EFFECTS OF THE KENOW WILDFIRE ON AMPHIBIAN POPULATIONS IN WATERTON LAKES NATIONAL PARK

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EFFECTS OF A SEVERE WILDFIRE ON AMPHIBIAN POPULATIONS IN WATERTON LAKES NATIONAL PARK

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ABSTRACT

As extreme events become more common, understanding how they impact wildlife populations, and imperiled wildlife populations in particular, is of heightened importance. In this thesis, I aimed to characterize how a very severe wildfire impacted amphibian populations in Waterton Lakes National Park in southwestern Alberta, Canada. In chapter one, I first reviewed the literature, highlighting gaps in our understanding of the impacts of wildfire on amphibian populations. I then conducted two studies to address a number of these gaps. Specifically, in chapter two, I investigated potential changes to breeding pond occupancy and species richness for four amphibian species in response to the Kenow wildfire. In chapter three of this thesis, I quantified changes to genetic diversity in long-toed salamanders using tissues collected in both burnt and unburnt parts of the park at time points spanning this severe wildfire. My results suggest that the Kenow wildfire did not have a major impact on amphibian occupancy in Waterton Lakes National Park. I further found that, although levels of genetic diversity changed for some sites across time points, the magnitude and direction of change varied considerably among sites, including among sites in both burnt and unburnt parts of the park. Altogether, these results suggest that the amphibian populations studied here were mostly unaffected by the wildfire. However, downward trends in occupancy and signatures of increased inbreeding for long-toed salamanders in the burn zone, highlight the need for continued monitoring of these populations and for evaluation of potential longer-term impacts of the Kenow wildfire on amphibians in the park.

PREFACE

The (modified) text presented in Chapter 2 of this thesis was submitted for peer-reviewed publication in October 2022 and at time of thesis submission was under review. I am the lead author on this manuscript. Lea Randall from the Calgary Zoo taught me about some of the analysis techniques, specifically those with the formal occupancy modelling software “PRESENCE”. Kim Pearson and Helena Mahoney provided the data for the analyses and informed me on specifics on the collection of the monitoring data and other details specific to Waterton Lakes National Park. Dr. Julie Lee-Yaw provided guidance during the design and execution of the study and writing support during manuscript preparation. All authors provided feedback on the manuscript before submission to the journal. Tissues to produce the genetic data presented Chapter 3 were collected in the summers of 2009 and 2020 in Waterton Lakes National Park under Parks Canada Agency Research and Collection Permit (permit nos. JP-2009-2252 and WL-2020-35977). Animal handling was performed under Animal Care permits (A07-0632 issued by the University of British Columbia for the 2009 collection and permit no. 1912 issued by the University of Lethbridge for the 2020 collection).

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CHAPTER 1: INTRODUCTION

1.1. The emerging need to understand the impact of extreme events on wildlife populations

Extreme events such as droughts, floods, heatwaves, and severe wildfire are increasing in frequency around the globe (Easterling *et al*., 2000; IPCC, 2014; Jentsch *et al*., 2007; Papalexiou and Montanari, 2019; Ummenhofer and Meehl, 2017). Such events may lead to both direct mortality of wildlife (*e.g.* Webb and Shine, 2008) and changes to habitat (*e.g.* Saracco *et al*., 2018; Schultz *et al*., 2007). Therefore, extreme events have the capacity to impact populations (*e.g.* Maxwell *et al*., 2019; Palmer *et al*., 2017), communities (Husson *et al*., 2022; Robson *et al*., 2018; Saracco *et al*., 2018), and entire ecosystems (Harris *et al*., 2018). As a result, extreme events may represent a key driver in shaping regional biodiversity and may pose a threat to imperiled taxa (Maron *et al*., 2015). Evaluating how populations and communities respond to extreme events is thus of increasing interest in biodiversity science (Bailey and van de Pol, 2016), and of pressing importance for conservation (Maxwell *et al*., 2019).

Globally, amphibians are the most threatened group of vertebrates, with up to 40% of species facing extinction (IUCN 2022; Wake, 2012). Although threats to amphibian populations are multifaceted (Grant *et al*., 2016; Hof *et al*., 2011), climate-related threats are of particular concern for amphibian conservation (Hoff *et al*., 2011; Wake, 2012). Changing climates have the potential to push aquatic breeding environment temperatures beyond what many species can tolerate (Duarte *et al*., 2012), affect pond hydroperiods (Pilliod *et al*., 2003), reduce terrestrial moisture levels (Hossack *et al*., 2009), and amplify the effects of amphibian pathogens (Hof *et al*., 2011). Extreme events associated with climate change may more acutely impact amphibian populations (Maxwell *et al*., 2019). Yet, studies addressing the effects of extreme events on amphibian populations and communities are limited, with most research focused on the effects of drought on occupancy and occurrence (*e.g.* Mac Nally *et al*., 2017; Moss *et al*., 2021; Scheele *et* *al*., 2013). Less is known about the how other types of extreme events impact this sensitive taxonomic group. In this thesis, I investigate the effects of a severe wildfire on amphibian populations in western North America, thereby adding to our understanding of the impact of climate change on amphibian populations.

1.2. Amphibians and wildfire: A review

Two seminal reviews have synthesized the literature with respect to amphibian responses to fire. Pilliod *et al*. (2003) reviewed published accounts of amphibian responses to fire and outlined potential direct and indirect effects of fire on amphibians. They found that amphibian responses to fire were highly variable among species and regions and that most species that responded to fire, responded positively (Pilliod *et al*., 2003). However, as the authors noted, most studies in their review were based on the response of species to prescribed burns (Pilliod *et al*., 2003), which are typically conducted during wetter seasons, are generally of low severity, and therefore have different effects from wildfire (Arkle and Pilliod, 2010). In a subsequent review, Hossack and Pilliod (2011) reviewed studies examining the response of amphibians in western North American to wildfire specifically. They categorized the response of species as positive, negative, or neutral (Hossack and Pilloid, 2011). They observed considerable variation in the direction of species' responses and proposed that habitat preferences explain some of this variation (Hossack and Pilliod, 2011). For instance, whereas pond-breeding species fared relatively well in the face of wildfire, terrestrial breeders (*i.e.* plethodontid salamanders) and stream-breeding amphibians often fared poorly (Hossack and Pilliod, 2011; also reported by Pilliod *et al*. 2003). However, most of the studies included in these reviews were limited to the United States. Furthermore, very few of these studies investigated wildfires of the type of magnitude becoming more common under shifting wildfire regimes.

More than a decade has passed since these two reviews. To update our understanding of amphibian responses to wildfire, I conducted a forward-in-time Web of Science search for studies that cited either Pilliod *et al*. (2003) or Hossack and Pilliod (2011), or both. Although this is not an exhaustive search, studies retrieved by this search should allow for an assessment of any general patterns that have emerged for this group in the recent literature. As per Hossack and Pilliod (2011), I limited my review to the effects of wildfire on amphibians. However, unlike previous reviews, I did not restrict my search to studies in North America. To be included in my review, studies had to have reported population-level responses to wildfire. Overall, 13 studies were returned by my search. These studies jointly reported information for 44 species-response combinations (Table 1). Below, I synthesize these reports, focusing on different types of population responses.

1.2.1. Occupancy and occurrence

The majority of recent studies examining the impacts of wildfire on amphibians focused on occupancy and/or occurrence (hereafter jointly referred to as "occupancy"; Table 2). With respect to the impacts of wildfire on occupancy, most species studied were either unimpacted by or responded positively to wildfire (Table 2). For example, in terms of positive responses, Hossack and Corn (2007) found that western toads (*Anaxyrus boreas*) colonized previously unoccupied wetlands following a wildfire in Montana, likely because of increased terrestrial temperatures in burnt habitat. In contrast, a species of tree frog (*Ischnocnema juipoca*) was not detected in any of the years following a severe wildfire in Brazil (Drummond *et al*., 2018).

Table 1. Recent studies examining amphibian responses to wildfire. Studies were retrieved through a Web of Science search of studies citing Pilliod *et al*. (2003) and Hossack and Pilliod (2011). Wildfire severity rating is based on assessment or descriptions given by the study authors. Direction of response refers to whether occupancy, abundance, vital rates, or genetic diversity increased (positive), stayed the same (neutral), or decreased (negative).

Response type*	**Species (or genus)**	**Order**	**Life-history**	**Wildfire Severity**	**Direction of Response**	**Location**	**Study**
Occupancy / Occurrence	*Ambystoma macrodactylum*	Urodela	pond breeding	mixed	neutral	Western U.S.	Hossack and Corn (2007)
Occupancy / Occurrence	*Aneides ferreus*	Urodela	terrestrial	moderate	negative	Western U.S.	Chelgren *et al*. (2011)
Occupancy / Occurrence	*Ascaphus montanus*	Anura	pond breeding	mixed	neutral	Western U.S.	Dunham *et al*. (2007)
Occupancy / Occurrence	*Batrachoseps wrighti*	Urodela	terrestrial	moderate	negative	Western U.S.	Chelgren *et al*. (2011)
Occupancy/ Occurrence	*Bufo boreas*	Urodela	pond breeding	mixed	positive	Western U.S.	Hossack and Corn (2007)
Occupancy/ Occurrence	*Dendropsophus minutus*	Anura	pond breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Ensatina eschscholtzii*	Urodela	terrestrial	moderate	negative	Western U.S.	Chelgren *et al*. (2011)
Occupancy / Occurrence	*Ischnocnema juipoca*	Anura	terrestrial	severe	negative	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Leptodactylus cunicularius*	Anura	pond breeding †	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Leptodactylus furnarius*	Anura	pond breeding †	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Leptodactylus fuscus*	Anura	pond breeding †	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Leptodactylus jolyi*	Anura	pond breeding	severe	neutral	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Leptodactylus latrans*	Anura	pond breeding	severe	neutral	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Physalaemus cuvieri*	Anura	pond breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Physalaemus erythros*	Anura	pond breeding†	severe	positive	Eastern Brazil	Drummond *et al*. (2018)

