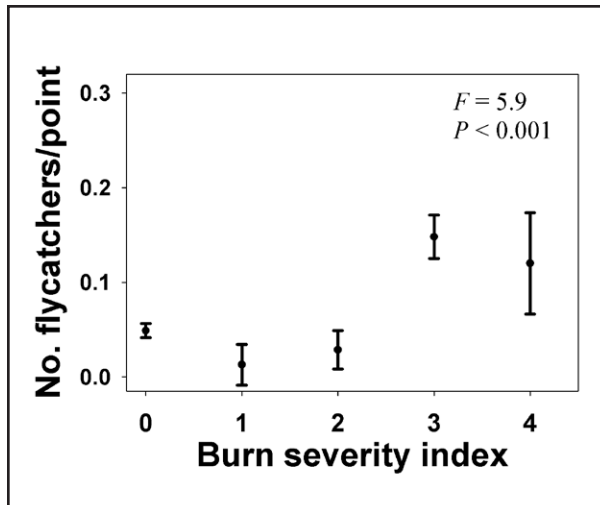


Figure 1. The Buff-breasted flycatcher is nearly absent in areas that had no evidence of recent fire (severity index 0) and areas with recent low-severity (severity index 1-2) fire but is much more common in areas with recent high-severity (severity index 3-4) fire within the low-elevation ponderosa pine forests in southern Arizona (from Conway and Kirkpatrick 2007).

fires than any other in the region during the past 20 years (Kirkpatrick *et al.* 2006).

The association between buff-breasted flycatchers and fire is not immediately obvious because these flycatchers do not colonize burned forest immediately after fire, and low- to moderate-severity fires in historically fire-suppressed areas do not appear to be sufficient to create optimal conditions for this species. Once an area has not burned for several decades or more, buff-breasted flycatchers may require a patchy high-severity fire to open the forest to an extent needed to produce the conditions sufficient for colonization. After a severe fire event, however, regular low- or moderate-severity fires may then be sufficient to maintain optimal conditions. At this point in time, we know only that this species is most abundant in areas that received a patchy high-severity crown fire roughly five years previously. Hence, fire frequency and fire severity both play a role in creating optimal conditions for buff-breasted flycatchers.

Lewis's Woodpecker (Melanerpes lewis)

Lewis's woodpecker is a patchily distributed but often locally abundant species that nests primarily in ponderosa pine and cottonwood (*Populus* spp.) riparian forests throughout the western United States (Tobalske 1997). The breeding distribution of Lewis's woodpecker closely follows the range of ponderosa pine, suggesting that this species may have evolved in ponderosa pine systems (Saab and Vierling 2001). Unlike most woodpeckers that bore for bark- and wood-dwelling insects, Lewis's woodpecker is an aerial forager that requires open habitats for aerial maneuvers involved in flycatching.

This species is considered a burn specialist due to its relatively high nesting success and high breeding densities in burned ponderosa pine forests (Saab and Vierling 2001, Gentry and Vierling 2007, Saab *et al.* 2007). Conditions created after moderate- to high-severity crown fires in ponderosa pine forests are known to provide ideal breeding habitat throughout the range of Lewis's woodpecker for at least a dozen years following fire (e.g., Raphael and White 1984, Haggard and Gaines 2001, Bock and Block 2005, Saab *et al.* 2007). Burned ponderosa pine forests likely provide a suitable breeding and foraging environment for Lewis's woodpecker because of the high snag abundance therein, and because of the relatively open canopy that allows for shrub development and associated arthropod prey (Bock 1970), good visibility, and perch sites for foraging, and space for foraging maneuvers (Saab and Vierling 2001).

Northern Hawk Owl (Surnia ulula)

The northern hawk owl is one of the least-studied birds in North America. It occurs from Alaska to Newfoundland and also from Scandinavia to Siberia. Although northern hawk owls are known to occupy burned forests

(Duncan and Duncan 1994), the importance of burned vs. unburned forests is still largely unknown. In the only published comparison of northern hawk owl relative abundance between burned and unburned conifer-dominated boreal forest in North America, northern hawk owls were detected only in post-fire forest and were not detected in nearby unburned coniferous forest (Hannah and Hoyt 2004). There was also a significant negative exponential relationship between northern hawk owl abundance and time since fire, suggesting that burns were suitable for only about eight years following fire. Thus, there is some evidence that the northern hawk owl is yet another species that depends on (is relatively restricted to) conditions created by severe, stand-replacement fires in boreal forests of Canada.

