Contributed Paper

Rapid Increases and Time-Lagged Declines in Amphibian Occupancy after Wildfire

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Abstract: *Climate change is expected to increase the frequency and severity of drought and wildfire. Aquatic and moisture-sensitive species, such as amphibians, may be particularly vulnerable to these modified disturbance regimes because large wildfires often occur during extended droughts and thus may compound environmental threats. However, understanding of the effects of wildfires on amphibians in forests with long fire-return intervals is limited. Numerous stand-replacing wildfires have occurred since 1988 in Glacier National Park (Montana, U.S.A.), where we have conducted long-term monitoring of amphibians. We measured responses of 3 amphibian species to fires of different sizes, severity, and age in a small geographic area with uniform management. We used data from wetlands associated with 6 wildfires that burned between 1988 and 2003 to evaluate whether burn extent and severity and interactions between wildfire and wetland isolation affected the distribution of breeding populations. We measured responses with models that accounted for imperfect detection to estimate occupancy during prefire (0–4 years) and different postfire recovery periods. For the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*), occupancy was not affected for 6 years after wildfire. But 7–21 years after wildfire, occupancy for both species decreased ≥25% in areas where >50% of the forest within 500 m of wetlands burned. In contrast, occupancy of the boreal toad (*Anaxyrus boreas*) tripled in the 3 years after low-elevation forests burned. This increase in occupancy was followed by a gradual decline. Our results show that accounting for magnitude of change and time lags is critical to understanding population dynamics of amphibians after large disturbances. Our results also inform understanding of the potential threat of increases in wildfire frequency or severity to amphibians in the region.*

Keywords: climate change, colonization, detection, disturbance, extinction, fire severity, isolation, population dynamics

Incrementos Rápidos y Declinaciones Desfasadas en la Ocupación de Anfibios Después de un Incendio

Resumen. *Se espera que el cambio climático incremente la frecuencia y severidad de sequías e incendios. Las especies acuáticas y sensibles a la humedad, como los anfibios, pueden ser particularmente vulnerables a estos regímenes de perturbación modificados porque los incendios extensivos a menudo ocurren durante sequías prolongadas y por lo tanto pueden agravar las amenazas ambientales. Sin embargo, el entendimiento de los efectos de incendios sobre anfibios en bosques con intervalos de retorno de incendio largos está limitado. Desde 1988 han ocurrido números incendios en el Parque Nacional Glacier (Montana, E.U.A.), donde hemos monitoreado anfibios a largo plazo. Medimos las respuestas de 3 especies de anfibios a incendios de diferente tamaño, severidad y edad en un área geográfica pequeña con manejo uniforme. Utilizamos datos de humedales asociados con 6 incendios entre 1988 y 2003 para evaluar si la extensión y severidad del incendio y las interacciones entre incendios y el aislamiento del humedal afectaron la distribución de poblaciones*

reproductivas. Medimos respuestas con modelos que explicaron la detección imperfecta para estimar la ocupación durante años previos al incendio (0–4 años) y durante diferentes períodos de recuperación después del incendio. Para la salamandra (Ambystoma macrodactylum) y la rana (Rana luteiventris), la ocupación no fue afectada durante 6 años después del incendio. Pero 7–21 años después del incendio, la ocupación de ambas especies disminuyó ≥25% en áreas donde se quemó ≥50% del bosque a 500 de un humedal. En contraste, la ocupación de sapo (Anaxyrus boreas) se triplicó en los 3 años después de que se quemaron los bosques en altitudes bajas. Este incremento en la ocupación fue seguida por una declinación gradual. Nuestros resultados indican que la explicación de la magnitud de cambio y los desfases temporales es crítica para el entendimiento de la dinámica poblacional de anfibios después de perturbaciones extensivas. Nuestros resultados también informan sobre el entendimiento de la amenaza potencial de los incrementos de la frecuencia o severidad de los incendios para los anfibios de la región.

Palabras Clave: Aislamiento, cambio climático, colonización, detección, dinámica poblacional, extinción, perturbación, severidad del incendio

Introduction

Global climate change and a growing human population are expected to increase the frequency and severity of many disturbances and to have broad effects on biological diversity (McKenzie et al. 2004; Scholze et al. 2006; IPCC 2007). How species respond to disturbance depends on the type and magnitude of disturbance, the amount and configuration of remaining habitat, and their life-history characteristics (Prugh et al. 2008; Kuussaari et al. 2009). Responses to disturbance and changing climate can also be counter to expectations that occupancy and vital rates will decline (e.g., Ferraz et al. 2007; Ozgul et al. 2010). Such counterintuitive responses highlight the need for greater knowledge of how disturbance affects species across a broad range of life-history strategies.