Occupancy / Occurrence	*Pithecopus ayeaye*	Anura	stream breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Plethodon dunni*	Urodela	terrestrial	moderate	negative	Western U.S.	Chelgren *et al*. (2011)
Occupancy / Occurrence	*Plethodon neomexicanus*	Urodela	terrestrial	mixed	neutral	Western U.S.	Cummer and Painter (2007)
Occupancy / Occurrence	*Plethodon vehiculum*	Urodela	terrestrial	moderate	negative	Western U.S.	Chelgren *et al*. (2011)
Occupancy / Occurrence	*Rana luteiventris*	Anura	pond breeding	mixed	neutral	Western U.S.	Hossack and Corn (2007)
Occupancy / Occurrence	*Rhinella crucifer*	Anura	pond breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Scinax curicica*	Anura	pond breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Scinax fuscovarius*	Anura	pond breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Scinax rogerioi*	Anura	pond breeding	severe	positive	Eastern Brazil	Drummond *et al*. (2018)
Occupancy / Occurrence	*Scinax squalirostris*	Anura	pond breeding	severe	neutral	Eastern Brazil	Drummond *et al*. (2018)
Abundance	*Ambystoma macrodactylum*	Urodela	pond breeding	mixed	negative	Western U.S.	Hossack *et al*. (2013a)
Abundance	*Anaxyrus houstonensis*	Anura	pond breeding	severe	neutral	Southern U.S.	Duarte *et al*. (2014)
Abundance	*Ascaphus montanus*	Anura	stream breeding	severe	negative	Western U.S.	Hossack and Honeycutt (2017)
Abundance	*Ascaphus montanus*	Anura	stream breeding	severe	negative	Western U.S.	Hossack *et al*. (2006)
Abundance	*Bufo (Anaxyrus/Incilius)*	Anura	pond breeding	mixed	neutral	Southern U.S.	Brown *et al*. (2014)
Abundance	*Desmognathus ocoee*	Urodela	terrestrial	mixed	negative	Eastern U.S.	Gould *et al*. (2022)
Abundance	*Eurycea wilderae*	Urodela	terrestrial	mixed	negative	Eastern U.S.	Gould *et al*. (2022)
	Gastrophryne						

Abundance	*spp.*	Anura	terrestrial	mixed	neutral	Southern U.S.	Brown *et al*. (2014)
Abundance	*Plethodon shermani*	Urodela	terrestrial	mixed	neutral	Eastern U.S.	Gould *et al*. (2022)
Abundance	*Rana luteiventris*	Anura	pond breeding	mixed	positive	Western U.S.	Hossack *et al*. (2013a)
Abundance	*Scaphiopus spp.*	Anura	pond breeding	mixed	neutral	Southern U.S.	Brown *et al*. (2014)
Vital Rates / Demographics	*Anaxyrus boreas*	Anura	pond breeding	mixed	neutral	Western U.S.	Barille *et al*. (2022)
Vital Rates / Demographics	*Ascaphus montanus*	Anura	stream breeding	severe	negative	Western U.S.	Hossack *et al*. (2006)
Vital Rates / Demographics	*Desmognathus ocoee*	Urodela	terrestrial	mixed	negative	Eastern U.S.	Gould *et al*. (2022)
Vital Rates / Demographics	*Eurycea wilderae*	Urodela	terrestrial	mixed	positive	Eastern U.S.	Gould *et al*. (2022)
Vital Rates / Demographics	*Plethodon neomexicanus*	Urodela	terrestrial	mixed	neutral	Western U.S.	Cummer and Painter (2007)
Vital Rates / Demographics	*Plethodon shermani*	Urodela	terrestrial	mixed	neutral	Eastern U.S.	Gould *et al*. (2022)
Vital Rates / Demographics	*Scaphiopus hurterii*	Anura	pond breeding	severe	positive	Southern U.S.	Brown *et al*. (2014)
Genetic diversity	*Hyla femoralis*	Anura	pond breeding	mixed	neutral	Southern U.S.	Robertson *et al*. (2018)

* Occurrence refers to presence or absence at specific localities, whereas occupancy refers a probability that a locality is occupied that applies to all sites on a landscape. Vital Rates/Demographics refers to changes in population statistics, population age structure, and measures of survivorship, recruitment, colonization and extirpation.

† Species lays eggs underground, but majority of larval development occurs in shallow wetlands (Colli *et al*., 2004; Nascimento *et al*., 2004; Reynolds *et al*., 2004; Caramaschi, 2004).

Table 2. Summary of recent studies looking at amphibian population-level responses to wildfire. See Table 1 for full set of studies.

Response-type	**Direction of response**			**Number of responses**
	Negative	Neutral	Positive	
Occupancy / Occurrence	6	8	11	25 (57%)
Abundance	5	5	1	11 (25%)
Population demography/Vital rates	2	3	2	7 (16%)
Genetic diversity	0	1	0	1 (2%)
Total	13 (30%)	17 (39%)	14 (32%)	44 (100%)

However, most of the cases reviewed here come from two studies, each of which focused on just a single wildfire in Oregon (Chelgren *et al*., 2011) and Brazil (Drummond *et al*., 2018) respectively. Thus it is difficult to draw additional general conclusions from studies published since Pilliod *et al*. (2003) and Hossack and Pilliod (2011). Nevertheless, results to date suggest that wildfires often have either neutral or positive effects on amphibian occupancy.

1.2.2. Abundance

Abundance was the second most common metric used to understand how amphibian populations respond to wildfire (Table 2). In contrast to occupancy, only one species responded positively to wildfire in terms of abundance. Specifically, Hossack *et al*., (2013a) reported that Columbia spotted frogs (*Rana luteiventris*) increased in abundance following a wildfire in Montana. In this case, the authors suggest that wildfire might have improved habitat quality by increasing wetland exposure to solar radiation (Hossack *et al*., 2013a). Roughly half of the cases reviewed reported no response to wildfire in terms of abundance (Table 1). However, an equal number of cases reported negative impacts of wildfire on amphibian abundance. Notably, majority of these decreases were reported for stream-breeding species (*i.e. Ascaphus montanus*; Hossack and Honeycutt, 2017) and terrestrial salamanders (*i.e.* plethodontid salamanders; Gould *et al*., 2022), consistent with a greater impact of wildfire on species with these life-history characteristics (Hossack and Pilliod 2011). Overall, these findings suggests that, in contrast to occupancy, amphibian responses to wildfire in terms of abundance are often neutral or negative. This suggests it may be insufficient to measure occupancy alone when characterizing the impacts of wildfire on amphibian populations.

1.2.3. Population demography and vital rates

Five studies considered changes to amphibian demography or vital rates following wildfire (Table 2). Brown *et al*. (2014) found that Hurter's spadefoot toad (*Scaphiopus hurterii*) experienced increased survivorship in Texas following a severe wildfire. Gould *et al*. (2022) likewise found evidence of increased recruitment following a wildfire in North Carolina for the plethodontid salamander *Euryce wilderae*. On the other hand, the same wildfire led to decreases in recruitment for *Desmognathus ocoee*, another plethodontid salamander (Gould *et al*., 2022). Hossack *et al*. (2006) also reported reduced recruitment in the stream-breeding tailed frog, *Ascaphus montanus*, following a wildfire in Montana. Most recently, Barille *et al*. (2022) examined survivorship and recruitment of western toads (*Anaxyrus boreas*) in response to a wildfire in Wyoming, in this case finding no impact of the wildfire on the species. Thus, to date, studies have reported mixed results in terms of the impact of wildfire on amphibian population demographics and vital rates. However, the limited number of studies investigating population responses at this level represents an important gap in our understanding of the impacts of wildfire on amphibian populations as measures of population performance and vital rates speak to whether populations are likely to experience positive or negative growth rates.

1.2.4. Genetic diversity

My search returned only one study that characterized changes to genetic diversity following wildfire in amphibian populations. Robertson *et al*. (2018) studied the effects of wildfire on the population genetics of a tree frog in Florida (*Hyla femoralis*). Although there were positive trends between effective population size and the severity of the most recent wildfire, and between allelic richness and the number of past wildfires experienced by a site, these relationships were not statistically significant (Robertson *et al*., 2018). The authors provide some potential reasons for these results, such as rapid recovery facilitated by high levels of connectivity, or increases in recruitment associated with improved habitat suitability following wildfire (Robertson *et al*., 2018). Beyond this study, I know of only one other study (not returned by my search) investigating the effects of wildfire on genetic diversity in amphibians. Potvin *et al*. (2017), also focused on hylid frogs, examined the responses of two species (*Litoria ewingii* and *L. paraewingi*) to very severe wildfire in Australia using a before-after study design. In contrast to the minimal impacts of wildfire on hylid frogs observed by Robertson *et al*. (2018), Potvin *et al*. (2017) found that heterozygosity and allelic richness decreased, and inbreeding increased for both species following wildfire. With just two studies in hylid frogs from very different parts of the world, our understanding of the effects of wildfire on genetic diversity in amphibians remains limited. This represents a fundamental gap in our understanding of the ultimate impacts of wildfire on amphibian populations, as genetic diversity is expected to influence the long-term performance (Leimu *et al*., 2006; Reed and Frankham, 2003) and adaptive potential (Agashe *et al*., 2011) of populations.