Kirtland's Warbler (Dendroica kirtlandii)

One of the most celebrated examples of a fire specialist is the Kirtland's warbler. The fire-specialist status of this bird species emerges from knowledge of its restricted habitat distribution. The Kirtland's warbler occurs nearly exclusively in young (5-year- to 23-year-old) jack pine (*Pinus banksiana*) forest created historically by fire (Walkinshaw 1983). In addition, pairing success is significantly higher in burned (98 %) than in unburned (58 %) forests (Probst and Hayes 1987). The need for severe fire is obvious not only because it historically took severe fire to stimulate succession and the creation of a young fire-dependent jack pine forest, but because of the difficulty that managers have had in trying to re-create conditions that mimic natural post-fire conditions with techniques that applied thinning followed by burning at lower severities (Probst and Donnerwright 1983).

Bachman's Sparrow (Aimophila aestivalis)

The Bachman's sparrow is an example of a fire specialist endemic to the longleaf pine (*Pinus palustris*) forest system, and it exhibits features that are consistent with adaptation to frequent fire. Individuals of this species forage and nest on the ground and, with the exception of singing males, seldom leave the ground. They prefer a dense groundcover of grasses and forbs with few or no hardwood shrubs or midstory trees, exactly the conditions produced by frequent surface fires (Dunning 1993). Sparrow densities are highest 1 yr to 3 yr post-fire and decline after three years (Dunning and Watts 1990, Shriver and Vickery 2001, Tucker et al. 2005). Thus, the conditions to which the species is adapted are dependent on fire and occur immediately following fire, but are highly ephemeral and persist only briefly. A species with these characteristics could be successful only under a frequent fire regime, supporting the conclusion that the prehistoric fire regime in longleaf forests consisted of frequent, low-severity surface fires.

Red-cockaded Woodpecker (Picoides borealis)

The endangered red-cockaded woodpecker is also a fire specialist characteristic of longleaf pine ecosystems, yet is a highly sedentary species, with family groups occupying the same territories continuously for decades (Conner et al. 2001). The sedentary nature of the species is tied to its unique habitat of excavating cavities for nesting and roosting in live pine trees. These cavities can be used for a decade or more, and take equally long to excavate (Harding and Walters 2002, 2004), so cavity-bearing trees are a highly valuable resource. Birds compete to inherit clusters of cavity trees and their associated territories rather than carving out new territories (Walters et al. 1992).

The initial declines of the species were due to the precipitous loss of habitat to logging around the beginning of the twentieth century, which reduced the vast longleaf forests of the southeast US to only 3 % of their original extent (Frost 1993). However, the more recent declines of the 1970s and 1980s were due to habitat changes following fire suppression, which promoted development of dense hardwood midstory and greatly reduced groundcover vegetation (Conner and Rudolph 1989, Conner *et al.* 2001). When hardwood midstory begins to reach cavity-level height, the birds abandon their cavities and associated territories (USFWS 2003). The declines of the 1970s and 1980s were characterized by abandonment of territories in fire-suppressed areas and not by reduced survival or productivity, or by loss of territories to timber cutting (Walters 1991). Also, the birds prefer to forage in habitat with a rich groundcover dominated by grasses and forbs and little or no hardwood midstory, and reproductive success is higher and group size larger in territories with more such habitat (USFWS 2003). Thus, both foraging habitat preferences and dependence on fire to maintain habitat suitability qualify the red-cockaded woodpecker as a fire specialist.

Frequent, low-severity surface fires produce optimal foraging conditions, suggesting the species is adapted to such a fire regime. Furthermore, the species exhibits a unique adaptation, the use of live pines for cavity trees. Selection for these trees can only be imagined if habitat can be occupied continuously for many decades, yet habitat becomes unsuitable in 10 yr to 20 yr (depending on the site) in the absence of fire. That the species can be sedentary yet dependent on fire suggests that fires were frequent in this system prehistorically. In the case of the red-cockaded woodpecker, reliance on live pines for cavities further suggests that crown fires were infrequent, and that it evolved in association with a low-severity fire regime.