The need to understand how increases in wildfire will affect native species and conservation planning is especially important for aquatic and moisture-sensitive species, such as amphibians, because large wildfires frequently occur during periods of extended drought (Westerling et al. 2006), when individuals may already be stressed (Pechmann et al. 1991; Lake 2003). In most cases, wildfire is likely not an immediate threat to the persistence of amphibian populations because individuals can seek refuge underground or in water (Russell et al. 1999), but numerous factors may interact after disturbance to reduce vital rates. Drought can cause cessation of breeding and eventual extirpation of isolated populations (Corn & Fogleman 1984; Church et al. 2007), and accelerated development triggered by drying water can reduce juvenile size and immune function (Semlitsch et al. 1988; Gervasi & Foufopoulos 2008). Individuals that disperse from disturbed areas, such as logged or burned forest, also face increased risk of desiccation and predation (Semlitsch et al. 2008; Rittenhouse et al. 2009). Persistent reductions in vital rates can cause gradual losses of populations (Ligon & Stacey 1996; Brooks et al. 1999); thus, it is important to measure responses across several wildfires and with long time series of data.

There is limited understanding of the effects of wildfire on amphibians in forests with long fire-return intervals because the few published studies have been short-term and often considered a single wildfire. Since 1988, several large wildfires have burned areas in Glacier National Park (Montana, U.S.A.), where we monitored wetland occupancy of the long-toed salamander (*Ambystoma macrodactylum*), Columbia spotted frog (*Rana luteiventris*), and boreal toad (*Anaxyrus boreas*). Although these species breed primarily in temporary wetlands, their terrestrial ecology differs. Like most ambystomatids, long-toed salamanders are fossorial after breeding and are likely limited to areas near wetlands (Rittenhouse & Semlitsch 2007). The Columbia spotted frog (hereafter, spotted frog) is highly aquatic, but often moves seasonally among different water bodies to breed, forage, and hibernate (Werner et al. 2004). The boreal toad hibernates terrestrially; thus, relative to the spotted frog it is less dependent on water (Werner et al. 2004). Occupancy of these 3 species did not decline in the 3 years after a 2001 wildfire in Glacier National Park (Hossack & Corn 2007); however, the severity of this fire was low and the length of the study was likely too short to detect time-lagged effects.

We used additional long-term monitoring data to evaluate whether burn extent and severity and interactions between wildfire and wetland isolation or forest structure affected occupancy of these 3 species. Specifically, we predicted the long-toed salamander would decline gradually after wildfire, especially in areas that burned severely and had few wetlands. We predicted no change to occupancy of spotted frog except where populations were most isolated. If dispersal is risky in a burned landscape, isolation should increase extinction risk (e.g., Brown & Kodric-Brown 1977). Finally, we expected a postfire increase in boreal toad occupancy, but only in low-elevation forests. This species is rare in low-elevation dense forests but common in high-elevation subalpine forests and tundra meadows (Hossack et al. 2006), and it often responds positively to disturbance (Crisafulli et al. 2005; Pearl & Bowerman 2006). Collectively, these

long-term data are critical for forming accurate assessments of how current and future wildfire regimes might affect the distribution and population dynamics of wetland-associated amphibians.

Methods

Study Area

We focused on 6 stand-replacing wildfires that occurred on the west side of Glacier National Park between 1988 and 2003 (Table 1 & Fig. 1). Four wildfires occurred primarily in low-elevation areas (Red Bench, Moose, Robert, and Middle Fork fires; wetland elevations 982–1464 m) and burned dense coniferous forests. These forests were historically replaced by fire every 140–340 years (Barrett et al. 1991). Two wildfires occurred at high elevation (McDonald Creek and Trapper Creek fires; wetland elevations 1867–2133 m) in areas of open, subalpine forests established in approximately 1735 (Barrett 1988). Because of the naturally long fire intervals, fire suppression has not greatly altered the natural succession of most forest stands in this area (Barrett 2002).

