Forum Article

Amphibian Responses to Wildfire in the Western United States: Emerging Patterns from Short-Term Studies

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ABSTRACT

The increased frequency and severity of large wildfires in the western United States is an important ecological and management issue with direct relevance to amphibian conservation. Although the knowledge of fire effects on amphibians in the region is still limited relative to most other vertebrate species, we reviewed the current literature to determine if there are evident patterns that might be informative for conservation or management strategies. Of the seven studies that compared pre- and post-wildfire data on a variety of metrics, ranging from amphibian occupancy to body condition, two reported positive responses and five detected negative responses by at least one species. Another seven studies used a retrospective approach to compare effects of wildfire on populations: two studies reported positive effects, three reported negative effects from wildfire, and two reported no effects. All four studies that included plethodontid salamanders reported negative effects on populations or individuals; these effects were greater in forests where fire had been suppressed and in areas that burned with high severity. Species that breed in streams are also vulnerable to post-wildfire changes in habitat, especially in the Southwest. Wildfire is also important for maintaining suitable habitat for diverse amphibian communities, although those results may not be evident immediately after an area burns. We expect that wildfire will extirpate few healthy amphibian populations, but it is still unclear how populations will respond to wildfire in the context of land management (including pre- and post-fire timber harvest) and fragmentation. Wildfire may also increase the risk of decline or extirpation for small, isolated, or stressed (e.g., from drought or disease) populations. Improved understanding of how these effects vary according to changes in fire frequency and severity are critical to form more effective conservation strategies for amphibians in the western United States.

Keywords: amphibian, conservation, decline, fire effects, forest management, fragmentation, life history strategies, population, wildfire

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INTRODUCTION

The widespread decline of amphibians has been one of the most visible conservation issues during the past two decades (Stuart *et al.* 2004). At the same time, the increase in large wildfires in western North America, where wildfire severity is expected to increase further under future climate conditions (Westerling *et al.* 2006, Morgan *et al.* 2008), has emerged as an important issue with direct relevance to amphibian conservation. Some amphibian species will decline after wildfires cause habitat changes, whereas other species will thrive in the early successional or patchy environments that often result. How amphibians respond to wildfire likely depends on their evolutionary history with fire, as well as the life history characteristics that influence their resistance and resilience.

The contemporary distribution and population trends of amphibians are, in part, a reflection of dynamic landscapes shaped by a range of disturbances and ecological processes, including beaver activity, debris flows, drought, and wildfire (Petranka *et al.* 2004, Means 2006, Swanson *et al.* 2011). Wildfire is an important agent in structuring diverse amphibian communities in fire-adapted ecosystems, like those in the southeastern US where frequent (e.g., 1 yr to 4 yr), low-severity fire is critical for maintaining suitable conditions for many species (Russell *et al.* 1999, Means 2006). Our definition considers severity to represent loss of biomass that results from fire (Keeley 2009). Although wildfire has likely served a similar role in structuring amphibian communities in some parts of the western United States (hereafter, the West), there are few studies from this region, and it is uncertain how broadly studies from other ecosystems apply because of differences in fire regimes and species assemblages. Also, interactions between land management and climate change may be resulting in fire characteristics different from those that populations have experienced in recent centuries, including less frequent but more severe wildfire in dry forests (e.g., ponderosa pine [*Pinus ponderosa* C. Lawson] in the southwestern US) or more frequent wildfire in forests that rarely burned historically (e.g., cold mesic forests; Agee 1993, DeBano *et al.* 1998).

More than half of the native anuran species (frogs and toads) in the West have suffered serious declines (Bradford 2005). Salamanders are thought to have experienced fewer declines than anurans, but the status of several species is uncertain because of limited data (Bradford 2005). Recent wildfire activity in the West has overlapped a large portion of the range of many amphibian species, making an improved understanding of the effects of wildfire on amphibian populations important for prioritizing conservation efforts. For example, more than 25% of the estimated range for the federally endangered mountain yellow-legged frog (*Rana muscosa* Camp., *sensu stricto*) in southern California has burned since 1987 (Figure 1). Approximately 24% of the range of the Rocky Mountain tailed frog (*Ascaphus montanus* Mittleman and Myers) has burned during the same period (Figure 1).

Pilliod *et al.* (2003) reviewed the effects of fire on North American amphibians and found only two studies conducted west of the Great Plains. Although knowledge of wildfire effects on amphibians is still limited compared to studies on other vertebrates, much more research has been completed in the West since 2003. We provide an updated review of the effects of wildfire on amphibians and their habitats in the West, where recent and projected fire activity could have important implications for populations. We discuss separately the

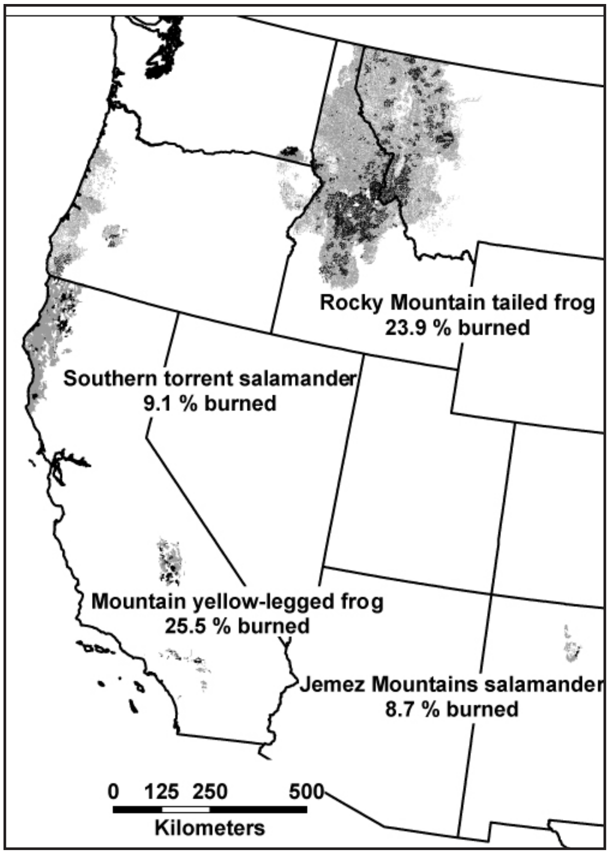

Figure 1. Overlap of areas burned by wildfire in the western United States since 1987 (in black) with the distribution of select amphibian species (in gray) that represent a range of the life-history strategies and fire regimes. Species distributions were mapped using a combination of Amphibian Atlas and Gap Analysis data. Wildfire data were compiled from several sources (unpublished data, USGS Snake River Field Station).