DISCUSSION

Thousands of years of evolution speak volumes in terms of understanding what constitutes the natural environmental condition within which a given species evolved, and fire specialists (those species that are relatively restricted to a narrow range of post-fire conditions) can provide a window into what probably constitute natural fire regimes. A number of bird species clearly require fire to be successful, and the type of fire matters. We now discuss the kinds of fire regimes that must have occurred prehistorically in the regions occupied by these bird species as evidenced by the post-fire conditions with which these bird species are positively associated.

Ponderosa Pine System

Prehistorically, frequent surface fires are thought to have characterized the dry, warm woodlands and open-canopy ponderosa pine forests of the American southwest and the more xeric low-elevation ponderosa pine forests elsewhere (Schoennagel *et al.* 2004). Fire intervals were probably shorter in the more xeric southwestern ponderosa pine than in the more mesic stands that occur along the Colorado Front Range, Black Hills of Wyoming and South Dakota, and the eastern Cascades (Agee 1993, Brown and Sieg 1996, Shinneman and Baker 1997, Veblen *et al.* 2000, Ehle and Baker 2003, Wright and Agee 2004). Nonetheless, evidence of natural, mixed-severity fire regimes is found in some ponderosa pine forests (Mast *et al.* 1999, Kaufmann *et al.* 2000, Ehle and Baker 2003), and both surface and crown fires occurred prehistorically in pure or nearly pure ponderosa pine forests of Montana (Arno *et al.* 1995), South Dakota (Brown and Sieg 1996, Shinneman and Baker 1997), and other locations in the Rocky Mountain region (Brown *et al.* 1999, Mast *et al.* 1999, Baker and Ehle 2001, Ehle and Baker 2003).

A collective consideration of the biology of Lewis's woodpecker, black-backed woodpecker, and buff-breasted flycatcher appears to underscore the prehistorical presence of an unknown amount of mixed- and high-severity fire within the ponderosa pine forest type. Each of these species occurs predominantly in the moderate to severe end of the fire severity spectrum, and each fails to show the same kind of positive response to low-severity surface fires. Although the black-backed woodpecker is not distributed throughout the range of ponderosa pine, it does occupy the more northerly portions where ponderosa pine most often occurs as a co-dominant in the low- to mid-elevation mixed-conifer forests. In addition, the black-backed woodpecker is nearly restricted in its distribution to the more severely burned portions of those forests. The naturally occurring severely burned forest conditions to which the black-backed woodpecker is adapted may well be in the mid- to high-elevation forests, although nesting and foraging individuals also successfully use high-severity burns within low-elevation ponderosa pine forests (Dudley and Saab 2007, Russell *et al.* 2007). The fact that black-backed woodpeckers feed primarily on fire specialist wood-boring beetle larvae in ponderosa pine and other thick-barked tree species (Hutto 1995) strongly suggests that forests containing ponderosa pine (particularly the more mesic ponderosa pine and mid-elevation mixed-conifer forests) harbored mixed- or high-severity fire, at least at a very local scale, in the past.

The death of large ponderosa pine trees, in particular, appears to be a necessary requisite for Lewis's woodpecker. This species differs from other woodpeckers in that it lacks several anatomical adaptations that facilitate wood excavation (i.e., fused vertebrae, thickened skull; Goodge 1972). Perhaps due to these characteristics, it nests primarily in snags or soft-wooded trees, such as heavily decayed

conifers and cottonwoods. Ponderosa pines are more readily excavated than other conifer tree species because they contain a relatively thick layer of sapwood with a hardened exterior shell. Ponderosa pine is also more easily excavated by cavity-nesting birds if the sapwood has decayed (Bull *et al.* 1997). Importantly, the sapwood of fire-killed ponderosa pine begins to soften in the third year after death, allowing for easier cavity excavation after that time. Thus, nesting densities of Lewis's woodpecker tend to increase from 5 yr to 12 yr after fire (Saab *et al.* 2007). Taken together, the distribution and ecology of all of these bird species suggest that high-severity fires were prehistorically more common across the variety of ponderosa pine systems than what conventional tree-ring records from the past several hundred years have led us to believe (see also Schoennagel *et al.* 2004, Baker *et al.* 2007, Sherriff and Veblen 2007).