Sampling Design

To measure whether amphibian occupancy changed in response to wildfires, we surveyed wetlands within each of the 6 wildfire perimeters and all neighboring, unburned reference wetlands outside of each wildfire perimeter. Areas surveyed before 2002 were part of a long-term monitoring program and were selected without respect to wildfire boundaries (Corn et al. 2005). After the 2001 Moose fire and subsequent 2003 wildfires burned areas where we had data on amphibian occupancy (Table 1), we incorporated these areas into our annual monitoring program so we could determine whether wildfire affected the distribution of amphibians. To provide a longer-term perspective on changes in amphibian

occupancy after wildfire, we also surveyed wetlands in and adjacent to areas burned by the 1988 and 1998 wildfires (Table 1).

Logistical and environmental constraints limited sampling efforts in some years, so we did not sample wetlands associated with all wildfires in all years. But each year we sampled wetlands associated with a particular wildfire, we surveyed both unburned reference and burned wetlands to provide a representative measure of occupancy. Reference wetlands had not burned since at least 1967; most had not burned in over 80 years before our surveys.

We used dip nets to sample 268 wetlands for the 3 focal species. We captured amphibian larvae along the perimeter and in shallow areas (≤ 0.5 m depth) of each wetland (Corn et al. 2005). We considered a wetland occupied only if we detected embryos, larvae, or recently metamorphosed juveniles. Most wetlands were sampled twice per summer (<2 weeks between surveys). During each visit to a wetland, we recorded habitat characteristics that we expected would affect occupancy or detection of amphibians: wetland size, maximum depth, extent of emergent vegetation, and percent of each wetland ≤ 0.5 m deep (Corn et al. 2005). Wetlands ranged in size from 0.01 to 15.6 ha (median = 0.10 ha); most were <1 m maximum depth. Most of these wetlands fill from snowmelt and rain in the spring, support extensive emergent vegetation (primarily *Carex* spp.), and are dry by mid-August.

Spatial Analyses

We used a geographic information system (ArcGIS 9.2) to measure landscape characteristics that we expected could affect presence of amphibians. All characteristics were measured in 500-m areas around the perimeter of wetlands. In a related study in the same area, we used data from 500-m and 2-km wetland areas and found nearly identical relations between environmental variables and amphibian abundance (B.R.H., W.H.L., R.K.H., S.A.P., and

Table 1. Wildfires in Glacier National Park, Montana (U.S.A.) sampled to measure changes in wetland occupancy by amphibians.

Wildfire	Fire size (ha)	Wetlands surveyed (unburned/ burned)	Area severely burned (%)*	Years sampled
1988 Red Bench	14,584	11/21	51.3 (4.9–83.8)	2001–2005, 2008–2009
1998 McDonald Creek	3544	6/9	28.9 (2.0–80.2)	2001–2002, 2004–2009
2001 Moose	28,574	41/42	17.5 (0.1–70.4)	1999–2006, 2008–2009
2003 Middle Fork	4855	4/9	0.40 (0.0–1.5)	2001, 2004–2009
2003 Robert	21,908	17/92	38.9 (0.4–98.9)	1999–2009
2003 Trapper Creek	7446	6/10	46.9 (1.7–78.7)	2001–2002, 2004–2009