documented or expected responses of amphibians to wildfire according to their life history strategies and the habitats they occupy. We also focus primarily on amphibian responses to wildfires rather than prescribed fires because the two types of fire manifest different change (e.g., Arkle and Pilliod 2010). Prescribed fires are usually set during cool seasons, burn with lower intensities than wildfires that occur during summer droughts, and are often used for management of fuels rather than achieving ecological objectives (Stone *et al.* 2010). Finally, we emphasize research gaps that should be addressed to help identify and form effective conservation strategies.

EFFECTS OF WILDFIRE ON AMPHIBIAN HABITATS

Unless a species has an extremely limited distribution or is isolated, we expect the immediate effects of wildfire such as mortality of some individuals or failed reproduction will be a small threat to most healthy populations. Instead, most declines probably result from sublethal effects imposed by persistent habitat change or synergistic effects with other stressors like drought. Because many amphibian species have discrete terrestrial and aquatic phases, they experience changes in both aquatic and terrestrial environments. This biphasic life style may expose some species to stressors in two environments, but it can also help insulate populations from catastrophic losses in a particular environment (e.g., aquatic larvae die but terrestrial adults survive).

Wetland Habitats

Of the three habitats frequented by amphibians (wetland, stream, terrestrial), we expect wetland environments would experience the smallest fire-related changes and may be the most likely to experience advantageous changes for larvae. We use the term "wetland" to include all non-flowing waters, including vernal pools, ponds, and lakes. We suspect amphibian populations in large wetlands and lakes will be less susceptible than populations in smaller water bodies simply because large sites tend to have longer hydroperiods and their basins are less likely to burn (Gresswell 1999). Increased productivity in lakes that sometimes results after fire could also improve foraging opportunities for grazing tadpoles and predatory salamanders (Scrimgeour *et al.* 2001, Charette and Prepas 2003).

In contrast, the high perimeter-to-surface ratio of small wetlands strengthens their connection with the surrounding terrestrial environment, likely increasing post-fire changes in habitat relative to large water bodies (Batzer *et al.* 2000, Palik *et al.* 2001). Small wetlands cover <5 % of the landscape in the West (Dahl 1990), yet they are critical habitats for many species and are the dominant breeding habitat for resident amphibians. In deciduous and mixed conifer-deciduous forests in other regions of the US, periodic events that open the canopy strongly influence amphibian communities through changes in the light regime, temperature, and hydroperiod of wetlands (Werner and Glennemeier 1999, Halverson *et al.* 2003). Frequent, low-severity wildfires in the southeastern US historically served a similar role in retarding encroachment of woody vegetation in wetlands and were critical for maintaining suitable habitat for several amphibian species (Russell *et al.* 1999, Means 2006).

There has been less research on the importance of wildfire to wetlands in the West. Suppression of wildfires in northern California has been associated with encroachment of trees into open meadow habitats and subsequent loss of amphibian breeding sites (Fellers and Drost 1993). Most larvae of wetland-breeding amphibians require sustained hydroperiods of warm water to complete development. Woody vegetation tends to either shorten hydroperiods or reduce water temperatures through evapotranspiration and shading. Contrary to this supposition, water temperatures on the north shoreline (where amphibians typically deposit eggs) of burned and unburned temporary wetlands in Glacier National Park, Montana, were not significantly different in the first year after a mixed-severity wildfire (Hossack and Corn 2008). However, all of the wetlands had fairly open canopies before the fire and we suspect that temperatures would have increased had they been heavily shaded before the fire.

Stream Habitats

Streams are critical to much of the West's diversity and may experience changes in structure and function after wildfire (Corn *et al.* 2003, Dunham *et al.* 2007). In the Southwest, debris flows are common after severe wildfires consume most surface vegetation, and can greatly reduce breeding and rearing habitat for local amphibians. Where pools do not fill completely with sediments, they may hold less water and dry before larvae can metamorphose (Sredl and Wallace 2000).

Population connectivity is often critical for recovery of stream species. There are several examples of fishes getting extirpated from stream reaches after wildfire, but in most cases they recolonize within one or two years, and populations recover to pre-fire levels within several years (Dunham *et al.* 2003). One important difference between stream fishes and amphibians is that recovery of many amphibians is expected to occur slowly. For example, experimental removal of Pacific giant salamanders (*Dicamptodon tenebrosus* Baird and Girard) from stream reaches 25 m to 40 m long showed that recolonization from adjacent areas within streams could take up to 42 months (Ferguson 2000). Recent evidence also indicates that the amount of terrestrial versus aquatic dispersal could strongly influence connectivity and recolonization. Giant salamanders that are more closely tied to their streams (Cope's giant salamander [*Dicamptodon copei* Nussbaum], Idaho giant salamander [*Dicamptodon aterrimus* Cope]) experience less gene flow among populations than the more terrestrial Pacific giant salamander (Steele *et al.* 2009, Mullen *et al.* 2010). Tailed frogs and torrent salamanders are likely weaker dispersers than Pacific giant salamanders and could take longer to recolonize habitats, or may experience reduced gene flow if wildfire makes the terrestrial environment less hospitable (Nijhuis and Kaplan 1998, Miller *et al.* 2006, Spear and Storfer 2008).

Southwestern anurans that breed in warm streams are more vagile than amphibians that occupy cold streams in the Northwest, but the stream habitats in the Southwest often occur in highly fragmented landscapes or contain introduced predators that may inhibit dispersal and recolonization (Riley *et al.* 2005, Wallace *et al.* 2010). Perhaps paradoxically, greater vagility may increase short-term risk of species to habitat loss and fragmentation, because dispersers can settle or die in unsuitable habitats (Funk *et al.* 2005, Fahrig 2007).