Mixed-conifer and Boreal Forest Systems

The bird species that appear to be most restricted to and, therefore, most dependent upon, burned forests in these systems (black-backed woodpecker, and northern hawk owl) clearly require severe fires. This is entirely consistent with our current understanding that infrequent, severe fires dominate fire regimes in the boreal conifer forest system (Johnson *et al.* 2001), and it also reinforces the idea that the extensive mixed-conifer forest zones throughout the western US were probably historically dominated by mixed-fire regimes that included either some infrequent severe fire events or, more likely, always included patches of severe fire during fire events that occurred at intermediate frequencies. This conclusion corresponds well with the fact that mixed- and high-severity fire regimes characterize the majority (see data from LANDFIRE) of forest types in North America (Johnson *et al.* 2001,

Graham 2003, Franklin *et al.* 2005, Noss *et al.* 2006), including even the more mesic ponderosa pine forests (Schoennagel *et al.* 2004, Baker *et al.* 2007, Sherriff and Veblen 2007).

Jack Pine System

There is little doubt that severe fires were a necessary part of the natural fire regime in conifer forests dominated by jack pine. Kirtland's warbler requires an abundance of young trees that still have their branches touching the ground. The only way such conditions could have been created over large areas in the absence of artificial means would have been through the tree death and regeneration caused by severe fire.

Southeastern Pine System

The longleaf pine forest of the southeast US is one system for which all approaches provide evidence that frequent, low-severity fires represent the prehistoric fire regime. In this case, the primary evidence emerges from studies of the organisms inhabiting the system, specifically plant species, rather than from tree-ring studies. This system exhibits the highest plant diversity recorded in the temperate zone at several scales (Walker and Peet 1983, Hardin and White 1989, Walker 1993), and maximum plant diversity occurs under a frequent (i.e., 2 yr to 5 yr fire return interval) fire regime (Walker and Peet 1983, Mehlman 1992, Glitzenstein *et al.* 1998, Walker 1998, Provencher *et al.* 2001). A rich groundcover of grasses and forbs accounts for this plant diversity, and is promoted by frequent, low-severity surface fires that do little more than scorch the trunks of the overstory pines.

Significantly, the adaptations of many of the organisms inhabiting this system reflect such a regime, in contrast to the adaptations of

the other species we have discussed. The Bachman's sparrow is adapted to conditions that exist for only a few years following fire, whereas the red-cockaded woodpecker depends on fire being sufficiently frequent to prevent habitat from ever succeeding to an unsuitable state. Interestingly, much less is known about prehistorical fire regimes and avian adaptations to fire in other habitat types within the longleaf zone such as pocosin, a coastal evergreen shrub bog, in which fires are infrequent and severe. One would expect fire specialists in these habitats to be more like those in western forests—less sedentary than red-cockaded woodpeckers and less ephemeral (i.e., persisting much longer in burned patches) than Bachman's sparrows.

Management Implications

Large-scale efforts to restore forests to pre-settlement conditions, especially in the western US, are based largely on information drawn from tree-ring and other historical studies. Before such efforts are implemented broadly, we need to consider the effects of these proposed restoration efforts on the organisms that live in those systems. If we rely entirely on tree-ring and other historical approaches without considering the needs of fire-dependent plants and animals to determine what constitutes a natural fire regime, we run the risk of producing forest conditions that lead to decreases in, rather than the maintenance of, populations of native fire-dependent species.

While our understanding of what constitutes a natural fire regime in the longleaf pine system has emerged largely from careful study of the adaptations of flora and fauna (Engstrom *et al.* 2005, Allen *et al.* 2006), our understanding of the same in most western forest systems has emerged primarily from tree-ring and other historical studies (see Agee 1993). We believe that a combination of ecological and historical approaches, including

fire-scarred tree rings, stand-age data (Agee 1993), paleo-environmental data preserved in sediments (Pierce *et al.* 2004, Whitlock 2004), and studies of adaptations of plants and animals should be used to understand the environments within which extant living organisms evolved. This is especially important because an ecological approach can lead to an understanding that may be at odds with the understanding gained from historical approaches, many of which date only into the relatively recent past 400 years or so (Whitlock 2004, Franklin *et al.* 2005). Living plants and animals carry adaptations that indicate the kind of environment within which they do well, and it would behoove us to pay close attention to what plants and animals are telling us about fire regimes. Once a fire-dependent species demonstrates that a particular kind of fire is necessary for its persistence or success, that information should be used to help guide management and restoration decisions.