Mean (range in parentheses) area that was severely burned within a 500-m radius of the wetland.
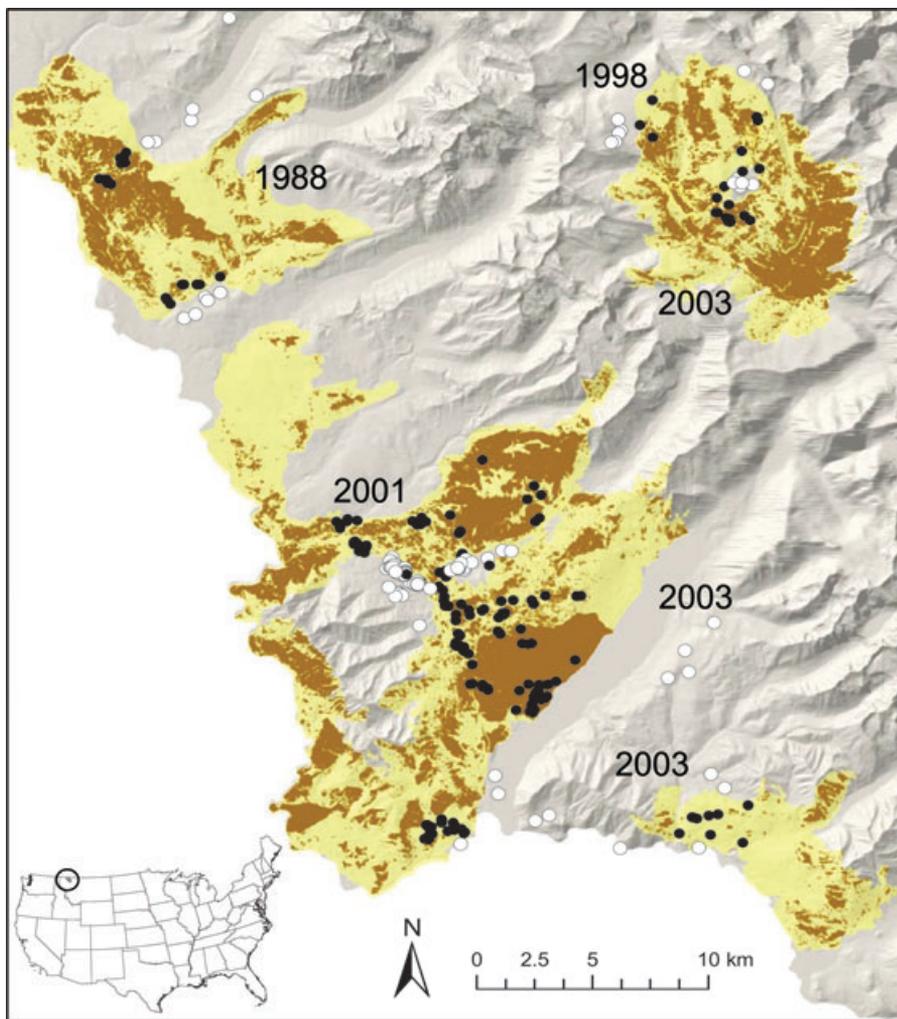
Figure 1. Location of 85 unburned wetlands (white circles) and 183 burned wetlands (black circles) associated with 6 wildfires that occurred in Glacier National Park, Montana (U.S.A.), between 1988 and 2003 (dark brown, severely burned areas; beige, burns of low or moderate severity).

P.S.C., unpublished manuscript). We obtained information on wildfires from the Monitoring Trends in Burn Severity project (MTBS), which uses pre- and postfire Landsat satellite imagery to delineate fire perimeters and quantify burn severity for each 30-m pixel (Eidenshink et al. 2007). We considered that pixels with differenced normalized burn ratio (dNBR) values between 550 and 1300 (Key & Benson 2006) were exposed to high-severity fire. The dNBR is derived from changes in vegetation after fire. We used National Wetlands Inventory (2008) data to measure area of wetlands within 500 m of wetland perimeters (USFWS 2008).

Statistical Analyses

To determine whether wildfire resulted in changes to amphibian occupancy, we organized data by wetland and on the basis of years before and after wildfire. For example, for the 2003 Robert fire, we coded surveys conducted in 1999 as 4 years prefire, surveys conducted immediately before the fire as 0 years prefire, and surveys conducted

in 2009 as 6 years postfire. This coding scheme resulted in 5 seasons of prefire data and 17 seasons of postfire data that corresponded to 4 years before a wildfire to 21 years after a wildfire. This hybrid space-for-time approach allowed us to model occupancy as a function of wildfire and time-since-fire simultaneously across data sets from each of the 6 wildfires.

We used the multiseason implicit-dynamics model in Presence (version 3.1) to account for variation in detection probability of each species and produce unbiased estimates of occupancy (Hines 2006; MacKenzie et al. 2006). The implicit-dynamics model applies a single-season occupancy model to each season of data and does not estimate local colonization or extinction rates. This model assumes wetlands are closed to changes in occupancy within a season, but allows for changes in occupancy between seasons.

We used a multistage modeling approach to identify the most parsimonious set of covariates to describe variation in detectability and occupancy for each species before evaluating hypotheses of interest. First, we modeled

detectibility for each species by evaluating the effect of wetland size (normalized), vegetative cover, maximum wetland depth, and percent of each wetland that was ≤0.5 m deep. Also, we made the a priori decision to include a wildfire as a detection covariate in all models to account for bias related to burn status. After identifying the detection model with the smallest Akaike information criterion (AIC) for each species (Burnham & Anderson 2002), we evaluated the effects of the same habitat covariates plus wetland elevation on the probability of wetland occupancy. Elevation was coded as low (982–1464 m) or high (1867–2133 m) to account for elevation-related variation in habitat. For each species, we added all habitat covariates to the best detection model and eliminated variables until we identified model that minimized AIC. This process resulted in a basic detection and occupancy model for each species that we used as the basis to measure support for hypotheses about the effects of wildfire and wetland isolation.