1.2.5. Summary

Across all studies and population response types, the greatest number of responses were categorized as neutral (Table 2). Thus, overall, recent studies suggest that wildfire does not pose a ubiquitous threat to amphibian populations. However, several gaps remain in our understanding of the impacts of wildfire on amphibian populations. First, my Web of Science search for studies citing two prominent reviews returned just 14 published papers. Although I may have missed some papers, the limited number of studies retrieved by my search suggests that this topic needs more attention in general. Furthermore, there is a need for studies that consider more than one type of population response. For example, Gould *et al*. (2022) reported declines in abundance for two plethodontid salamanders (*i.e. E. wilderae* and *D. ocoee*) following a wildfire. However, whereas recruitment also declined in one of the species (*D. ocoee*), recruitment increased in the other species, suggesting population recovery in the latter (Gould *et al*., 2022). Thus, measuring multiple types of population responses is important for a comprehensive understanding of the overall impacts of wildfire on amphibians, yet few studies have looked multiple responses in a single system. Few studies have likewise characterized the effects of wildfire on population parameters that reflect overall population health and processes that can eventually lead to smaller population sizes, and local extirpations (*i.e.* changes to population demography, vital rates, and genetic diversity). Finally, in their reviews, both Pilliod *et al*. (2003) and Hossack and Pilliod (2011) emphasized the need for studies investigating the effects of severe wildfire on amphibian populations. However, in the decade that has followed from these reviews, only six studies have investigated the impacts of severe wildfire on amphibian populations. Global amphibian declines and increases in the frequency of severe wildfire events make this an urgent priority for this taxonomic group at this juncture.

1.3. Thesis overview: Amphibian responses to the Kenow wildfire

The above synthesis of studies highlights the need for additional research on the impact of wildfire, and severe wildfire in particular, on amphibian populations. My thesis addresses several of the gaps identified above, using a case study of amphibian responses to a severe wildfire in southwestern Alberta. Specifically, my thesis focuses on the effects of the Kenow wildfire on amphibian populations in Waterton Lakes National Park (known as *Paahtómahksikimi* to the region's Blackfoot inhabitants; hereafter referred to as "Waterton").

Waterton is situated at the ecotone between the Rocky Mountains and the Canadian Prairies and is inhabited by six pond-breeding amphibian species from diverse genera: long-toed salamanders (*Ambystoma macrodactylum*), western toads (*Anaxyrus borealis*), Columbia spotted frogs (*Rana luteiventris*), western tiger salamanders (*Ambystoma mavortium mavortium*), Northern leopard frogs (*Lithobates pipiens*), and boreal chorus frogs (*Pseudacris maculata*). Waterton and the surrounding region typically experience a mean fire return interval of about 36-62 years, with an average burn size of about 1900 hectares (Rogeau, 2016). By comparison, the Kenow wildfire burned approximately 19,303 hectares in Waterton in the late summer of 2017, representing 39% of the park. This area was burned with unusual uniformity, with 88% of the burn classified as being extreme or high severity (Eisenberg *et al*., 2019).

Several features of the Kenow wildfire make this an excellent opportunity to assess the impacts of severe wildfire on amphibian populations. First, the wildfire impacted roughly half of known amphibian breeding ponds in the park, which allowed for before-after and control-impact comparisons (Underwood, 1992). Second, the timing of the wildfire was such that young-of-the-year for all focal species would have already metamorphosed. With most individuals in the terrestrial environment at the time of the wildfire, the potential for the fire to lead to direct mortality was high. Finally, the wildfire burned soils to a depth of up to 0.7 m in some areas of Waterton (Eisenberg *et al*., 2019), increasing the risk of direct mortality for amphibians, which are known to take refuge in fossorial environments during wildfire (reviewed by Pilliod *et al*., 2003)

The overarching goal of my thesis was to understand how the Kenow wildfire impacted amphibian populations in Waterton. The rest of my thesis is organized as follows:

- In Chapter 2, I used a long-term amphibian monitoring dataset maintained by Parks Canada to quantify changes to breeding pond occupancy and species richness for four of the most common amphibian species in Waterton.

- In Chapter 3, I used tissue samples from one of the species included in Chapter 2 (long-toed salamanders) collected at two time points (before and after the fire), to examine changes to intrapopulation genetic diversity in burnt and unburnt parts of the park.
- In Chapter 4, I summarize my findings in light of the above literature review and outline future directions for further study.

Overall, this work advances our understanding of how severe wildfire effects amphibian populations at a time when severe fire events have become an annual occurrence. I discuss the implications of my findings for the management of amphibians in fire-prone regions of Alberta.

CHAPTER 2: SHORT-TERM RESILIENCE OF PERIPHERAL POPULATIONS OF FOUR AMPHIBIAN SPECIES TO SEVERE WILDFIRE

2.1. Abstract

Fire is a natural part of the disturbance regime of many ecosystems. However, the increasing frequency and severity of wildfires has the potential to negatively impact sensitive species and alter the composition of species in a region. These effects may be more pronounced at the edges of species' ranges and along ecotones where population sizes may be naturally low. In this study, I used a long-term monitoring dataset to investigate the immediate impacts of a particularly severe wildfire on peripheral populations of four amphibian species along an ecotone in western Canada. Specifically, I assessed potential population losses following the Kenow wildfire in Waterton Lakes National Park and compared occupancy before and after the wildfire in affected and unaffected (control) regions to examine the short-term effects of the fire. I also used species accumulation curves to assess changes in species richness following the fire. I found that the populations studied were largely resilient to the effects of the wildfire, at least within the time frame considered. Specifically, I found limited evidence for an effect of the fire on overall patterns of breeding pond-occupancy and species richness across the region. However, downward trends in occupancy for one of the species suggest that there is reason to be cautious in concluding that these populations were unaffected by this event. I discuss the implications of my results for the long-term stability of this ecotone and for the management of at-risk amphibian populations following severe wildfire.

2.2. Introduction

Wildfire shapes ecosystems around the world (Bond *et al*., 2005). Species that occur in fire-prone habitats often exhibit behavioural (*e.g*. Banks *et al*., 2012; Grafe *et al*., 2002; Hale *et al*., 2021) and/or physiological adaptations (*e.g*. Stromberg, 1997) that allow them to contend with fire (reviewed by Pausas and Parr, 2018). However, wildfires are becoming more frequent and severe (Liu *et al*., 2010; Wotton *et al*., 2017). Forecasts of extreme fire events for the foreseeable future (Coogan *et al*., 2019) make it important to assess the impacts of these events on wildlife populations, and especially populations of species that are of conservation concern.

Peripheral populations may be particularly vulnerable to extreme events, including severe wildfire. Peripheral populations may be more isolated (Johannesson and André, 2006; Tóth *et al*., 2019) and suffer greater demographic instability than more central populations (*eg*. Angert, 2009; Curnutt *et al*., 1996; Gerst *et al*., 2011; but see Pironon *et al*., 2017), increasing their risk of extinction following major disturbance (Foley, 1994; Treurnicht 2021). Peripheral populations may also exhibit reduced levels of genetic diversity (Eckert *et al*., 2008; but see Pironon *et al*., 2017), which may limit their ability to contend with environmental change following disturbance (*e.g*. Hughes and Stachowicz, 2004). At the same time, peripheral populations may harbour distinct genotypes (Friedline *et al*., 2019) or adaptations (Bontrager *et al*., 2021) that make them valuable from an evolutionary perspective, and an important reservoir of variation that can facilitate adaptation in the face of climate change (Keller *et al*., 2018; Rehm *et al*., 2015). Thus, population losses following severe wildfire at the edge of species' ranges may have ramifications for the long-term persistence of species.

Major disturbance events at the edge of species' ranges may also have implications for the overall distribution of species. Population losses or gains at the edge of the range can lead to range contractions or expansions. For example, Hill and Field (2021) found that range shifts in response to climate change were hastened by the occurrence of wildfire for some tree species. Similarly, Smale and Wernberg (2013) found that an extreme warming event drove a large range contraction for a habitat-forming seaweed. In the case of parapatric ranges, differences among species in their response to major disturbance may influence the boundaries between interacting species (*e.g.* Brice *et al*., 2019; Santos *et al*. 2019). Thus, severe and more frequent wildfires have the potential to impact species' range limits and reconfigure the boundaries between different communities.

Globally, amphibians are the most threatened vertebrate group, with up to 40% of species facing extinction (IUCN 2022; Wake, 2012). Along with other threats to this group (Hof *et al*., 2011), understanding how amphibians respond to extreme events associated with climate change is necessary to better protect these species. The effects of fire on amphibian populations in fire-prone areas is of particular interest (reviewed by Hossack and Pilliod, 2011; Pilliod *et al*., 2003). Some species appear to do well following fire events, with individuals exhibiting a preference for recently burned areas (*e.g*. western toad*s*: Guscio *et al*., 2008; Hossack *et al*., 2009). However, other studies have reported negative impacts of wildfire on amphibian occupancy (*e.g.* five species of plethodontid salamanders in western North America: Chelgren *et al*., 2011; three amphibian species in western North America: Rochester *et al*., 2010), abundance (*e.g*. two plethodontid salamanders in eastern North America: Gade *et al*., 2019; Rocky Mountain tailed-frogs: Hossack and Honeycutt, 2017), breeding success (*e.g*. California newts: Gamradt and Kats, 1997; ten amphibian species in Spain: Muñoz *et al*., 2019), and genetic diversity (*e.g*. two species of tree frog in Australia: Potvin *et al*., 2017). Nevertheless, much of what we know about amphibian responses to fire comes from studies of prescribed burns or low- to moderate-severity wildfires. Relatively little is known about amphibian responses to severe wildfires of the magnitude forecasted for the future.

Here, I use data from a long-term amphibian monitoring program to examine how a particularly severe wildfire affected four species of pond-breeding amphibians at the edge of their ranges along an ecotone boundary in Western Canada. I specifically ask: 1) were there breeding population losses in the years immediately following the fire for any of the species? 2)

How has breeding pond occupancy changed in this region since the fire? and 3) Are there patterns consistent with an impact of the fire on species richness? In general, my study represents a rare case of having pre-event information about populations against which to assess the impacts of an extreme event on at-risk populations, and has implications for understanding the resilience of edge populations to climate change.