Terrestrial Habitats

Most aquatic-breeding amphibians spend the majority of their lives in terrestrial or riparian habitats. Thus, even for aquatic-breeding species, the terrestrial environment can be a stronger driver of population dynamics than the aquatic environment (Biek *et al.* 2002, Trenham and Shaffer 2005), and terrestrial habitat characteristics are often better predictors of the composition and abundance of larval amphibian communities (Van Buskirk 2005, Piha *et al.* 2007). The importance of terrestrial habitat in structuring aquatic communities reflects the strong connection between terrestrial and aquatic environments, but also emphasizes the importance of the terrestrial environment on dispersal and survival.

Changes to temperature and moisture regimes are likely to be two of the biggest challenges facing amphibians after wildfire (Hossack *et al.* 2009, Semlitsch *et al.* 2009). Wildfire increases recruitment of coarse wood to the forest floor (although oftentimes slowly), which can help offset the greater soil temperatures and risk of evaporative water loss that result from reduced canopy (Lindenmayer and Noss 2006). However, if wildfire occurs in early seral stages or forests that have been logged, there may be little large wood on the forest floor to provide refugia for animals (Major 2005). Variation in burn severity within the fire perimeter may also be critical for providing refugia and sources of future colonists to the surrounding habitats. These legacy patches could be especially important for species like plethodontid salamanders that have limited colonization abilities, but can persist in small remnants of intact forest (Gibbs 1998, Noël *et al.* 2007).

EFFECTS OF WILDFIRE ON AMPHIBIAN POPULATIONS

Amphibians have a broader range of life-history strategies than any other vertebrate class (Duellman and Treub 1986), and understanding and accounting for these strategies is critical for predicting responses to wildfire. Vulnerability of a species to direct (mortality) and indirect (habitat change) effects of wildfire will depend largely upon how individuals use and perceive their environment and how their habitats change after fire. Most western amphibians can be placed into three general groups based on breeding habitats and reproductive characteristics: 1) species that breed in standing water or slow, warm streams; 2) species in the Northwest and northern Rocky Mountains that breed in small, cold streams; and 3) lungless salamanders (family Plethodontidae) that are not reliant upon water for breeding. Most species in these last two categories have delayed maturity, are long lived, and have low fecundity relative to most species that breed in warm waters, and thus may take longer to respond to or recover after wildfire. We used these life-history characteristics and associated breeding habitats to frame expected effects of wildfire on amphibian populations.

Wetland and Warm Stream Breeders

Most studies of effects of wildfire on wetland amphibians in the West have occurred in the northern Rocky Mountains, the region that has experienced the largest increase in recent fire activity (Westerling *et al.* 2006). Many of the studies in this region have been in Glacier

National Park, Montana, where fires burned areas that were part of a long-term amphibian monitoring program. After a 2001 mixed-severity fire burned forest surrounding 42 previously surveyed wetlands, there was no change in occupancy of breeding sites by the long-toed salamander (*Ambystoma macrodactylum* Baird) or Columbia spotted frog (*Rana luteiventris* Thompson), whereas western toads (*Anaxyrus boreas* Baird and Girard) colonized several wetlands they did not use for breeding before the fire (Table 1; Hossack and Corn 2007). Western toads also colonized >20 previously vacant wetlands after another stand-replacement fire in Glacier National Park in 2003 (Hossack and Corn 2007).

In this same area of Glacier that was colonized by toads after fire, a radio telemetry study showed that adult western toads used severely burned areas more than moderately burned forest (there was little unburned forest in the area; Guscio *et al.* 2008). In contrast, adult western toads did not use burned habitats more than expected in an area of northeast Oregon that included three fires that burned 6 yr to 10 yr prior, but they did use open habitats more than expected (Bull 2006). Different responses between study areas may be related to the age of the fires or because the fires in Oregon burned relatively open subalpine forests that included extensive meadows, whereas the fires in Glacier National Park occurred in dense forest. Consistent with the positive responses to fire in Glacier National Park, western toad populations near areas burned by the 1988 fires in Yellowstone National Park had greater genetic connectivity than populations farther from burned areas (Murphy *et al.* 2010). These data suggest that landscape-level factors such as wildfire may facilitate dispersal and connectivity.

The threat of wildfire to amphibian populations is probably greater in the Southwest than other regions of the West. The Southwest is also the region with the highest proportion of imperiled species (Bradford 2005). Persistent drought, large wildfires, and widespread alteration of water bodies (including the presence of non-native amphibians and fishes), combined with an already challenging landscape, magnify the threats to these species (Clarkson and Rorabaugh 1989, DeBano *et al.* 1998, Sredl and Wallace 2000, Olden and Poff 2005). Comparison of pre- and post-fire data after two large wildfires in southern California revealed that the western toad was detected in fewer plots (using drift fence arrays) in chaparral habitats after they burned, but the capture rate did not change across the study area and toads remained the most common amphibian (Rochester *et al.* 2010). The distribution and capture rate of the Pacific treefrog (*Pseudacris regilla* Baird and Girard) in terrestrial plots was not affected by the wildfires in either chaparral or coastal sage scrub habitats. Captures of treefrogs in stream-side habitats, which may be more relevant to population dynamics, were insufficient to evaluate effects of the wildfires (Rochester *et al.* 2010).

Landslides and other sedimentation events are common after intense wildfires in the Southwest, often altering stream channels and filling breeding habitats. In Arizona, the lowland leopard frog (*Lithobates yavapaiensis* Platz and Frost) has suffered widespread declines and often breeds in bedrock pools called tinajas, which are the only breeding habitats that last through the winter in some areas (Clarkson and Rorabaugh 1989, Parker 2006). Many of these pools filled with coarse sediments following several large wildfires since 1989, and frogs remain rare in areas most affected by large sedimentation events (Parker 2006). Post-wildfire landslides and debris flows in southern California have reduced breeding habitat of many stream-associated species and may have extirpated one of the largest remaining populations of the federally endangered mountain yellow-legged frog (Backlin *et al.* 2004). Recent wildfires have burned approximately 25 % of the range of this endangered species in southern California,

Table 1. Summary of effects of wildfire on amphibian populations and their habitats in the western United States. Studies are sorted by species, with the direction of the response (if apparent) indicated. Timeline refers to number of years before and after the wildfire occurred. The superscripted letter references the study, listed below the table.

