



Short communication

Declines revisited: Long-term recovery and spatial population dynamics of tailed frog larvae after wildfire



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ABSTRACT

Drought has fueled an increased frequency and severity of large wildfires in many ecosystems. Despite an increase in research on wildfire effects on vertebrates, the vast majority of it has focused on short-term (< 5 years) effects and there is still little information on the time scale of population recovery for species that decline in abundance after fire. In 2003, a large wildfire in Montana (USA) burned the watersheds of four of eight streams that we sampled for larval Rocky Mountain tailed frogs (*Ascaphus montanus*) in 2001. Surveys during 2004–2005 revealed reduced abundance of larvae in burned streams relative to unburned streams, with greater declines associated with increased fire extent. Rocky Mountain tailed frogs have low vagility and have several unusual life-history traits that could slow population recovery, including an extended larval period (4 years), delayed sexual maturity (6–8 years), and low fecundity (< 50 eggs/year). To determine if abundance remained depressed since the 2003 wildfire, we repeated surveys during 2014–2015 and found relative abundance of larvae in burned and unburned streams had nearly converged to pre-fire conditions within two generations. The negative effects of burn extent on larval abundance weakened > 58% within 12 years after the fire. We also found moderate synchrony among populations in unburned streams and negative spatial autocorrelation among populations in burned streams. We suspect negative spatial autocorrelation among spatially-clustered burned streams reflected increased post-fire patchiness in resources and different rates of local recovery. Our results add to a growing body of work that suggests populations in intact ecosystems tend to be resilient to habitat changes caused by wildfire. Our results also provide important insights into recovery times of populations that have been negatively affected by severe wildfire.

1. Introduction

Changes in precipitation regimes and increased temperatures have intensified drought and increased the frequency and severity of large-scale disturbances (Dennison et al., 2014; IPCC, 2014). Increases in drought severity and length often lead to large, severe wildfires that alter habitats and affect the distribution and abundance of wildlife (McKenzie et al., 2004; Morgan et al., 2008; Swanson et al., 2011). However, we still know little about short-term effects of wildfire on many vertebrates, and we know even less about long-term effects (Fontaine and Kennedy, 2012). Furthermore, short-term and long-term measures of species' responses can sometimes provide surprisingly different results (Evans et al., 2017; Hossack et al., 2013a).

Population-level effects of wildfire on amphibians depend upon many interrelated factors, including the frequency and severity of burns, habitat isolation, management history of the landscape, and the persistence of habitat change that results from fire (Hossack et al., 2013b; Hossack and Pilliod, 2011; Westgate et al., 2012). Further,

declines in occupancy and extirpations of wildlife after disturbance may not be evident for several years. For example, following a series of wildfires in the Rocky Mountains, reductions in wetland occupancy of some amphibian species were not evident for > 6 years (Hossack et al., 2013a). Collectively, these studies show that responses—whether negative or positive—are strongly context dependent.

Despite the increased knowledge of wildfire effects on amphibians and other vertebrates, few studies have addressed the temporal scale of post-fire population recovery. Highly-mobile species such as many birds and fishes often quickly recolonize areas where they were extirpated (Bixby et al., 2015; Dunham et al., 2007; Smucker et al., 2005). However, species with narrow environmental tolerances and low rates of dispersal and population growth, including many headwater stream amphibians, are vulnerable to changes in habitat such as increased water temperature and sedimentation that can occur after wildfire (Corn et al., 2003; Green, 2003; Welsh and Ollivier, 1998). For example, Rocky Mountain tailed frogs (*Ascaphus montanus*) are limited to permanent streams because the larvae require approximately 4 years to

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metamorphose. This species is also among the slowest anurans to reach maturity (6–8 years after hatching), it is long-lived (> 14 years), and females have low fecundity (< 50 eggs/year) (Daugherty and Sheldon, 1982). These life history traits and habitat associations could limit recovery. But they also make tailed frogs and other stream amphibians ideal models for studying disturbances (Green, 2003; Welsh and Ollivier, 1998).

In 2003, a large wildfire in western Montana (USA) burned four of four watersheds (hereafter burned or unburned streams) where we sampled for larval tailed frogs. The Robert Fire was one of six large wildfires in the park that summer, when severe drought dried forest fuels to record low levels and contributed to the park's largest fire season on record. Post-fire sampling during 2004–2005 revealed a reduction in abundance of larvae in burned relative to unburned streams, possibly because of limited recruitment that was evident by skewed age distributions (Hossack et al., 2006). To determine if abundance of larvae had recovered since 2004–2005, we re-sampled the same eight streams during 2014–2015. We also investigated patterns of population synchrony to determine how fire affected local spatial population dynamics.

2. Materials and methods

2.1. Study system

The Robert Fire was ignited by an escaped campfire on 23 July 2003 on the Flathead National Forest and entered the west side of Glacier National Park later that day, burning 16,527 ha inside the park (Fig. 1). The fire burned mixed conifer forests that have a mean fire frequency interval of 140–340 years (Barrett et al., 1991). Seven of the eight streams were inside the park, where forests have not been logged since at least 1910, when the park was established. One unburned stream (Pinnacle Creek) was on US Forest Service land that is managed for multiple uses, including timber harvest (Fig. 1).