We expected the presence of neighboring wetlands would increase the probability that a wetland was occupied by the long-toed salamander and spotted frog. Therefore, we included area of wetland habitat within 500 m of the perimeter of each surveyed wetland as an occupancy covariate in all models, except in the basic habitat model described above and in an intercepts-only model. We did not estimate the effect of wetland isolation on toad occupancy. On the basis of 11 years of surveying wetlands in Glacier NP and previous descriptions of toad responses to wildfire and other disturbances (Crisafulli et al. 2005; Pearl & Bowerman 2006; Hossack & Corn 2007), we did not expect isolation would affect toad occupancy at the scale of our study.

We used a before-after-control-impact (BACI) design to evaluate changes in amphibian occupancy after wildfire (Underwood 1992). For long-toed salamanders and spotted frogs, we started with the basic habitat and detection model described above and added a location term that described whether a wetland was inside or outside a fire perimeter and a time effect that corresponded to the number of seasons before or after a wildfire. In this same model structure, we then added a location × time term (hereafter, burn effect) that measured the effect of wildfire on occupancy. To determine whether the effect of wildfire differed on the basis of isolation, we fit a subsequent model with a burn effect × isolation interaction term. We used this same model structure to estimate occupancy as a function of the amount of severely burned forest within 500 m of wetlands, the result of which was 4 models of changes in mean prefire (1–5 seasons) and postfire (1–21 seasons) occupancy that included additive and interactive effects of isolation.

We used the same models to estimate postfire occupancy separately for 2 categories of postfire recovery: 1–6 years after wildfire and 7–21 years after wildfire.

These separate postfire estimates allowed for detection of nonlinear responses over time, like those that may be expected from a gradual decline or a temporary decline-and-recover response (Whelan et al. 2002). We chose these time periods because 6 years after fire represents the longest continuous time series of data for any fire in our dataset (the 2003 Robert fire), and because it encompasses at least 1 generation for each species.

We used a similar modeling approach to estimate occupancy of boreal toads as a function of wildfire, but did not include isolation effects in any models. Instead, on the basis of prior knowledge of the study system (Burnham & Anderson 2002), we expected different population responses between open forests at high elevations and dense forests at low elevations, similar to responses of many bird species that differ according to forest structure before wildfire (e.g., Kotliar et al. 2002). To measure responses at different elevations, we included burn effect × elevation and burn severity × elevation interactions. Results of previous analyses show transient occupancy dynamics after wildfire are driven by changes in colonization and extinction (Hossack & Corn 2007), so we estimated occupancy separately for postfire seasons 1–3, 4–6, and 7–21 years in addition to the basic prefire versus postfire models.

In total, we fit 12 models for each of the 3 species. All burn-effects models were parameterized so that we estimated the effect of wildfire (including interaction terms) with its own intercept and slope for each time period. We measured support for models with differences in AIC and Akaike weights (w_i), which represent the probability that a particular model is the best for a set of data and fitted models (Burnham & Anderson 2002).

Results

In the basic detection and occupancy model we used as the starting point before estimating effects of wildfire, occupancy of long-toed salamanders was negatively related to elevation ($b = -1.99$ [SE = 0.27]) and positively related to wetland vegetation ($b = 2.19$ [0.34]) (Supporting Information). Detection probability for long-toed salamanders increased from 0.82 (0.03) before wildfire to 0.89 (0.01) after wildfire, but it increased equally in unburned and burned wetlands. The 5 models we fitted with 3 time periods received almost all model support, which indicated occupancy differed between pre- and postfire periods and between the 2 postfire periods (1–6 years after fire and 7–21 years after fire, respectively). The best model for salamanders showed that occupancy did not differ with regards to burn severity during the first 6 years following fire, but 7–21 years after fire it decreased, especially in areas with extensive high-severity fire (Table 2 & Fig. 2a). Models that described salamander occupancy as simply a function of time and space

Table 2. Models used to estimate the effects of burn extent and severity on wetland occupancy (Ψ) by breeding populations of the long-toed salamander (*Ambystoma macrodactylum*) after accounting for the effects of wetland elevation, vegetation, and wetland isolation.[*]