2.3. Methods

2.3.1. Study system

This study focuses on the impacts of a severe wildfire that took place in Waterton Lakes National Park (known as *Paahtómahksikimi* to the region's Blackfoot inhabitants), in the southwestern corner of Alberta, Canada. The park (hereafter referred to as "Waterton") is situated within the ecotone between the Rocky Mountains and the Canadian Prairies and is home to peripheral populations of six amphibian species. Long-toed salamanders (*Ambystoma macrodactylum*), western toads (*Anaxyrus borealis*), and Columbia spotted frogs (*Rana luteiventris*) are Western species that are broadly distributed across forested, montane habitats of western North America. Western tiger salamanders (*Ambystoma mavortium mavortium*), Northern leopard frogs (*Lithobates pipiens*), and boreal chorus frogs (*Pseudacris maculata*) are more central species that are associated with grassland and parkland habitats of the northern Great Plains. In this study, I focus on the impacts of a severe wildfire on populations of boreal chorus frogs, Columbia spotted frogs, western toads and long-toed salamanders in foothill, parkland, and montane habitats in Waterton (western tiger salamanders and northern leopard frogs in the park were excluded from my study as the former occupy a limited number of sites in the park and all contemporary populations of the latter have been recently reintroduced). Of the four focal species, all but boreal chorus frogs are listed as "Sensitive" or "Special Concern" at the Provincial or Federal level in Canada (COSEWIC, 2012; James, 1998; Wilkinson, 2016).

In late summer/early fall 2017, the Kenow wildfire burned approximately 19,303 hectares in Waterton (39% of the park). The area impacted was more than 10-fold greater in size than most fires in the region in recent decades (historical fires have been less than 1900 hectares in size: [Rogeau, 2016]). Furthermore, the Kenow wildfire was particularly severe and unusually uniform in its severity, with 88% of the burn classified as extreme or high severity (Eisenberg *et al*., 2019). Besides being a stand-replacing fire, the fire burned soils to a depth of up to 0.7 m in some areas of the park (Eisenberg *et al*., 2019), potentially increasing the risk of direct mortality for amphibians, which are known to take refuge in fossorial environments during fire (reviewed by Pilliod *et al*., 2003). Furthermore, young-of-the-year of all focal species would have metamorphosed by late summer when the fire occurred, and all age classes would have been in the terrestrial environment at the time of the fire. Thus, populations may not have been buffered during the fire by life-stages in the aquatic environment. The severity and timing of the Kenow wildfire therefore represents a unique opportunity to explore the limits of the ability of amphibian populations to tolerate severe wildfire.

2.3.2. Long-term monitoring data

My study takes advantage of a long-term amphibian monitoring dataset developed and maintained by Parks Canada (Parks Canada Waterton Lakes Field Unit, 2021; see Table S1 for summary of monitoring program). I used data from 2008 to 2021, representing ten years of monitoring before the Kenow wildfire and three years of monitoring following the fire (note: the COVID-19 pandemic precluded monitoring in 2020 and there are no data available for that year). Thus, my study focuses on the short-term effects of the wildfire on amphibian populations in the park. The 41 monitoring sites included in the dataset are split between burnt and unburnt regions of the park (20 burnt sites, 21 unburnt sites; Figure 1), creating a natural before-after control-impact study design (Underwood, 1992).

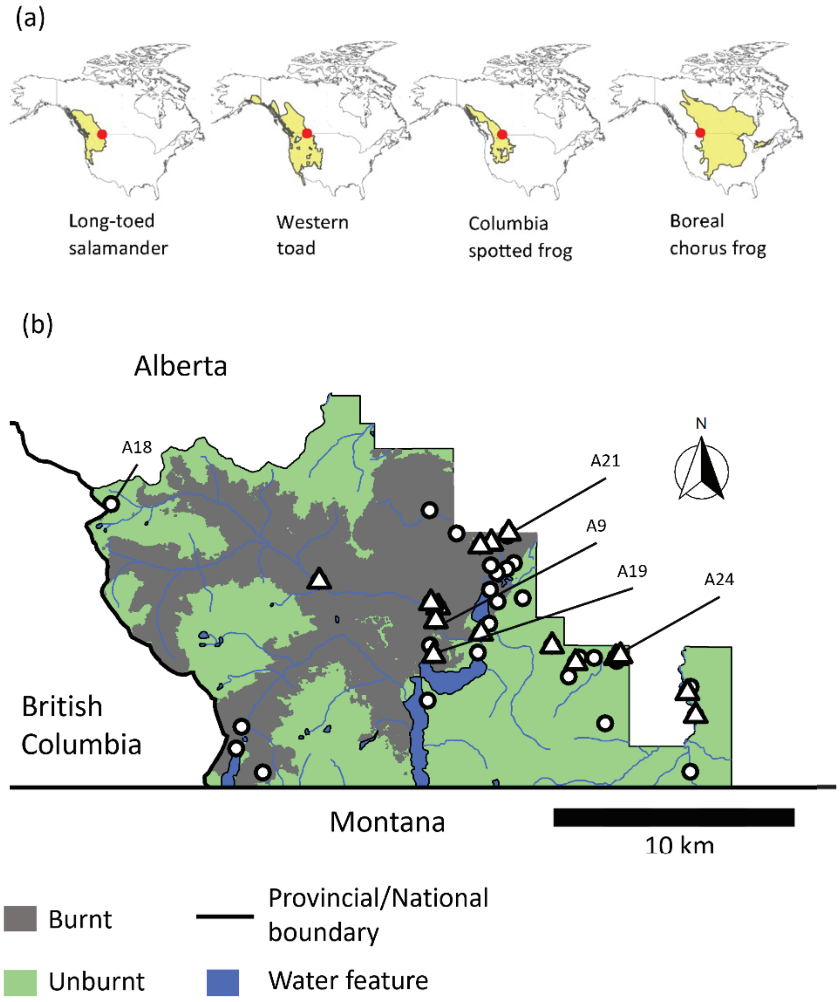


Figure 1. Species and sites used to explore the effects of severe wildfire on peripheral populations of long-toed salamanders (*Ambystoma macrodactylum*), western toad (*Anaxyrus boreas*), Columbia spotted frog (*Rana luteiventris*), and boreal chorus frogs (*Pseudacris maculata*). The geographic range of each species is shown as a yellow polygon in (a), with the location of Waterton Lakes National Park, Canada depicted as a red dot in each map. The park boundary and the distribution of the 41 monitoring sites (circles and triangles) with respect to the 2017 Kenow wildfire (grey shading) are shown in (b). The 15 core amphibian monitoring sites (see main text) are distinguished from the other monitoring sites as triangles. Sites referred to in the main text are labelled.

Over the thirteen years of monitoring, sites were visited two or three times in the spring (predominately in May but with visits occurring up until July for some sites in earlier years; see Table S1). During each visit, two trained technicians recorded the presence of all amphibian species during 60-minute audiovisual shoreline surveys. The dataset consists of 1126 people-hours of observation from 563 visits to the 41 sites. Of these 41 sites, only 30 were visited following the fire (Table S1). However, data from other sites are useful for establishing overall estimates of occupancy and probabilities of detection. Of the 30 sites with data available before and after the fire, 15 sites were visited consistently every year from 2012-2016 (pre-fire) and 2018-2021 (post-fire; Table S1). Thus, I used this subset of sites (hereafter referred to as the "core monitoring sites") for those analyses that required continuous data before and after the wildfire.

2.3.3. Assessing population loss following the wildfire

I first examined the potential for populations to have been lost following the fire. For this analysis, I focused on the 15 core monitoring sites. I pooled the monitoring data from all visits to a given site for a given year to score each site as present or absent for that year. I considered a population to be putatively lost if the species was detected in at least two of the years between 2012 and 2016 and went undetected in the three years of monitoring following the fire.

To distinguish population loss from issues with detection, I calculated the probability of false absence for each putative loss using an approach similar to that of Moritz *et al*. (2008). Specifically, I used the following equations to calculate the probability of false absence:

(1) $P_y = 1 - (1 - P)^v$

(2) $P_{fa} = (1 - P_y)^n$

Equation (1) calculates the annual cumulative probability of detecting a given species for each site (P_y) across v visits, based on the average per-visit probability (P) of detecting the species (given that it is present). In my case, sites under consideration (*i.e.* the core sites in the *pre-fire* years; Table S1) were visited three times per year, so $v = 3$. Equation (2) uses P_y to calculate the probability of *not* detecting the species in question at the focal site when it is present across n years of observation (*i.e.* the probability of false absence; P_{fa}). In my case, there were three years of monitoring post-fire so $n = 3$.

Estimates of P were produced in the program PRESENCE version 2.13.10 (Mackenzie *et al.*, 2003). PRESENCE uses occurrence data collected over multiple visits to a set of sites to estimate probability of detection per visit (as well as overall occupancy across a region; see below). I used the pre-fire detection history for each putative population loss and the multi-season modelling algorithm in PRESENCE to generate a site-specific estimate of P. This value was then used to estimate the average annual probability of detection following equation (1) and the probability of mistakenly calling a species absent for the three post-fire years following equation (2). A value of $P_{fa} < 0.05$ (Moritz *et al.*, 2008) would suggest that the absence of a species at a site for the three post-fire years in question likely represents a true population loss rather than an issue with detection. Because using PRESENCE to estimate P based on data from a single site results in estimates that have limited precision (J.E. Hines, *pers. comm.*), I also calculated P_{fa} using values of P generated by grouping the pre-fire detection history of each site of interest with the pre-fire detection history of its nearest neighbour (sensitivity test 1) and its four nearest neighbours (sensitivity test 2), which were identified using the Euclidean distance between sites as measured in Google Earth (version 7.3.4).

2.3.4. Wildfire effects on breeding pond occupancy

In addition to exploring specific population losses following the fire, I examined changes in overall occupancy for each species. I was specifically interested in whether there were differences in occupancy between burnt and unburnt parts of the park that depended on time with respect to the fire (*i.e.* before versus after the fire), which would signal an effect of the fire on occupancy (*e.g.* following Hossack and Corn, 2007). Thus, I modelled occupancy as a function of the interaction between region (in or out of the burn zone) and time-period (pre- or post-fire) for each species (hereafter referred to as the “Fire” model). Models were generated using the multi-season algorithm in PRESENCE with the implicit-dynamics parameterization (Mackenzie *et al*., 2003). The implicit dynamics model uses data from each year independently to produce estimates of occupancy that apply across years and can accommodate missing visits in the monitoring data. Thus, I was able to use data from all 41 sites and from all 13 years for this analysis.