Species	Location	Timeframe	Effect	Description
Ambystoma macrodactylum[a]	Western Montana	–3 to +3	none	No change in occupancy of breeding sites.
Anaxyrus californicus[b]	Southern California	–2 to +1	positive	Increased breeding after post-fire transport of coarse sediments to low-gradient streams.
Anaxyrus boreas[a]	Western Montana	–3 to +3	positive	Colonization of several wetlands after they burned.
Anaxyrus boreas[a]	Western Montana	–4 to +1	positive	Colonization of several wetlands after they burned.
Anaxyrus boreas[c]	Western Montana	+1	positive	Adults used severely burned forest more than expected.
Anaxyrus boreas[d]	Northeastern Oregon	+6 to +10	none	No selection for burned habitats by adults.
Anaxyrus boreas[e]	Western Wyoming	+16 to +18	positive	Greater gene flow among populations near areas burned in 1988.
Anaxyrus boreas[f]	Southern California	–5 to +2	none	Reduced occupancy of terrestrial plots in chaparral habitats but no change in abundance. No change in occupancy or abundance in grassland, coastal sage scrub, or woodland-riparian habitats.
Ascaphus montanus[g]	Western Montana	–2 to +2	negative	Reduced relative abundance and a shift in age-class structure of larvae.
Ascaphus montanus[h]	Idaho	+9 to +11	none	No difference in patch occupancy by larvae.
Batrachoseps major[f]	Southern California	–5 to +2	negative, none	Reduced occupancy of terrestrial plots in chaparral habitats. No change in occupancy in grassland, coastal sage scrub, or woodland-riparian habitats.
Lithobatesy avapaiensis[i]	Southern Arizona	+5 to +15	negative	Persistent sedimentation of breeding habitats linked to declines in frog counts.
Plethodon elongatus[j]	Northern California	+1 to +2	negative	Less frequent detection associated with more severe wildfire and loss of cover.
Plethodon neomexicanus[k]	Northern New Mexico	–4 to +4	negative, none	Change in size classes toward more small salamanders and fewer adults. No change in body condition.
Plethodon spp.[l]	Western Oregon	+2	mixed	Weak support for lower surface occupancy by 5 species of plethodontid salamanders.
Pseudacris regilla[f]	Southern California	–5 to +2	none	No change in occupancy or abundance in terrestrial plots.
Rana luteiventris[a]	Western Montana	–3 to +3	none	No change in occupancy of breeding sites.
Rana muscosa[m]	Southern California	–2 to +1	negative	Likely extirpation of a population of federally endangered *R. muscosa* after fire and debris flows.
Taricha torosa[n]	Southern California	–1 to +3	negative	Fewer egg masses after landslides reduced pool and run habitats in streams.

[a] Hossack and Corn 2007
[b] Mendelsohn *et al.* 2005
[c] Guscio *et al.* 2008
[d] Bull 2006
[e] Murphy *et al.* 2010
[f] Rochester *et al.* 2010
[g] Hossack *et al.* 2006
[h] Dunham *et al.* 2007
[i] Parker 2006
[j] Major 2005
[k] Cummer and Painter 2007
[l] Chelgren *et al.* 2011
[m] Backlin *et al.* 2004
[n] Gamradt and Kats 1997

likely increasing the risk of extinction of some isolated populations (Figure 1). Similar changes to streams following other wildfires in southern California led to reduced numbers of egg masses of the California newt (*Taricha torosa* Rathke) (Gamradt and Kats 1997), but improved breeding habitat of the federally endangered arroyo toad (*Anaxyrus californicus* Camp) (Mendelsohn *et al.* 2005). These different responses illustrate the often species- and context-specific responses by amphibians to wildfire.

Cold Stream Breeders

The Pacific Northwest hosts three endemic families of amphibians (Ascaphidae, Dicamptodontidae, Rhyacotritonidae) that are restricted to or reach peak abundances in small, cold streams (Corn *et al.* 2003). There is still little published research on the effects of wildfire on these species, in part because some species (e.g., torrent salamanders of the family Rhyacotritonidae) occupy habitats that rarely burn. All research on effects of wildfire on stream amphibians in the Pacific Northwest has focused on tailed frogs (*Ascaphus* spp.), especially in the Rocky Mountains, where >20% of the range of the Rocky Mountain tailed frog (*Ascaphus montanus* Mittleman and Myers) has burned since 1987 (Figure 1). Tailed frogs reside primarily in cold headwater streams, have long larval periods that can exceed 3 years, and often decline in numbers after disturbances that increase sedimentation or water temperature (Corn *et al.* 2003). Therefore, tailed frogs are expected to be sensitive to wildfire-induced changes to habitat (Pilliod *et al.* 2003). Notably, Noble and Putnam (1931) speculated 80 years ago that wildfire resulted in the local extirpation of coastal tailed frogs (*Ascaphus truei* Stejneger) in the Olympic Mountains of Washington.

Research to date does not indicate that wildfire is likely to extirpate tailed frog populations, although declines may occur. After a 2003 wildfire in Glacier National Park, comparison of one year of pre-fire data and two years of post-fire data on Rocky Mountain tailed frogs showed that larvae in burned streams were less abundant and were dominated by older age classes compared to larvae in unburned streams (Hossack *et al.* 2006). However, Dunham *et al.* (2007) did not find evidence that significant changes to channel structure after wildfire affected the distribution or abundance of Rocky Mountain tailed frog larvae in 6 streams that were sampled 9 yr to 11 yr after burning, suggesting that this species may be more resistant or resilient to wildfire than thought.

Terrestrial Breeders

Plethodontid salamanders are the most species-rich family of amphibians in the West. These lungless salamanders are associated primarily with mature forest and moist talus slopes or stream sides, where they lay terrestrial eggs that develop directly (no aquatic stage). Direct development from terrestrial eggs has evolved independently in several amphibian families and is thought to be an adaptation to predictable environments (Duellman and Trueb 1988). Species with low vagility and restricted microclimate associations like plethodontid salamanders are often expected to be the most sensitive to disturbance because they have limited capacity for population growth and recolonization of vacant habitats (Russell *et al.* 1999, Pilliod *et al.* 2003). For example, plethodontids were the slowest group of amphibians to recover after the eruption of Mount St. Helens in Washington (Crisafulli *et al.* 2005). Some plethodontids occupy habitats that are unlikely to burn, such as talus slopes. The subterranean habits of most salamanders likely also buffer them from the direct effects of wildfire, especially because most salamanders probably retreat underground during summer drought, when wildfires are more likely to occur. However, these habits will also make it more difficult to detect population-level changes in plethodontids, because only a small fraction of the population may be available to sample at any given time (Chelgren *et al.* 2011).