Model	Time	$-2log(L)$	k	ΔAIC	w_i
Ψ (elevation, vegetation, isolation, severity)	3	2186.96	12	0.00	0.57
Ψ (elevation, vegetation, isolation, location)	3	2193.29	10	2.33	0.18
Ψ (elevation, vegetation, isolation, burned)	3	2189.35	12	2.39	0.17
Ψ (elevation, vegetation, isolation, severity, isolation × severity)	3	2191.09	13	6.13	0.03
Ψ (elevation, vegetation, isolation, burned, isolation × burned)	3	2191.48	13	6.52	0.02
Ψ (elevation, vegetation)	1	2206.18	6	7.22	0.02
Ψ (elevation, vegetation, isolation, severity, isolation × severity)	2	2199.12	11	10.16	0.00
Ψ (elevation, vegetation, isolation, severity)	2	2201.31	10	10.35	0.00
Ψ (elevation, vegetation, isolation, burned)	2	2203.64	10	12.68	0.00
Ψ (elevation, vegetation, isolation, location)	2	2205.85	9	12.89	0.00
Ψ (elevation, vegetation, isolation, burned, isolation × burned)	2	2204.59	11	15.63	0.00
Ψ (.)	1	2489.53	2	282.57	0.00

[*]*We used the same detection structure (P) for all models (P [location, before vs. after wildfire]) except for the intercepts-only model, where P(.).Key: $-2log(L)$, -2 log-likelihood; k, number of model parameters; AIC, Akaike information criterion; ΔAIC, difference in the AIC between a particular model and the top-ranked model.*

(no fire effect) or that described variation in occupancy as a function of wildfire extent received moderate support (Table 2). Models that included interactions between fire effects and wetland isolation received little support (Table 2), likely because isolation by itself was only weakly associated with occupancy (0.04 [0.10]).

Occupancy of the spotted frog increased as a function of wetland size (4.32 [SE 0.56]) and vegetation (1.92 [0.35]) and was negatively related to elevation (−1.33 [0.46]) (Supporting Information). Detection probability was a function of wetland size (−0.51 [0.12]) and increased from 0.77 (0.05) before wildfire to 0.88 (0.02) after wildfire and increased to a greater extent after fire in burned wetlands. More-isolated wetlands were also more likely to be occupied (0.21 [0.09]). The top-ranked model for the spotted frog was clearly the best of the set ($w_i = 0.96$) (Supporting Information) and described occupancy as an interaction between time-since-fire and burn severity. Occupancy was not affected by burn severity in the first 6 years after wildfire, but it decreased as a function of the amount of high-severity burns near wetlands 7–21 years after fire (Fig. 2b). The second-ranked model for this data set described stable occupancy in unburned sites, but showed a small increase in occupancy for burned sites 1–6 years after wildfire and then decrease for 7–21 years after fire. These results are similar to the burn-severity model.

Occupancy of boreal toads increased as a function of elevation (4.28 [SE 0.39]), wetland size (0.66 [0.20]), and vegetative cover (0.62 [0.51]) (Supporting Information). Detection was high across the study period, but it decreased from 0.95 (05) to 0.90 (0.02) after wildfire because detection probability decreased in wetlands that burned. The model that described occupancy as an interaction between burn extent and elevation was clearly the best model ($w_i = 0.99$) (Supporting Information). At low elevations, occupancy increased substantially in the first 3 years after fire and then gradually declined 4–6 and 7–21 years after wildfire (Fig. 3a). The increase in the first 3 years was driven by colonization of previously unoccupied wetlands the first year after wildfire. For example, in the areas burned by the 2003 Robert and Middle Fork wildfires, there was an approximate 10-fold increase in occupancy the first year after the area burned. But within 4 to 5 years after fire, occupancy returned to near prefire levels. In contrast, toads occupied most high-elevation wetlands regardless of wildfire (Fig. 3b). Occupancy in high-elevation wetlands declined in both burned and unburned wetlands over time, and these declines were slightly greater in burned wetlands.