PRESENCE takes imperfect detection into account when modelling occupancy. In this case, I included standardized Julian date as a covariate when modelling probability of detection to account for differences in amphibian activity across the monitoring season (as a result, these estimates of probability of detection differ from the site averages used above). Because amphibians often demonstrate differences in breeding phenology across elevation (*e.g*. Howard and Wallace, 1985), I also tested whether including standardized elevation when modelling the probability of detection improved model fit. For each species, the final set of covariates used for modeling probability of detection was chosen by selecting the set of covariates with the lowest Akaike Information Criterion score (corrected for small sample sizes; AICc: Burnham and Anderson, 2002; Table S2). The final occupancy model for each species thus modelled the effects of wildfire after accounting for differences in the probability of detection associated with survey date, and/or elevation, depending on the species. These models do not have a formal goodness-of-fit test. To explore whether the ranking of models was sensitive to overdispersion, I toggled the variance inflation factor ($\hat{c}$) in PRESENCE to values between 1 and 2 in increments of 0.1.

I compared the performance of the above wildfire model for each species to simpler models that looked at the separate effects of region (“Region” model) and time period (“Time” model) on occupancy. The Region model for each species explored overall differences in the proportion of sites occupied between unburnt and burnt parts of the park across all years. Given the specific configuration of the area affected by the fire, this model essentially examines differences in occupancy between eastern and Western parts of the park. The Time model explored overall differences in the proportion of sites occupied across the park between the two time periods of interest and thus probes general changes in occupancy over time. Finally, I generated an intercept-only model that produced a single estimate of occupancy for each species across all sites and years. I used AICc to select the model that best explains patterns of occupancy in the park for each species. Because not all 41 sites were visited following the wildfire, I re-ran all models using the subset of 30 sites that were visited post-fire to test the sensitivity of my results to differences in which sites were monitored between time periods. Furthermore, a single unburnt site (A18) occurs in the otherwise burnt, western part of the park, and I re-ran the analyses without this site to explore the impacts of omitting this site.

2.3.5. Impacts on species richness

I used rarefied species accumulation curves to assess changes to species richness (S) in burnt and unburnt parts of the park following the fire. Species accumulation curves quantify the relationship between survey effort (number of sites visited) and the number of species detected, and are typically used to guide survey design. However, differences in the shape of these curves across space and/or time can also signal differences in species richness among regions or time periods (*e.g.* Loehle *et al*., 2005). I use this approach here to evaluate the effects of the wildfire on amphibian species richness as the limited number of amphibian species in the park precluded us from using more traditional community ecology metrics such as changes in beta or gamma diversity.

I created species accumulation curves for burnt and unburnt parts of the park for the three years immediately before the wildfire (*i.e.* 2014, 2015, and 2016) and for the three post-fire years for which monitoring data were available (*i.e.* 2018, 2019, and 2021). For this analysis, I focused on the 15 core monitoring sites. I pooled the monitoring data from all visits to a given site for a given year to score each site as present or absent for that year. A species accumulation curve was generated for each of the six years using the sample-based method without randomization in EstimateS, version 8.2.0 (Colwell *et al*., 2012).

2.4. Results

2.4.1. Population losses following the fire

I used the detection histories of each species to evaluate putative population losses in both burnt and unburnt parts of Waterton Lakes National Park following the Kenow wildfire. Resident species observed before the fire were observed in at least one monitoring year following the fire for most of the eight sites considered in the burn zone (Figure S1). Nevertheless, I identified two sites in the burn zone where one or more species was regularly detected before the fire but has not been observed post-fire (Figure S1). Specifically, long-toed salamanders, western toads, and boreal chorus frogs were observed at site A9 in at least two of the five years immediately predating the fire but have not been observed at this site since the fire. For long-toed salamanders, the probability of false absence (P_{fa}) was <0.001 regardless of how the site-specific probability of detection (P) in equation 1 was calculated (Table S3). For boreal chorus frogs and western toads, the P_{fa} ranged from < 0.001 to 0.19 and 0.001 to 0.32 respectively at this site (Table S3). Thus, my estimates were sensitive to how P was calculated for these species, and I cannot say with certainly that their absences from A9 following the fire represent true population losses. Western toads were likewise observed at A21in pre-fire years but not after; however, in this case, P_{fa} was high, ranging from 0.13 to 0.32 (Table S3).

I assessed putative population losses in unburnt parts of the park over the same period for comparison. Most of the species observed at the seven unburnt sites before the fire were observed in at least one of the post-fire monitoring years (Figure S1). However, long-toed salamanders appear to have been lost at A19 (P_{fa} values were <0.001 across all sensitivity tests;

Table S3). Western toads were not observed at site A24 in the three post-fire years, but P_{fa} was sensitive to my estimates of P (range < 0.001 to 0.14; Table S3).

2.4.2. Effects of the fire on breeding pond occupancy

Formal occupancy modelling revealed differences among species with respect to the factors influencing detection (Table S2) and best predicting occupancy in the park (Table 3). With respect to the main model of interest (*i.e.* the "Fire" model), estimates of occupancy for long-toed salamanders increased from pre-fire years to post-fire years in unburnt regions of the park but decreased from pre-fire years to post-fire years in burnt regions of the park (Figure 2, Table 3). In contrast, estimates of occupancy for the other three species either decreased (Columbia spotted frogs and western toads) or slightly increased (boreal chorus frogs) in unburnt parts of the park and increased in burnt parts of the park following the fire (Figure 2, Table 3). However, in all cases, the 95% confidence intervals around the estimates for each time period in each region were overlapping.

Model selection based on AICc did not support the Fire model as the best model to explain occupancy for most species (Table 3). Instead, occupancy was best modelled as a single, park-wide value for long-toed salamanders ($\Psi = 0.58$, SE = 0.04). Occupancy was best explained by incorporating differences between regions for western toads (unburnt region: $\Psi = 0.77$, SE = 0.06; burnt region: $\Psi = 0.42$, SE = 0.06) and boreal chorus frogs (unburnt region: $\Psi = 0.90$, SE = 0.04; burnt region: $\Psi = 0.80$, SE = 0.05), although the Intercept and Time models were also competitive (*i.e.* ΔAICc < 2) for the boreal chorus frog (Table 3). For the Columbia spotted frog, the Fire model had the lowest AIC but this result appears to be driven by a decrease in occupancy from pre- to post-fire years in unburnt parts of the park rather than changes in burnt parts of the park (Figure 2).

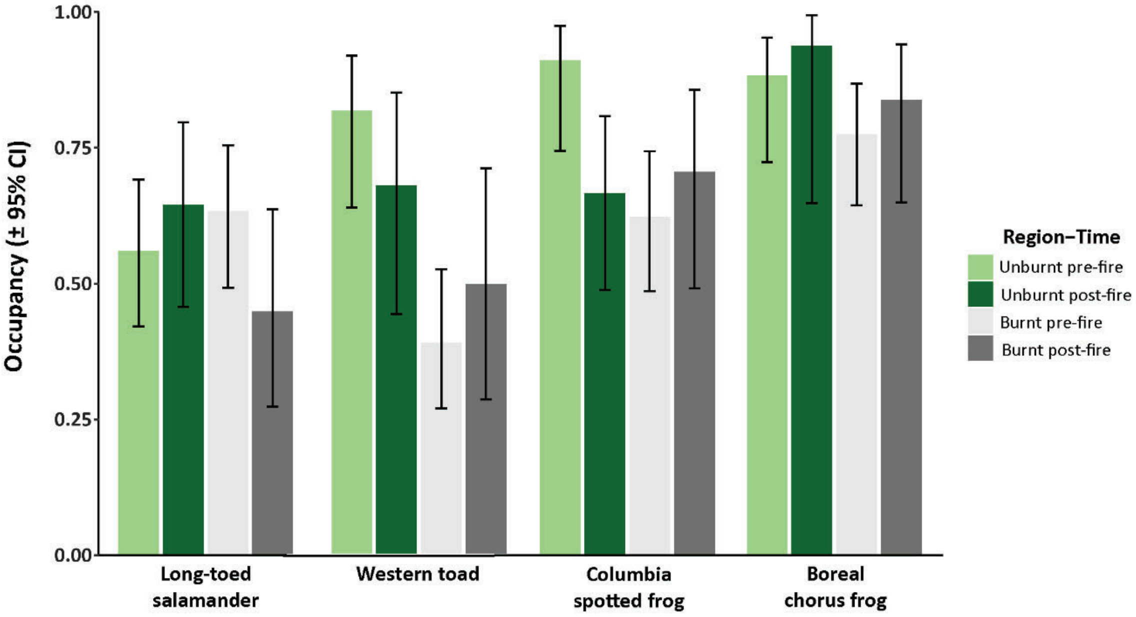


Figure 2. Estimates of occupancy for the four species of amphibians before (2008 – 2017) and after (2018-2021) the 2017 Kenow wildfire in unburnt (green) and burnt (grey) parts of Waterton Lakes National Park based on 41 monitoring sites. Error bars represent 95% confidence intervals.

The Region model was also competitive for this species (Table 3) and the ranking of these two models was sensitive to changes to ĉ, with the Region model being the top model at ĉ ≥ 1.3 and the fire model no longer being competitive when ĉ ≥ 1.9. Thus, overdispersion may impact results for this species. The top model selected based on AICc was sensitive to either the subset of sites considered (Table S4) or the exclusion of the lone unburnt site in the Western part of the park (Tables S5) for all species. However, in no case was the Fire model competitive for the other three species.