Fire severity or pre-fire habitat conditions may be more important for predicting effects on terrestrial salamanders than for any other group of western amphibians. Detection of the garden slender salamander (*Batrachoceps major* Camp) and the ensatina (*Ensatina escholtzii* Gray) in drift fence arrays declined after intense wildfires in southern California (Rochester *et al.* 2010). These declines were most significant in chaparral forests, where little soil litter remained after the fires. After a 2009 ha wildfire burned in an ancient forest in western Oregon, Chelgren *et al.* (2011) found only weak support for a reduction in surface occupancy by five species of plethodontid salamanders in burned plots (0.16 ha) compared to unburned plots. In this study, the large volume of downed wood in the mature forest may have offered sufficient post-fire habitat to reduce the effects of the wildfire. Results from a prescribed fire in the Sierra Nevada in California support the hypothesized link between burn severity and effects on salamanders. Capture rates of the Sierra Nevada ensatina (*Ensatina eschscholtzi platensis* Jimenez de la Espada) and gregarious slender salamander (*Batrachoseps gregarius* Jockusch, Wake, and Yanev) were not affected by spring burning, probably because patches of deep litter remained after the fire and overstory canopy closure was unaffected (Bagne and Purcell 2009).

We expect the threat of wildfire to amphibians could be especially serious in fire-suppressed forests that burn with greater intensity than they did historically, because resident species are not adapted to a high-severity fire regime. In recently burned, fire-suppressed Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco)–tanoak (*Lithocarpus densiflorus* [Hook. and Arn.] Rehder) forests in northern California, Del Norte salamanders (*Plethodon elongates* Van Denburgh) were detected more frequently in stands that burned with low or moderate severity, and there were large amounts of downed wood, compared with lower detection rates in severely burned stands that retained less woody debris (Major 2005). After a stand-replacement wildfire burned a fire-suppressed landscape in New Mexico that historically burned with low- or mixed-severity fires, microhabitat temperatures in severely burned habitats consistently exceeded preferred temperatures (and occasionally the critical thermal maximum) of the Jemez Mountains salamander (*Plethodon neomexicanus* Stebbins and Riemer) (Cummer and Painter 2007; Figure 1). A comparison of pre- and post-wildfire data revealed no difference in naïve capture rates of surface-active salamanders, but the mean size of salamanders in the burned area decreased during the 4 years after the fire. This shift in size could have several explanations, including reduced surface activity by larger salamanders, reduced growth rates, or increased mortality of adults (Cummer and Painter 2007). Similar differences in body size or body condition of amphibians have been documented in comparisons of amphibians from harvested and unharvested forest and may be indicative of a gradual decline in population size that is difficult to detect (Karraker and Welsh 2006, Neckel-Oliveira and Gascon 2006).

SUMMARY AND RECOMMENDATIONS

Seven studies have compared pre- and post-wildfire data on a variety of metrics ranging from amphibian occupancy to demographic patterns. Two of these studies detected positive changes and five detected negative changes to population- or individual-level data on at least one species (Table 1). Of the seven studies that used a retrospective approach to investigate effects of wildfire on amphibians, two reported positive effects, two did not find any effects, and three reported negative effects from wildfire. Across all studies, there is no clear pattern to the effects that were documented and time-since-fire, in part because there are not enough studies for most species. However, the positive responses after wildfire were from the western toad and the arroyo toad, which is consistent with the affinity of some toad species for disturbed habitats (Hossack *et al.* 2007, Warren and Büttner 2008). Furthermore, all four studies that included plethodontid salamanders reported negative effects on populations or individuals (Table 1), which supports our prediction that these species would be the most sensitive to changes in habitat affected by wildfire.

Importantly, there are still few published studies on the effects of wildfire on amphibians in the West, and most studies (including our own) have been poorly replicated, included only a few sites, and have been short-term. Studies we reviewed covered only 14 species, and publication bias (i.e., not reporting cases where no changes were found) could have important implications for our perception of the effects of wildfire on amphibians. We emphasize three areas that require further research to clarify the threat of wildfire to amphibian populations. These topics are not mutually exclusive, and include 1) synergisms with land management and effects of fragmentation like timber harvest and roads; 2) effects of fire frequency and severity, which may be especially relevant in landscapes where the fire regime has been altered; and 3) more robust or longer-term estimates of population responses.

There is a large body of literature describing the often negative effects of timber harvest or fragmentation by forest roads on amphibian populations and habitats (e.g., Marsh and Beckman 2004, Karraker and Welsh 2006, Semlitsch *et al.* 2009), but to our knowledge, no studies have explicitly measured the combined effects of wildfire and timber harvest. Research on synergies between wildfire and disturbances will be especially important in areas that have been harvested after wildfire because characteristics of forests that have been salvaged logged (e.g., reduced recruitment of large wood, increased soil heating; Lindenmayer and Noss 2006) suggest that the combined effect of wildfire and harvest could be more harmful to forest amphibians than either factor alone. Negative interactive effects of wildfire and timber harvest or fragmentation may be more likely for isolated populations, where there are greater physiological costs of dispersal and reduced likelihood of rescue from neighboring populations.

A greater understanding of the effects of wildfire frequency and severity on populations will also be important for developing effective management strategies, especially in fire-suppressed forests that may burn more intensely than they did historically. Based on our summary, more severe wildfires seem to increase the likelihood of harmful changes to habitats or decreases in populations, especially for stream habitats and plethodontid salamanders (Backlin *et al.* 2004, Major 2005, Cummer and Painter 2007). Importantly, however, fire severity usually has not been quantified using a standard method like the Normalized Burn Ratio (Key and Benson 2005) in the studies that we reviewed, which limits our ability to make general comparisons across studies. Changes in the frequency and intensity of wildfire are particularly important in the Southwest, especially in areas where invasive plants might further alter the historical wildfire regime (Brooks *et al.* 2004).