On three of four burned streams, the sampled reaches were severely burned, leaving little understory vegetation. The sampled reach on Apgar Creek did not burn because it was near residential and administrative buildings that received fire suppression efforts; otherwise, this watershed was the most thoroughly burned. The burned and unburned catchments were similar before the fire (Table 1), except Sprague Creek flows through a temperate rain forest. All streams had mean gradients > 5% and had riffle–pool or step–pool morphologies dominated by cobble and boulder substrates.

2.2. Data collection

We originally sampled the eight streams during June 2001 to evaluate a time-constrained method for potential inclusion in a monitoring program. We sampled streams by turning rocks and disturbing the substrate in front of D-frame nets for 250 min, with surveyors progressing upstream. Surveyors focused on areas of optimal habitat (e.g., turbulent water, coarse substrates) to increase the likelihood of capturing larvae. Two surveyors sampled simultaneously for 5-min each (making one 10-min period) and called out captures to a data recorder. Surveyors alternated roles every five sampling periods. We excluded juveniles and adults from analyses because they use stream and forest habitats and are not sampled efficiently (Hossack et al., 2006).

After the 2003 fire burned four of the watersheds, we resurveyed the eight streams during 2004 and 2005 to evaluate the near-term effects of wildfire and again in 2014 and 2015 to evaluate population recovery. We used the same sampling methods and approximate starting point and sampled approximately the same distance in each stream, each year. All surveys were conducted after the peak of runoff.

2.3. Analyses

To measure the effects of the fire, we fit two linear mixed-effects models to test for changes in abundance of larvae in burned streams compared to unburned streams (package nlme in program R 3.3.1; Pinheiro et al., 2016). The first model included fixed effects of Fire, YearGroup, and a YearGroup \times Fire interaction. The Fire term designated whether a stream was within or outside of the (eventual) perimeter of the 2003 fire. YearGroup corresponded to counts in each stream during 2001, 2004–2005, and 2014–2015. The second model was structured the same as the first but used proportion of catchment burned (ProportionBurned; range: 0.17–0.98) as a predictor variable instead of designating catchments simply as burned or unburned. For both models, an effect of fire on relative abundance would be evident by non-zero interactions.

Prior to analyses, we centered the response data for each year by calculating the mean captures from all eight streams and subtracting that value from each stream's count. This step helped emphasize that our focus was on changes in abundance in burned streams relative to abundance in unburned streams, not trends in overall abundance, per se (Stewart-Oaten et al., 1986). We used random intercepts with compound symmetry correlation to account for repeated sampling of the same streams and assumed that sampling error was equal in burned and unburned streams (Pinheiro et al., 2016). Based on the sampling design and small number of streams, we are unaware of a way to explicitly incorporate detection error into models. We used a much more intensive sampling method than is typical for stream amphibians (e.g., Corn et al., 2003; Welsh and Ollivier, 1998), however, which increases the probability of acquiring a representative sample.

To ensure that our results were not confounded by positive spatial autocorrelation in abundance (i.e., population synchrony), we used a Mantel test to evaluate population synchrony (Pearson's correlation coefficient, r) based on log-transformed counts of larvae (range: 28–390) and Euclidean distance for all pairs of streams (R package APE; Koehnig, 1999; Paradis et al., 2004). We also compared population synchrony based on the burn status of stream pairs to determine if wildfire affected temporal variation in abundance between streams.

3. Results

In 2001, we captured an average of 15.38 (SE = 46.41) more larvae in streams that eventually burned versus those that did not (Fig. 2). The wildfire affected relative abundance of larvae, as indicated by significant YearGroup \times Fire ($F_{2,28} = 4.15$, $p = 0.027$) and YearGroup \times ProportionBurned interactions ($F_{2,28} = 3.98$, $p = 0.031$). These interactions reflect reduced captures of larvae in burned streams during 2004–2005 relative to pre-fire conditions (mean difference = -145.50 [56.77], $t_{28} = -2.56$, $p = 0.016$) that corresponded to the proportion of each catchment that burned ($b = -178.03$ [72.10], $t_{28} = -2.47$, $p = 0.020$). By 2014–2015, burned streams averaged only 67.75 (56.77) fewer captures than unburned streams, which did not differ from the relative difference in 2001 ($t_{28} = -1.19$, $p = 0.243$). There was still a negative relationship between proportion of a catchment burned and larval abundance in 2014–2015, but it was > 58% weaker ($b = -75.75$ [72.10], $t_{28} = -1.05$, $p = 0.302$) than in 2004–2005.

The distance between pairs of streams ranged from 1.11 km (McGee Creek and Fish Creek) to 56.96 km (McGee Creek and Autumn Creek), and the mean distance between burned streams was 6.15 km compared to 34.46 for unburned streams (Fig. 1). Abundance of larvae was positively correlated between all pairs of streams of the same burned status (both burned or unburned; mean $r = 0.47$, range: 0.03–0.81). Despite the close proximity of the four burned streams, there was no evidence of positive spatial autocorrelation across the study area (Mantel test: $z = 189.95$, $p = 0.516$). Population synchrony was greater in unburned streams ($r = 0.55$) than where both streams

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