Discussion

Changes in occupancy by breeding amphibians ranged from rapid increases by the boreal toad to time-lagged declines in occupancy by the long-toed salamander and spotted frog. Accounting for imperfect detection improved our ability to draw inferences related to the effects of wildfire, especially because detection for the spotted frog and boreal toad covaried with wildfire, but in
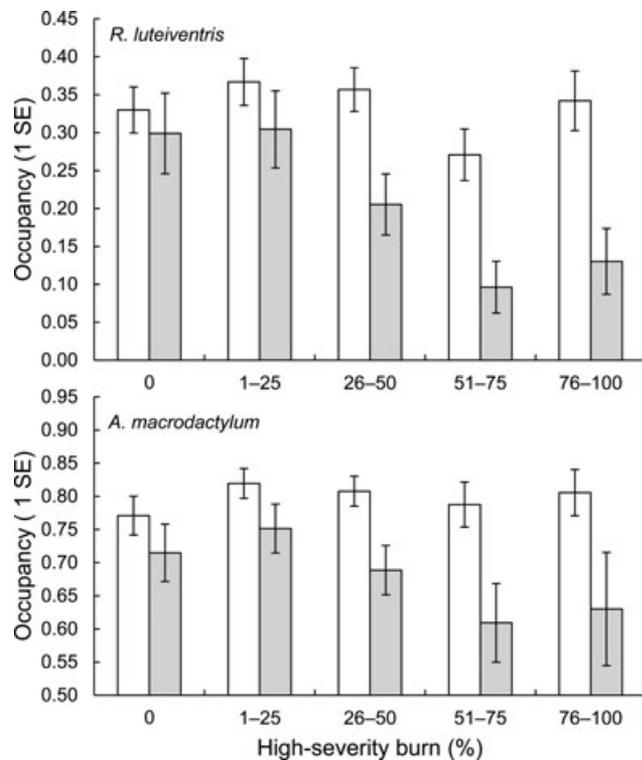
*Figure 2. Estimated occupancy (1 SE approximately) of the Columbia spotted frog (*Rana luteiventris*) and long-toed salamander (*Ambystoma macrodactylum*) relative to percentage of area that was severely burned within 500 m of wetlands (x-axis) during the first 6 years after wildfire (unshaded) and years 7–21 (shaded) after wildfire.*

*Figure 3. Estimated occupancy (1 SE approximately) of the boreal toad (*Anaxyrus boreas*) in unburned (unshaded) and burned wetlands (shaded) at low elevation (<1465 m) and high elevation (>1866 m) during the 5 summers before wildfire (years −4 to 0) and 1–21 years after wildfire (years 1–3, 4–6, 7–21).*

opposite directions. The relation between wildfire and occupancy of the long-toed salamander was weaker than for the spotted frog, but breeding populations of both species were less likely to occur in wetlands where burn severity was high. This severity effect was not evident for over 6 years. Declines in occupancy and extirpations after disturbance may not be evident for several years (e.g., Ligon & Stacey 1996; Findlay & Bourdages 2000). For example, severe drought and wildfire in eucalypt forests have been associated with persistent declines of small, ground-dwelling mammals and birds; the form and timing of responses also differ among species in these systems (Whelan et al. 2002; Recher et al. 2009; Kelly et al. 2011). Time-lagged reductions in occupancy for long-toed salamanders and spotted frogs suggest these changes were caused by reductions in vital rates rather than immediate extirpation.

Reduced colonization rates in disturbed or fragmented habitats can also be associated with time-lagged declines (Brown & Kodric-Brown 1977), but our data indicate habitat characteristics described more variation in occupancy than wetland isolation, regardless of burn severity. Occupancy of the long-toed salamanders was unrelated to

wetland isolation, perhaps because wetlands were abundant in our study area and salamanders occupied most potential breeding sites. Counter to our expectations, occupancy by spotted frogs increased with isolation in both unburned and burned areas. It is possible that measures of wetland isolation at 500 m, like those we used, are less useful for detecting demographic effects of isolation than measures at broader scales. However, the lack of an isolation effect is consistent with the results of studies that show turnover in occupancy of amphibians and other species is less common in intact landscapes than in fragmented landscapes (Marsh & Trenham 2001; Baguette 2004).

Mechanisms that drive population changes in amphibians after habitat disturbance are still not well understood. Removal of forest canopy and woody debris can reduce dispersal, survival, and other vital rates of juvenile amphibians (Semlitsch et al. 2009; Popescu & Hunter 2011). In areas where amphibian habitat is primarily of low quality, juveniles crowd into the few high-quality patches and experience strong density-dependent mortality (Patrick et al. 2008). A similar situation may exist in severely burned areas that lose woody debris and other cover, and population growth of long-toed salamanders

and spotted frogs is expected to be highly sensitive to reductions in juvenile survival (Biek et al. 2002; Vonesh & De la Cruz 2002). If survival of adults is also reduced, population growth would decline even more quickly, potentially increasing extirpation rates and resulting in the lower occupancy that we observed.