Last, we need population estimates or other adjusted estimates to form reliable conclusions about both the short- and long-term effects of wildfire. For example, differences in apparent abundance between burned and unburned habitats can result from different detection probabilities between areas. In the Chelgren *et al.* (2011) study, which compared occupancy of five species of plethodontid salamanders in burned and unburned forest, they detected more salamanders per unit effort in burned plots because there was less cover for salamanders to hide under than in unburned plots. After adjusting for the lower detection rates in unburned plots, they found weak evidence of a negative effect of fire on occupancy of salamanders. Similarly, Hossack *et al*. (2007) found that detection probabilities for Columbia spotted frogs increased during the course of their study. Without adjusting for these differences, they would have incorrectly reported a change in occupancy after the wildfire, when in fact there was no change. These studies underscore the need for reliable estimates to detect changes after wildfire. Long-term studies contrasting population and community dynamics in burned and unburned areas are also critical for measuring the effects of wildfires on amphibians in contrasting habitats or management scenarios because fire-related declines may not be evident for several generations (Findlay and Bourdages 2000, Metzger *et al.* 2009).

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LITERATURE CITED

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Covelo, California, USA.

Arkle, R.S., and D.S. Pilliod. 2010. Prescribed fires as ecological surrogates for wildfires: a stream and riparian perspective. Forest Ecology and Management 259: 893-903. doi: 10.1016/j.foreco.2009.11.029

Backlin A.R., C.J. Hitchcock, and R.N. Fisher. 2004. Survey results for the southern California populations of the mountain yellow-legged frog (*Rana muscosa*), 2004 Annual Report. US Geological Survey Technical Report. Western Ecological Research Center, Sacramento, California, USA.

Bagne, K.E., and K.L. Purcell. 2009. Response of two terrestrial salamander species to spring burning in the Sierra Nevada, California. USDA Forest Service Research Note RMRS-RN-41. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Batzer, D.P., C.R. Jackson, and M. Mosner. 2000. Influences of riparian logging on plants and invertebrates in small, depressional wetlands of Georgia, USA. Hydrobiologia 441: 123-132. doi: 10.1023/A:1017558523802

Biek, R., W.C. Funk, B.A. Maxell, and L.S. Mills. 2002. What is missing from amphibian decline research: insights from ecological sensitivity analysis. Conservation Biology 16: 728-734. doi: 10.1046/j.1523-1739.2002.00433.x

Bradford, D.F. 2005. Factors implicated in amphibian population declines in the United States. Pages 915-925 in: M.J. Lannoo, editor. Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, USA.

Brooks, M.L., C.M. D'Antonio, D.M. Richardson, J.B. Grace, J.E. Keeley, J.M. DiTomaso, R.J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. BioScience 54: 677-688. doi: 10.1641/0006-3568(2004)054[0677:EOIAPO]2.0.CO;2

Bull, E. 2006. Sexual differences in the ecology and habitat selection of western toads (*Bufo boreas*) in northeastern Oregon. Herpetological Conservation and Biology 1: 27-38.

Charette, T., and E.E. Prepas. 2003. Wildfire impacts on phytoplankton communities of three small lakes on the Boreal Plain, Alberta, Canada: a paleolimnological study. Canadian Journal of Fisheries and Aquatic Sciences 60: 584-593. doi: 10.1139/f03-049

Chelgren, N.D., M.J. Adams, L.L. Bailey, and R.B. Bury. 2011. Using multilevel spatial models to understand salamander site occupancy patterns after wildfire. Ecology 92: 408-421. doi: 10.1890/10-0322.1

Clarkson, R.W., and J.C Rorabaugh. 1989. Status of leopard frogs (*Rana pipiens* complex: Ranidae) in Arizona and southeastern California. Southwestern Naturalist 34: 531-538. doi: 10.2307/3671513

Corn, P.S., R.B. Bury, and E.J. Hyde. 2003. Conservation of North American stream amphibians. Pages 24-36 in: R.D. Semlitsch, editor. Amphibian conservation. Smithsonian Books, Washington, D.C., USA.

Crisafulli, C.M., L.S. Trippe, C.P. Hawkins, and J.A. MacMahon. 2005. Amphibian responses to the 1980 eruption of Mount St. Helens. Pages 183-197 in: V.H. Dale, F.J. Swanson, and C.M. Crisafulli, editors. Ecological responses to the 1980 eruption of Mount St. Helens. Springer. New York, New York, USA. doi: 10.1007/0-387-28150-9_13

Cummer, M.R., and C.W. Painter. 2007. Three case studies of the effect of wildfire on the Jemez Mountains salamander (*Plethodon neomexicanus*): microhabitat temperatures, size distributions, and a historical locality perspective. Southwestern Naturalist 52: 26-37. doi: 10.1894/0038-4909(2007)52[26:TCSOTE]2.0.CO;2

Dahl, T.E. 1990. Wetlands losses in the United States 1780s to 1980s. US Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

DeBano, L.F., D.G. Neary, and P.F. Ffolliott. 1998. Fire's effects on ecosystems. John Wiley and Sons, New York, New York, USA.

Duellman, W.E, and L. Trueb. 1986. Biology of amphibians. McGraw Hill Book Company, New York, New York, USA.

Dunham, J.B., M.K. Young, R.E. Gresswell, and B.E. Rieman. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fish invasions. Forest Ecology and Management 178: 183-196. doi: 10.1016/S0378-1127(03)00061-6

Dunham, J.B., A.E. Rosenberger, C.H. Luce, and B.E Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems 10: 335-346. doi: 10.1007/s10021-007-9029-8

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology 21: 1003-1015. doi: 10.1111/j.1365-2435.2007.01326.x

Fellers, G.M., and C.A. Drost. 1993. Disappearance of the Cascades frog *Rana cascadae* at the southern end of its range, California, USA. Biological Conservation 65: 177-181. doi: 10.1016/0006-3207(93)90447-9

Funk, W.C., A.E. Greene, P.S. Corn, and F.W. Allendorf. 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. Biology Letters 1: 13-16. doi: 10.1098/rsbl.2004.0270

Ferguson, H.M. 2000. Larval colonisation and recruitment in the Pacific giant salamander (*Dicamptodon tenebrosus*) in British Columbia. Canadian Journal of Zoology 78: 1238-1242.