2.4.3. Effects of the fire on species richness

I used species accumulation curves to examine changes in amphibian species richness associated with the wildfire. I generated separate curves for burnt and unburnt parts of the park, for three pre- and three post-fire years (Figure 3). Each curve plots the mean number of species encountered (*S*) on the y-axis as a function of the number of sites visited on the x-axis. Because all four species occur throughout the park, the asymptote of these curves is the same (*i.e.* = 4). Of interest were potential differences among the curves in the number of species observed at x = 1 (*i.e.* the mean number of species observed per visit to a single site) and the point on the x-axis at which the curve begins to approach the asymptote (assessed by eye). In terms of the number of species observed per visit to a single site, this value ranged from an average of 3.00 to 3.43 in pre-fire years, and 2.29 to 3.14 in post- fire years in unburnt parts of the park (Figure 3a). In burnt parts of the park, this value ranged from an average of 2.13 to 2.88 in pre-fire years, and 1.75 to 2.13 in post-fire years (Figure 3b). Thus, in both unburnt and burnt parts of the park, there was a slight depression in the mean number of species per visit to a single site following the fire, although these differences were not statistically significant (Figure 3). In terms of the number of sites at which the asymptote was reached, in unburnt parts of the park, one could expect to observe all four species after visiting four or five sites both before and after the fire (Figure 3a). In contrast, in burnt parts of the park, before the fire, all four species could be expected to be observed after visiting five to six sites, but visits to six to eight sites were required to see all four species after the wildfire (Figure 3b). However, again, the 95% CI were broad and overlapping across years in several cases.

2.5. Discussion

I set out to determine the impacts of severe wildfire on peripheral populations of four amphibian species along an ecotone boundary. Specifically, I examined changes in breeding pond occupancy and species richness in the years immediately following the Kenow wildfire in Waterton Lakes National Park in southwestern Alberta, Canada. Despite the potential for the extreme severity and timing of this wildfire to have resulted in high amphibian mortality, I found limited evidence for population loss or changes in breeding pond occupancy associated with the wildfire. These results, representing the response of four species from different genera and with different life-histories, behaviours, and habitat use, suggest that amphibian populations may, at least initially, be resilient to the type of severe wildfires forecast for the future in this part of the world. At the same time, the small number of populations for which data were available limited the power of some of my analyses. Furthermore, my analyses were limited to the immediate impacts of the wildfire, and thus I caution that more work is needed to understand the long-term impacts of this event on amphibian populations in the park.

2.5.1. Amphibian responses to severe wildfire

Although amphibians are known to exhibit a diversity of responses to wildfire (Hossack and Pilliod, 2011; Pilliod *et al*., 2003), little is known about their response to extreme wildfire events. I found limited evidence of an impact of the very severe Kenow wildfire on amphibian populations in Waterton Lakes National Park in Western Canada. Although long-toed salamanders appear to have been lost from one site in the burnt zone following the fire, the resident species of most sites within the burnt zone remained present following the fire. Furthermore, it is not uncommon for amphibians to exhibit metapopulation dynamics (Smith and Green, 2005), and for populations to be lost for other reasons over the time-spans considered here (*e.g.* Heard *et al*., 2012). Indeed, I also observed the probable loss of a population of long- toed salamanders in unburnt parts of the park in the same time period. Thus, the wildfire does not seem to have led to population losses in burnt parts of the park above and beyond that which might be expected based on natural metapopulation dynamics.

Table 3. Estimates of occupancy (Ψ) for four amphibian species in Waterton Lakes National Park based on monitoring data from 41 sites from 2008 to 2021, inclusive of the 2017 Kenow wildfire. The top model for each species is presented first and bolded with remaining models presented in ascending order of AICc scores.

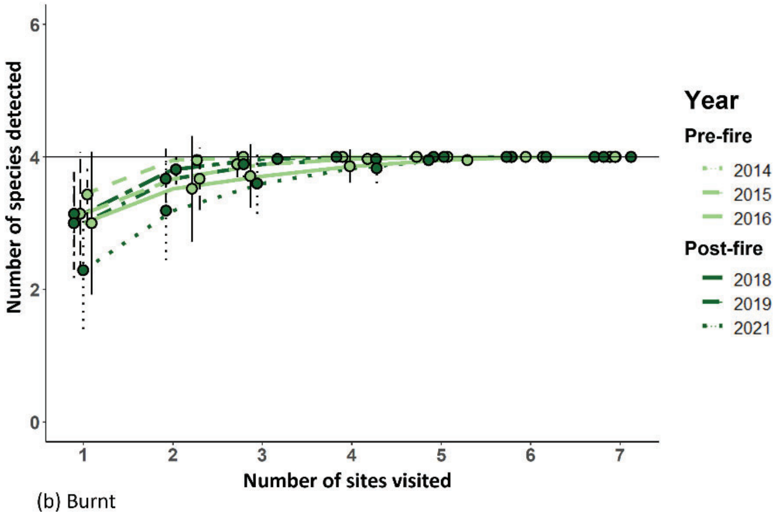
Species	**Detection covariates**[1]	**Model**	**Ψ**[2] **(SE**[3]**)**	***k***	**AICc**	**ΔAICc**	**AICc weight**
Long-toed salamanders	date + elevation	**Intercept**	**0.58 (0.04)**	**3**	**647.73**	**0.00**	**0.58**
		Time	0.60 (0.05); 0.56 (0.07)	4	649.97	2.24	0.19
		Region	0.59 (0.06), 0.57 (0.06)	4	650.14	2.41	0.17
		Fire	0.56 (0.07), 0.63 (0.07), 0.64 (0.09), 0.45 (0.10)	6	652.58	4.85	0.09
Western toads	date	**Region**	**0.77 (0.06), 0.42 (0.06)**	**3**	**600.14**	**0.00**	**0.83**
		Fire	0.81 (0.07), 0.39 (0.07), 0.68 (0.11), 0.50 (0.12)	5	603.36	3.22	0.17
		Intercept	0.59 (0.05)	2	614.43	14.29	< 0.00
		Time	0.58 (0.05), 0.60 (0.08)	3	616.73	16.59	< 0.00
Columbia spotted frogs	date + elevation	**Fire**	**0.91 (0.05), 0.62 (0.07), 0.66 (0.08), 0.70 (0.10)**	**6**	**698.97**	**0.00**	**0.52**
		Region	0.81 (0.05), 0.65 (0.06)	4	700.10	1.13	0.30
		Intercept	0.74 (0.04)	3	701.87	2.90	0.12
		Time	0.76 (0.05), 0.69 (0.06)	4	703.49	4.52	0.05
Boreal chorus frogs	date	**Region**	**0.90 (0.04), 0.80 (0.05)**	**3**	**705.90**	**0.00**	**0.42**
		Intercept	0.84 (0.03)	2	706.62	0.72	0.29
		Time	0.82 (0.04), 0.88 (0.05)	3	707.49	1.59	0.19
		Fire	0.88 (0.06), 0.77(0.06), 0.93 (0.07), 0.83 (0.07)	5	708.94	3.04	0.09

[1] The covariates used to estimate the probability of detection for each species were selected using a model selection procedure based on AICc or QAIC (Table S2).

[2] Order of Ψ estimates for the different models:
Time: pre-fire; post-fire
Region: unburnt, burnt
Fire: pre-fire unburnt, pre-fire burnt, post-fire unburnt, post-fire burnt

[3] Standard error was calculated using a non-parametric bootstrapping method.

(a) Unburnt



(b) Burnt

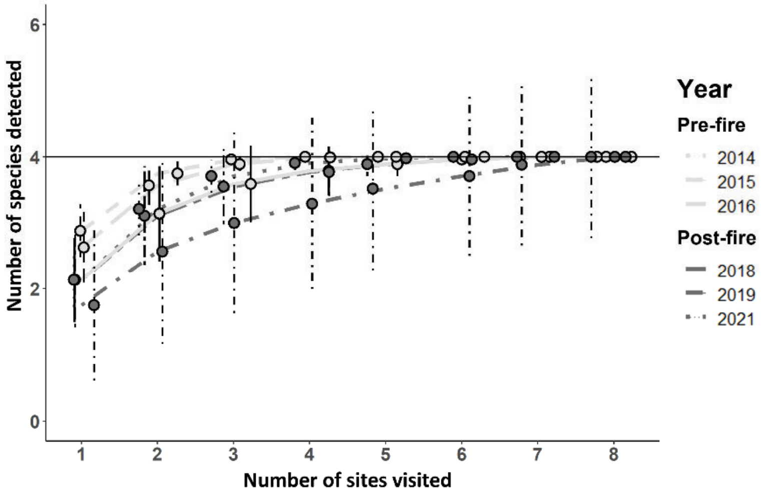


Figure 3. Amphibian species accumulation curves in Waterton Lakes National Park for three years before and three years after the 2017 Kenow wildfire based on data from the 15 core monitoring sites (see main text). Curves for unburnt (a) and burnt (b) parts of the park are shown separately. Error bars represent unconditional 95% confidence intervals around the mean.

Likewise, the wildfire does not appear to have had an impact on overall occupancy for these species across the park. In fact, although not statistically significant, there were upward trends in occupancy in burnt parts of the park for three of the four species studied here. In general however, breeding pond occupancy was best modelled as either a single value across the park for long-toed salamanders or as function of region for western toads, Columbia spotted frogs, and boreal chorus frogs, with higher occupancy in eastern parts of the park (noting that the Intercept and Time models were also competitive for the boreal chorus frog). The Fire model was competitive for Columbia spotted frogs, but this was largely driven by a decrease in occupancy in unburnt parts of the park and the model suffered from overdispersion. Finally, although species richness, as estimated using species accumulation curves, tended to decrease following the fire, these decreases were observed in both burnt and unburnt parts of the park and were not statistically significant. Therefore, my results suggest the populations studied here were not especially impacted by the Kenow wildfire, at least not in the years immediately following this event.

My results are in line with results from other studies examining the impact of fire on amphibian populations. For instance, Greenberg *et al*. (2018) found that capture rates of 12 species of amphibians in North Carolina were generally unaffected by prescribed fires. Most comparably, Hossack and Corn (2007) and Hossack *et al*. (2013b) examined the impacts of burns of varying severity in Montana on more central populations of three of the four species studied here (*i.e*. western toads, Columbia spotted frogs, and long-toed salamanders). They found no changes in occupancy following wildfires over similar timeframes. That I see a similar lack of response to a uniform, highly severe wildfire suggests that regardless of severity, wildfire may pose little threat to the persistence of some amphibian populations, at least in the short-term (but see Chelgren *et al*., 2011; Rochester *et al*., 2010).