Because wetlands burned by the oldest fire (1988 Red Bench fire) were surrounded by the highest mean severity, it is difficult to separate the effect of time-since-fire and burn severity. For both species, however, occupancy was similar among wetlands surrounded by few areas that were severely burned in years 1–6 and 7–21 after wildfire. Furthermore, mean severity around wetlands in the 2003 Trapper Creek fire was similar to that of wetlands in the 1988 Red Bench fire. Many wetlands within the perimeter of the 2003 Robert fire also burned more severely than those surrounded by the 1988 fire. Sampling wetlands associated with 6 wildfires from a small geographic area with uniform management provided a level of spatial and temporal replication that is uncommon in studies of wildlife responses to wildfire. Therefore, it seems unlikely that lower occupancy in areas that were severely burned reflect differences in habitat among areas.

In contrast to occupancy patterns of long-toed salamanders and spotted frogs, the response of boreal toads was rapid and positive and was driven by burn extent rather than severity. Boreal toad occupancy increased greatly during the first 3 years after wildfire in low-elevation forests and then decreased to near prefire levels 7–21 years after wildfire. This postfire increase was driven by colonization of previously unoccupied wetlands the first year after wildfire, a pattern that has been documented after other disturbances (Crisafulli et al. 2005; Pearl & Bowerman 2006). More than 20 years after extensive wildfires in Yellowstone National Park (Wyoming, U.S.A.), boreal toad populations near burned forests had greater genetic connectivity than populations farther from burned areas (Murphy et al. 2010). This pattern is similar to the pattern of increased colonization after wildfire we found. Some endangered toads in Europe are more abundant where frequent disturbances maintain diverse vegetative structure (Denton et al. 1997; Tockner et al. 2006; Warren & Büttner 2008). We do not know what triggers the response of boreal toads, the source of colonists, or why occupancy declines rapidly after an initial postfire colonization phase. But this pattern is typical of species that increase in abundance after a change in resources. Although changes in resources may be temporary, they can produce lasting effects on population structure and genetics (Whelan et al. 2002; Smucker et al. 2005).

Although the boreal toad and some other amphibians can respond positively to some disturbances, the response is context specific and cannot be generalized too broadly, as evidenced by the lack of change in occupancy after wildfire at high elevations. We suspect different responses at high elevations reflect changes effected by wildfire. Most low-elevation wetlands were embedded in dense forest, whereas high-elevation wetlands were in sparse forest or open meadows, where there was less change in canopy cover and insolation after wildfire. Similarly, responses of many birds to wildfire vary according to the magnitude of change caused by wildfire (Kotliar et al. 2002). Toads also bred in most high-elevation wetlands before wildfire.

Burn extent and severity distinctly affected the temporal and spatial patterns of amphibian occupancy. Wildfire was associated with increased occupancy of boreal toads, depending on forest structure. Our results and those of other researchers that show other species respond positively to wildfire reinforce the importance of maintaining natural disturbance regimes to maintain diverse biological communities (Russell et al. 1999; Smucker et al. 2005). We also found strong evidence of time-lagged declines in occupancy of the long-toed salamander and spotted frog, primarily in areas where >50% of the forest within 500 m of wetlands was severely burned. Only 30% of burned wetlands crossed this 50% threshold; thus, populations in areas that burned less severely could provide sources to recolonize wetlands where populations were extirpated. Because native species in the region evolved in ecosystems shaped by large disturbances (McKenzie et al. 2004), this pattern of temporary decline and recovery after large disturbances is not unexpected. However, measuring patterns of decline and recovery in protected landscapes is essential for predicting how species may respond to these disturbances. More importantly, our data highlight potential negative effects of expected changes to climate-associated disturbance regimes. Extending research outside of protected landscapes will be critical for predicting where and under what conditions wildfire is a significant threat to populations and for prioritizing conservation efforts.

Acknowledgments

Supporting Information

Occupancy and detection parameters from models used to measure the effect of wildfire on the distribution of 3 amphibian species (Appendix S1) and a list of occupancy models for the spotted frog (Appendix S2) and boreal toad (Appendix S3) are available online. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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