Across a wide variety of forest types and geographic locations (including the southwestern ponderosa pine system), there are bird species that are nearly restricted to, or perform relatively well in, more severely burned conditions. This fact runs counter to the currently accepted view that severe fires in those systems are unnatural. Without adopting the perspective of living organisms, we may overlook the importance of maintaining severe fire on the landscape. High-severity fires are every bit as natural as low-severity fires in most forest systems. Such fires should be allowed in the future if we want to manage our forests to retain the complete range of natural conditions used by endemic fauna. While patterns of bird distribution suggest that severe fires played a prehistorically important role across a wide range of forest types (even, perhaps, in low-elevation ponderosa pine forests), distribution patterns alone cannot tell us about the extent of such fires that occurred in the past or about the spatial and temporal

distribution of such fires needed in the future to provide suitable conditions for these fire-dependent species.

With respect to severe fire, fire ecologists (e.g., Agee 1993:Figure 1.6) have previously outlined that it is the relative frequency and size, not the presence, of severe fires that varies across fire regimes. Nonetheless, many have yet to accept that severe fire is a natural part of most forest systems. If data such as those I present here can help move us closer to accepting that severe fire is important, we can then move toward determining the proportion and extent of such fires that best reflect natural patterns and fire-dependent wildlife needs. Even more importantly, we can move toward building better public appreciation of the fact that fire-dependent plant and animal species require not only a specific fire severity, but the post-fire conditions (standing dead trees) associated with that severity as well. Salvage logging is not a substitute for high severity fire, because the species that most depend on post-fire conditions will not be retained (Hutto 2006).

Because different bird species respond positively to different fire severities within the low- to mid-elevation forest zones (Smucker *et al.* 2005), maintaining all fire severities within a mixed-severity fire regime in those vegetation types is an important fire management practice. While there are certainly many bird species that depend on the presence of unburned forest conditions or even on the presence of less severely burned conifer forest conditions (e.g., Smucker *et al.* 2005), the importance of severe fire in many forest systems is not always acknowledged. Indeed, despite recent calls for developing restoration guidelines that are compatible with the evolutionary history of fire-dominated systems (Moore *et al.* 1999, Mitchell *et al.* 2006), restoration practices are not generally driven by a solid understanding of the evolutionary history of indigenous species. Instead, management practices tend

to be focused on the use of mechanical treatments either to enhance wood production or to modify forest structure in a way that will reduce fire severity in the future (Fall *et al.* 2004, Loehle 2004, Arno and Fiedler 2005, Mason *et al.* 2006). The negative consequence of concentrating on altering fire behavior to the exclusion of ecological considerations is sometimes evidenced by bird community changes that are clearly unfavorable to the more fire-dependent species (Allen *et al.* 2006, Maron and Kennedy 2007). Forest restoration efforts should be based on a sound understanding of the ecological role of fire as an integral process; we need to develop the methods required to restore the full range of fire severities that plants and animals inform us were historically and evolutionarily associated with any given forest type (Johnson *et al.* 2003, DellaSala *et al.* 2004, Pierce *et al.* 2004, Fischer *et al.* 2006).

The longleaf pine and jack pine systems are now managed primarily to maintain natural fire regimes and only secondarily for other purposes, which illustrates what is possible when ecological considerations are considered primary. In the longleaf pine system, current management represents a reversal of previous

goals that were geared toward timber production and that led to an era of fire suppression. Consequently, there has been much success in restoring the diversity lost in the previous era through prescribed burning designed to mimic the prehistoric fire regime. That the endangered red-cockaded woodpecker is a fire specialist was fortuitous, as its management has tended to support restoration of the natural fire regime. Nevertheless, the risk in paying too much attention to the needs of endangered species is that their needs can be met through artificial means that mimic natural post-fire conditions (e.g., plantations rather than burned forests for Kirtland's warbler), rather than through the accommodation of natural fire events. We must not lose sight of the fact that it is the entire ecosystem and not merely a single endangered species that needs to be maintained through active management (Hutto *et al.* 1987). The ecology of selected species (in the present case, fire-dependent species) should be used to understand and embrace the natural processes that prehistorically produced conditions necessary for their maintenance, and not be used to devise artificial means to circumvent those natural processes.

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