2.5.2. Severe wildfire and peripheral populations

My results have implications for understanding the impact of extreme events on peripheral populations and species' range limits. Peripheral populations are thought to experience greater isolation (Johannesson and André, 2006; Tóth *et al*., 2019), higher demographic instability (Angert, 2009; Curnutt *et al*., 1996; Gerst *et al*., 2011), and reduced levels of genetic diversity (Eckert *et al*., 2008; Wood *et al*., 2021). Thus, peripheral populations might be expected to be more susceptible to extreme events than populations elsewhere in their range (Hadie and Hutchings, 2010). In contrast to this expectation, my results are indicative of the capacity of peripheral populations to withstand extreme events. One possibility to explain such resilience is that peripheral populations, rather than being more susceptible to disturbance, are pre-adapted to stress (Wood *et al*., 2021). If this is the case, it is also possible that peripheral populations could represent strongholds for species that are subject to changing disturbance regimes associated with climate change (Coleman and Wernberg, 2020; Rehm *et al*., 2015). However, comparisons of differences in the response of core versus peripheral populations to extreme events are needed to further assess this possibility.

Although amphibian populations in Waterton seem to have held their ground in the wake of this wildfire, it is possible that habitat changes resulting from the fire (Eisenberg *et al*., 2019; Lloren, 2021) have primed this region for future changes to the amphibian community. For example, Brice *et al*. (2019) found that historical disturbance, including wildfires, facilitated an ecotone transition in eastern North America, with broadleaf forest species moving northward and encroaching on coniferous species in disturbed areas faster than in undisturbed areas under changing climates. With respect to wildfire and herpetofauna specifically, Santos *et al*. (2019) found that habitat suitability increased along an ecotone boundary in southern France for open-habitat reptile and amphibian species following repeated wildfires over a 37-year time span. These changes in habitat suitability were associated with the replacement of forest-associated, medio-European species in the region (Santos *et al*. 2019), demonstrating the potential for repeated fire events to lead to shifts in ecotone boundaries over time. Therefore, although a single extreme event may not have much of an impact on communities, such events can have legacy effects that influence the longer-term stability of ecotones in the face of future climate-related events (Lindenmayer 2011 *et al*., 2011, Miller and Safford, 2020).

2.5.3. Implications for management

That I was able to compare occupancy before and after an extreme fire event was made possible by the availability of multiple years of amphibian monitoring data through the Ecological Integrity Monitoring Program of Waterton Lakes National Park. Thus, my study demonstrates the value of long-term monitoring programs for understanding environmental change and the impacts of extreme events on wildlife populations. In the present case, it was fortuitous that monitoring sites spanned burnt and unburnt parts of the park. However, the limitations of my study highlight important considerations for future monitoring programs. In particular, my study was limited by the number of sites for which data were available, limiting power and precluding consideration of additional environmental covariates in my models (*e.g.* vegetation type, isolation, *etc*.). Furthermore, inconsistency in monitoring efforts across years prevented us from estimating other parameters such as the probability of colonization and extinction (*e*.g. Hossack *et al*., 2013b; Moss *et al*., 2021). Thus, we recommend that in designing future monitoring programs, managers consider the number of sites needed for adequate statistical power for a range of occupancy analyses and ensure that sites are monitored consistently across years (see also Nelson *et al*. 2021).

In addition to the number of sites, those designing future monitoring programs may want to consider different environmental contrasts when selecting sites (Lepetz *et al*., 2009). Although the amphibian monitoring program in Waterton was designed to be representative of different ecoregions (Parks Canada Waterton Lakes Field Unit, 2021), a limited number of high-elevation amphibian breeding ponds in the park are monitored and none of these sites have been formally monitored since the fire. The exclusion of these sites from my study is unfortunate given that high-elevation amphibian breeding sites in the park are closest to the centre of the burn. Furthermore, high-elevation sites are thought to be more isolated than low-elevation sites for at least some of the species studied here (*i.e.* Columbia spotted frog: Funk *et al*., 2005; Long-toed salamanders: Giordano *et al*., 2007). Thus, my results may underestimate the impacts of the Kenow wildfire on amphibian populations in the park. Going forward, it may be worth expanding the monitoring program in Waterton to include high-elevation sites. More generally, we recommend that future monitoring programs in fire- prone areas be designed to span the entirety of key environmental gradients that may serve to modify the impact of fire events on populations.

Despite the limitations of my data, my results have important implications for the management of the populations studied here and for the post-fire management of amphibian populations in general. Although I found limited evidence for a change in occupancy, I did observe a downward trend in breeding pond occupancy in burnt parts of the park for long-toed salamanders following the wildfire. Hossack *et al*. (2013b) reported lags in the response of this species and of Columbia spotted frogs to a wildfire in Montana, with occupancy remaining relatively stable for up to six years post-fire and then dropping precipitously. Thus, it is possible that the downward trend in occupancy observed for the salamanders foreshadows future declines and that the apparent resilience to wildfire of this and the other species studied here may be relatively short-lived. However, initial persistence of amphibian populations following severe wildfire may present land managers with opportunities to mitigate against longer-term declines. For example, it may be possible to promote the continued persistence of populations through active habitat restoration or placement of supplemental cover objects (which are important for many amphibian species) around affected breeding sites (*e.g*., O’Donnell *et al*., 2017).

Furthermore, continued monitoring of amphibian populations in the park, coupled with assessment of successional changes to their habitat following the fire will allow for adaptive management of these populations in the long run.

2.5.4. Conclusions and future directions

Overall, I found that peripheral populations of the four species of amphibians examined here were mostly unaffected by a severe wildfire. These results give us reason to hope that severe wildfire events do not pose an immediate threat to the persistence of these species. At the same time, I caution that the short-term persistence of populations does not mean populations were unaffected by the wildfire. For instance, occupancy is not always correlated with abundance (Wilson, 2011; Rochester *et al*., 2010) and populations may have experienced numerical declines as a result of the fire (*e.g.* Potvin *et al*., 2017). Likewise, changes to both aquatic and terrestrial habitats following wildfire have the potential to impact the survival and reproductive success of individuals (*e.g*. Dudley *et al*., 2021; Munoz *et al*., 2019; O'Neil *et al*., 2020). Impacts on population size and recruitment may in turn lead to increased genetic drift and the loss of genetic diversity (*e.g*. Potvin *et al*., 2017), potentially influencing the long-term performance and persistence of populations (*e.g*. Rowe and Beebee, 2003). Thus, more work is needed to understand the potentially multifaceted and longer-term responses of these populations to this event. In the meantime, I encourage the continued monitoring of these populations and the establishment of carefully designed monitoring programs in other, fire-prone regions to generate baseline data against which the effects of forecasted extreme events can be assessed.

CHAPTER 3: EFFECTS OF SEVERE WILDFIRE ON GENETIC DIVERSITY IN LONG-TOED SALAMANDERS

3.1. Abstract

Understanding the effects of severe wildfire on biodiversity has become an important challenge in ecology and conservation biology. Amphibians are experiencing worldwide declines and might be particularly vulnerable to these events, yet studies addressing the impact of these events on amphibian populations limited. Here, I used genomic data to assess changes in genetic diversity in the long-toed salamander (*Ambystoma macrodactylum*) over two time points that span the occurrence of a very severe wildfire in southwestern Alberta, Canada. I found that there were increases in inbreeding four of the five in the burnt region following the wildfire. However, two of the sites in the burnt region exhibited increases in allelic richness and expected heterozygosity following the wildfire, possibly due to increased immigration. Although I did not detect a consistent effect of wildfire on genetic diversity across sites, the generally low levels of genetic diversity relative to amphibians elsewhere, and elevated levels of inbreeding for several populations in the park suggest that these populations may be susceptible to future disturbance and subsequent population declines. Therefore, continued genetic monitoring of these populations is recommended.

3.2. Introduction

Extreme, climate-related events, such as severe floods, drought, heat, and wildfire, are increasing in frequency (Jentsch *et al*., 2007; Nolan *et al*., 2021; Papalexiou and Montanari, 2019). Such events can have substantial impacts on wildlife populations (Gutschick and BassiriRad, 2003; Sergio *et al*., 2018), causing direct mortality (*e.g.* Shohami and Nathan, 2014; McKechnie *et al*., 2021) or by impacting critical habitat and resource availability (*e.g.* Boucek *et al*., 2022; Sergio *et al*., 2018). Thus, extreme events can have consequences for population demography, vital rates, and size (Andrello *et al*., 2012; Roland and Matter, 2016).

Changes in population size may in turn impact levels of genetic diversity (Banks *et al*., 2013; Davies *et al*., 2016; Filazolla *et al*., 2019; Gutschick and BassiriRad, 2003; Sergio *et al*., 2018). On the one hand, population bottlenecks and selective sweeps caused by extreme events can lead to reductions in genetic diversity in some populations (*e.g.* Coleman *et al*., 2020; Gurgel *et al*., 2020; Harvey *et al*., 2021; Janjoo *et al*., 2016; Shama *et al*., 2011; Potvin *et al*., 2017; Vincenzi *et al*., 2017). Other populations may experience an increase in genetic diversity following extreme events because of increased connectivity (*e.g.* floods may bring individuals into populations or increase connectivity for aquatic species). Finally, genetic diversity may be relatively unimpacted by extreme events in cases where populations are pre-adapted to stress (*e.g*. Blondel *et al*., 2021; Dolan *et al*., 2008; Poff *et al*., 2018; Suarez *et al*., 2012). However, relatively few studies have characterized the genetic response of populations to extreme events. Given that genetic diversity impacts population performance (Leimu *et al*., 2006; Reed and Frankham, 2003) and the ability of populations to adapt (Agashe *et al*., 2011), this represents a gap in our understanding of the impacts of climate change on biodiversity, especially in the case of threatened taxa. In this study, I expand on our understanding of extreme events to include the impacts of severe wildfire on an at-risk amphibian in western Canada.