Findlay, C.S., and J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology 14: 86-94. doi: 10.1046/j.1523-1739.2000.99086.x

Gamradt, S.C., and L.B. Kats. 1997. Impact of chaparral wildfire-induced sedimentation on oviposition of stream-breeding California newts (*Taricha torosa*). Oecologia 110: 546-549. doi: 10.1007/s004420050193

Gibbs, J.P. 1998. Genetic structure of redback salamander *Plethodon cinereus* populations in continuous and fragmented forests. Biological Conservation 86: 77-81. doi: 10.1016/S0006-3207(97)00173-0

Gresswell, R.E. 1999. Fire and aquatic ecosystems in forested biomes of North America. Transactions of the North American Fisheries Society 128: 193-221. doi: 10.1577/1548-8659(1999)128<0193:FAAEIF>2.0.CO;2

Guscio, C.G., B.R. Hossack, L.A. Eby, and P.S. Corn. 2008. Post-breeding habitat use by adult boreal toads (*Bufo boreas*) after wildfire in Glacier National Park, USA. Herpetological Conservation and Biology 3: 55-62.

Halverson, M.A., D.K. Skelly, J.M. Kiesecker, and L.K. Freidenburg. 2003. Forest mediated light regime linked to amphibian distribution and performance. Oecologia 134: 360-364.

Hossack, B.R., P.S. Corn, and D.B. Fagre. 2006. Divergent patterns of abundance and age-class structure of headwater stream tadpoles in burned and unburned watersheds. Canadian Journal of Zoology 84: 1482-1488. doi: 10.1139/z06-143

Hossack, B.R., and P.S. Corn. 2007. Responses of pond-breeding amphibians to wildfire: short-term patterns in occupancy and colonization. Ecological Applications 17: 1403-1410. doi: 10.1890/06-2037.1

Hossack, B.R., and P.S. Corn. 2008. Wildfire effects on water temperature and selection of breeding sites by the boreal toad (*Bufo boreas*). Herpetological Conservation and Biology 3: 46-54.

Hossack, B.R., L.A. Eby, C.G. Guscio, and P.S. Corn. 2009. Thermal characteristics of amphibian microhabitats in a fire-disturbed landscape. Forest Ecology and Management 258: 1414-1421. doi: 10.1016/j.foreco.2009.06.043

Karraker, N.E., and H.H. Welsh, Jr. 2006. Long-term impacts of even-aged timber management on abundance and body condition of terrestrial amphibians in northwestern California. Biological Conservation 131: 132-140. doi: 10.1016/j.biocon.2006.02.013

Keeley, J.E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. International Journal of Wildland Fire 18: 116-126. doi: 10.1071/WF07049

Key, C.H., and N.C. Benson. 2004. Landscape Assessment (LA) sampling and analysis methods. Pages LA1-LA55 in: D.C. Lutes, R.E. Keane, J.F. Caratti, C.H. Key, N.C. Benson, S. Sutherland, and L.J. Gangi. 2006. FIREMON: Fire effects monitoring and inventory system. USDA Forest Service General Technical Report RMRS-GTR-164CD. Rocky Mountain Research Station, Fort Collins, Colorado, USA.

Lindenmayer, D.B., and R.F. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology 20: 949-958. doi: 10.1111/j.1523-1739.2006.00497.x

Major, D.J. 2005. Effects of fire disturbance on terrestrial salamanders in mixed-coniferous forests of the Klamath/Siskiyou region of the Pacific Northwest. Dissertation, Utah State University, Logan, USA.

Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15: 40-49.

Marsh, D.M., and N.G. Beckman. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications 14: 1882-1891. doi: 10.1890/03-5179

Means, D.B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. Pages 157-213 in: S. Jose, E.J. Jokela, and D.L. Miller, editors. The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, New York, USA.

Mendelsohn, M.B., M.C. Madden-Smith, and R.N. Fisher. 2005. Post-cedar fire arroyo toad (*Bufo californicus*) monitoring surveys at Cuyamaca Rancho State Park, 2004, Final Report. US Geological Survey Technical Report. Western Ecological Research Center, Sacramento, California, USA.

Metzger, J.P, A.C. Martensen, M. Dixo, L.C. Bernacci, M.C. Ribeiro, A.M.G. Texeira, and R. Pardini. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142: 1166-1177. doi: 10.1016/j.biocon.2009.01.033

Miller, M.P., S.M. Haig, and R.S. Wagner. 2006. Phylogeography and spatial genetic structure of the southern torrent salamander: implications for conservation and management. Journal of Heredity 97: 561-570. doi: 10.1093/jhered/esl038

Morgan, P., E.K. Heyerdahl, and C.E. Gibson. 2008. Multi-season climate synchronized forest fires throughout the 20th century, northern Rockies, USA. Ecology 89: 717-728. doi: 10.1890/06-2049.1

Mullen, L.B., H.A. Woods, M.K. Schwartz, A.J. Sepulveda, and W.H. Lowe. 2010. Scale-dependent genetic structure of the Idaho giant salamander (*Dicamptodon aterrimus*) in stream networks. Molecular Ecology 19: 898-909. doi: 10.1111/j.1365-294X.2010.04541.x

Murphy, M.A., J.S. Evans, and A. Storfer. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. Ecology 91: 252-261. doi: 10.1890/08-0879.1

Neckel-Oliveira, S., and C. Gascon. 2006. Abundance, body size, and movement patterns of a tropical treefrog in continuous and fragmented forests in the Brazilian Amazon. Biological Conservation 128: 308-315. doi: 10.1016/j.biocon.2005.09.037

Nijhuis, M.J., and K.H. Kaplan. 1998. Movement patterns and life history characteristics in a population of the Cascade torrent salamander (*Rhyacotriton cascadae*) in the Columbia River Gorge, Oregon. Journal of Herpetology 32: 301-304. doi: 10.2307/1565317

Noël, S., M. Ouellet, P. Galoisand, and F.J. Lapointe. 2007. Impact of urban fragmentation on the genetic structure of the eastern red-backed salamander. Conservation Genetics 8: 599-606. doi: 10.1007/s10592-006-9202-1

Noble, P.G., and P.G. Putnam. 1931. Observations on the life history of *Ascaphus truei* Stejneger. Copeia 1931: 97-101. doi: 10.2307/1437329

Olden, J.D., and N.L. Poff. 2005. Long-term trends of native and non-native fish faunas in the American Southwest. Animal Biodiversity and Conservation 28: 75-89.

Palik, B., D.P. Batzer, R. Buech, D. Nichols, K. Cease, L. Egeland, and D.E. Streblow. 2001. Seasonal pond characteristics across a chronosequence of adjacent forest ages in northern Minnesota, USA. Wetlands 21: 532-542. doi: 10.1672/0277-5212(2001)021[0532:SPCAAC]2.0.CO;2

Parker, J.T.C. 2006. Post-wildfire sedimentation in Saguaro National Park, Rincon Mountain District, and effects on lowland leopard frog habitat. US Geological Survey Scientific Investigations Report 2006-5235. Arizona Water Science Center, Tucson, USA.

Petranka, J.W., C.K. Smith, and A.F. Scott. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. Ecological Applications 14: 1065-1078. doi: 10.1890/02-5394

Piha, H., M. Luoto, M. Piha, and J. Merilä. 2007. Anuran abundance and persistence in agricultural landscapes during a climatic extreme. Global Change Biology 13: 300-311. doi: 10.1111/j.1365-2486.2006.01276.x

Pilliod, D.S., R.B. Bury, E.J. Hyde, C.A. Pearl, and P.S. Corn. 2003. Fire and amphibians in North America. Forest Ecology and Management 178: 163-181. doi: 10.1016/S0378-1127(03)00060-4

Riley, S.P.D., G.T. Busteed, L.B. Kats, T.L. Vandergon, L.F.S. Lee, R.G. Dagit, J.L. Kerby, R.N. Fisher, and R.M. Sauvajot. 2005. Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. Conservation Biology 19: 1894-1907. doi: 10.1111/j.1523-1739.2005.00295.x

Rochester, C.J., C.S. Brehme, D.R. Clark, D.C. Stokes, S.A. Hathaway, and R.N. Fisher. 2010. Reptile and amphibian responses to large-scale wildfires in southern California. Journal of Herpetology 44: 333-351. doi: 10.1670/08-143.1

Russell, K.R., D.H. Van Lear, and D.C. Guynn, Jr. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 27: 374-384.

Scrimgeour, C.G., W.M. Tonn, C.A. Paszkowski, and C. Goater. 2001. Benthic macroinvertebrate biomass and wildfires: evidence for enrichment of boreal subarctic lakes. Freshwater Biology 46: 367-378. doi: 10.1046/j.1365-2427.2001.00682.x

Semlitsch, R.D., B.D. Todd, S.M. Blomquist, A.J.K. Calhoun, J.W. Gibbons, J.P. Gibbs, G.J. Graeter, E.B. Harper, D.J. Hocking, M.L. Hunter Jr., D.A. Patrick, T.A.G. Rittenhouse, and B.B. Rothermel. 2009. Effects of timber harvest on amphibian populations: understanding mechanisms from forest experiments. BioScience 59: 853-862. doi: 10.1525/bio.2009.59.10.7

Spear, S.F., and A. Storfer. 2008. Landscape genetic structure of coastal tailed frogs (*Ascaphus truei*) in protected vs. managed forests. Molecular Ecology 17: 4642-4656. doi: 10.1111/j.1365-294X.2008.03952.x

Sredl, M.S., and J.E. Wallace. 2000. Management of the amphibians of Fort Huachuca, Cochise County, Arizona. Nongame and Endangered Wildlife Program Technical Report 166. Arizona Game and Fish Department, Phoenix, USA.

Steele, C.A., J. Baumsteiger, and A. Storfer. 2009. Influence of life-history variation on the genetic structure of two sympatric salamander taxa. Molecular Ecology 18: 1629-1639. doi: 10.1111/j.1365-294X.2009.04135.x

Stone, K.R., D.S. Pilliod, K.A. Dwire, C.C. Rhoades, S.P. Wollrab, and M.K. Young. 2010. Fuel reduction management practices in riparian areas of the western USA. Environmental Management 46: 91-100. doi: 10.1007/s00267-010-9501-7

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783-1786. doi: 10.1126/science.1103538

Swanson, M.E., J.F. Franklin, R.L. Beschta, C.M. Crisafulli, D.A. DellaSala, R.L. Hutto, D.B. Lindenmayer, and F.J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9: 117-125. doi: 10.1890/090157

Trenham, P.C., and H.B. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15: 1158-1168. doi: 10.1890/04-1150

US Geological Survey National Amphibian Atlas. 2008. Version Number 1.0 US Geological Survey Patuxent Wildlife Research Center, Laurel, Maryland, USA. <http://www.pwrc.usgs.gov/naa>. Accessed 21 February 2011.

US National Gap Analysis Program. 2009. <http://gapanalysis.nbii.gov/portal/server.pt>. Accessed 8 June 2011.

Van Buskirk, J. 2005. Local and landscape influence on amphibian occurrence and abundance. Ecology 86: 1936-1947. doi: 10.1890/04-1237

Vredenburg, V.T., R. Bingham., R. Knapp., J.A.T. Morgan, C. Moritz, and D. Wake. 2007. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered mountain yellow-legged frog. Journal of Zoology 271: 361-374. doi: 10.1111/j.1469-7998.2006.00258.x

Wallace, J.E., R.J. Steidl, and D.E. Swann. 2010. Habitat characteristics of lowland leopard frogs in mountain canyons of southeastern Arizona. Journal of Wildlife Management 74: 808-815. doi: 10.2193/2009-207

Warren, D.D., and R. Büttner. 2008. Relationship of endangered amphibians to landscape disturbance. Journal of Wildlife Management 72: 738-744. doi: 10.2193/2007-160

Werner, E.E., and K.S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999: 1-12. doi: 10.2307/1447379

Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increases western US forest wildfire activity. Science 313: 940-943. doi: 10.1126/science.1128834