Amphibians are one of the most threatened taxonomic groups, with 40% of species facing declines and extinction (IUCN 2022; Wake, 2012). Several studies have investigated the impacts of wildfire on occupancy (*e.g*. Chelgren *et al*., 2011; Rochester *et al*., 2010), abundance (*e.g*. Hossack and Honeycutt, 2017; Potvin *et al*., 2017), and breeding activity (*e.g*. Munoz *et al*., 2019) in different amphibian taxa. These studies indicate that responses to wildfire vary considerably among species (reviewed in Chapter 1). However, our understanding of the effects of wildfire on genetic diversity in amphibians remains limited to the findings of only two studies

(Potvin *et al*., 2017; Robertson *et al*., 2018). Robertson *et al*. (2018) found that wildfire severity and frequency had positive effects on effective population size and allelic richness in a species of hylid frog (*Hyla femoralis*) in Florida. By contrast, Potvin *et al*. (2017) reported reduced estimates of allelic richness and heterozygosity, as well as increased inbreeding in two species of hylid frogs (*i.e. Litoria ewingii* and *L. paraewingi*) following a severe wildfire in Australia. With just two studies in hylid frogs from different parts of the world, our understanding of the effects of wildfire on genetic diversity in amphibians remains limited. Further studies from a wider range of amphibian taxa are needed to develop our understanding of how wildfire affects genetic diversity in amphibian populations.

The long-toed salamander (*Ambystoma macrodactylum*) is a pond-breeding amphibian in western North America. This species is of conservation concern in Alberta (Wilkinson, 2016), with the western part of the province representing the easternmost extent of its global distribution. Waterton Lakes National Park (hereafter "Waterton") in southwestern Alberta represents one of three concentrations of long-toed salamanders in the province, and the only stronghold for the Eastern long-toed salamander subspecies (Lee-Yaw and Irwin, 2012). In late summer and early fall of 2017, Waterton was impacted by the Kenow wildfire, a particularly severe fire that burned 19,303 hectares within the park boundaries (Eisenberg *et al*., 2019). The Kenow wildfire had the potential to be particularly impactful on amphibian populations in the park for two reasons. First, by late summer and early fall when the wildfire occurred, larval individuals would have metamorphosed and left aquatic environments, potentially subjecting them directly to the wildfire. Additionally, the wildfire and subsequent high winds removed up to 0.7 m of soil in some parts of Waterton (Eisenberg *et al*., 2019), which would have been detrimental to individuals sheltering in fossorial habitats (reviewed by Pilliod *et al*., 2003).

Here, I take advantage of a rare pre- and post-fire tissue collection to assess genome-wide changes in genetic diversity in response to wildfire using the long-toed salamanders in Waterton as a case study. I specifically asked whether there were changes in expected or observed heterozygosity, levels of inbreeding, and/or allelic richness at five sites that were impacted by the Kenow wildfire and how these compared to changes at three sites from unburnt parts of the park. My findings, shed light on the response of different populations of this at- risk species to an extreme event and speak to the overall evolutionary trajectory of salamanders in the park.

3.3. Methods

3.3.1. Sampling

Pre-fire and post-fire tissue samples were collected from eight wetland sites in Waterton in the summers of 2009 and 2020 respectively (Figure 4). Sites ranged in elevation from 1294 m to 1905 m, and include sites in the parkland, montane, and subalpine ecoregions found within the park. These sites represent both burnt and unburnt parts of the park, allowing me to partially disentangle the effects of the wildfire on genetic diversity from the effects of time. In particular, consistent changes in genetic diversity in burnt parts of the park that are unmatched or that differ in direction from changes in unburnt parts of the park would signal a strong impact of the fire on genetic diversity in this system.

Tissue sampling involved catching larval individuals by dipnet. To minimize the probability of collecting siblings, individuals were captured from different parts of each pond. Tail clips were taken from larger larvae. For larvae that were too small to tail clip, the whole organism was collected after being euthanized in buffered MS-222. Samples were immediately preserved in 95% ethanol and stored at -80°C once back in the lab.

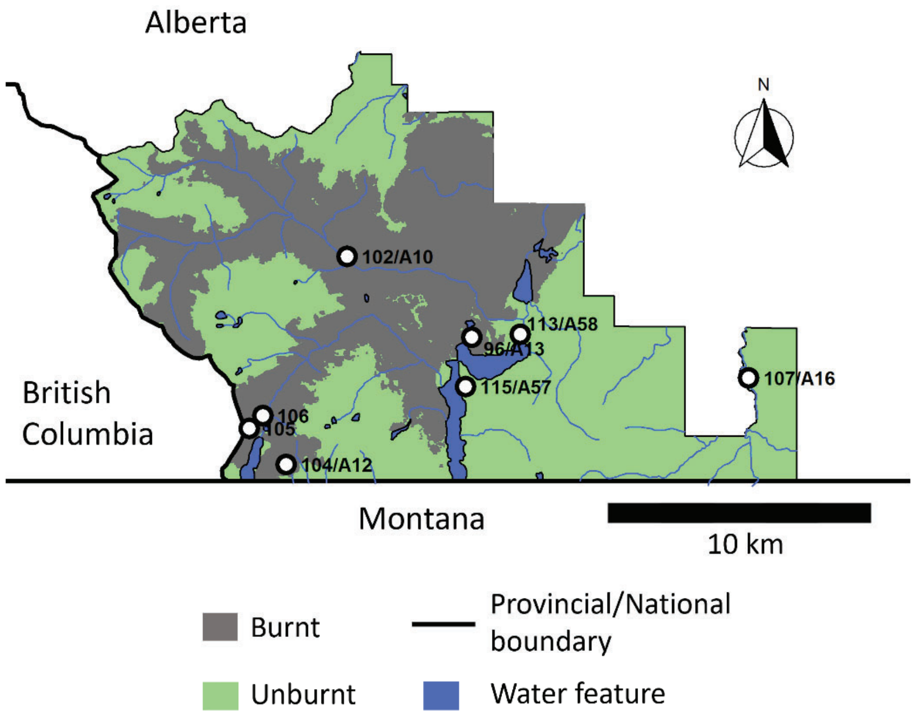


Figure 4. Long-toed salamander breeding ponds in Waterton Lakes National Park used to assess changes in genome-wide levels of genetic diversity following a severe wildfire. The extent of the 2017 Kenow burn is shown as grey shading. Tissue samples were collected from all sites in 2009 (pre-fire) and again in 2020 (post-fire). Sites are labelled as per the original number scheme of Lee-Yaw and Irwin (2012). Sites that were also included in Chapter 2 are indicated by the site identifying code used by Parks Canada.

3.3.2. DNA extraction and sequencing

Whole genomic DNA was extracted from five individuals per site per time period (N=80) using Qiagen DNeasy Blood and Tissue kits. Extractions followed the manufacturer's instructions, except that after initial overnight digestion, I added an additional 10µl of Proteinase K to the digested sample and incubated the tissues on a shaking heat block for an additional hour. The elution step followed the double elution option, using 160 µl of buffer AE. DNA was quantified using a Thermo Fisher Qubit 4 fluorometer (Thermo Fisher Scientific, Waltham, MA, USA). Samples were diluted to 20-25ng/µl and were sent to the Université of Laval Institute of

Integrative Biology and Systems for double digest restriction site-associated DNA (ddRAD; Petersen *et al*., 2012) sequencing library preparation. Specifically, double-stranded DNA was digested using the restriction enzymes *Sph1* (recognition sequence: CATGC) and *EcoR1* (recognition sequence: AATTC), both of which produce four-base overhangs (Nunziata *et al*., 2017). Unique barcode sequences corresponding to sample ID were ligated to the sticky ends of each fragment. These fragments were size selected for 150-bp reads, and then pooled for PCR amplification. Double-digest RAD libraries were then sent to Genome Quebec for paired-end sequencing on an Illumina NovaSeq 6000.

3.3.3. Assembly and filtering

De novo assembly of ddRAD loci, filtering, and SNP calling were performed in iPyrad v.0.9.82 (Eaton and Overcast, 2020). Individuals were first demultiplexed based on unique barcodes. Adaptors and restriction enzyme sites were trimmed, and only reads with a length of 35 bp or greater were retained. The maximum number of bases with low quality (*i.e.* Phred quality score < 20) was set to five per read. The minimum read depth for calling a base was set to six. To minimize missing data, a minimum of 75% of the individuals sequenced had to have data at a locus for the locus to be retained. To avoid inclusion of paralogous sites, iPyrad uses a default function that omits loci with three or more alleles when analyzing diploid organisms. The final assembly included individuals from another project in the lab. These individuals were removed and monomorphic sites resulting from their inclusion were removed ahead of the downstream analyses using the --non-ref-ac-any function in VCFtools (Danecek *et al*. 2011). The VCFtools function --thin was used to retain a single polymorphic site per RAD locus. The inclusion of close kin can impact estimates of genetic diversity (Goldberg and Waits, 2010). Although efforts were made during sampling to avoid sampling kin (see Sampling section above), I calculated kinship coefficients for each pair of individuals (Manichaikul *et al*., 2010) using the --relatedness2 program in VCFtools to ensure that the five individuals per site per time period were not full or half-siblings.

3.3.4. Changes in genetic diversity

I used four standard population genetic metrics to assess changes in genetic diversity: expected (H_S) and observed heterozygosity (H_O; Nei 1987), Wright's inbreeding coefficient (F_{IS}; Wright, 1951), and allelic richness (Nei, 1975). Expected heterozygosity reflects the probability that two alleles randomly selected from a population will be different alleles and is a measure of allelic diversity. This metric is sensitive to bottleneck events, especially in populations with small effective population sizes (Barrandeguy and Garcia, 2021). Observed heterozygosity measures the proportion of individuals with heterozygous genotypes for each locus. F_{IS} is calculated as $1 - (H_O/H_S)$ and is thus a measure of heterozygote excess or deficiency. Allelic richness measures the number of alleles present in a population, and is known to be more sensitive to population bottlenecks than expected heterozygosity (Leberg, 1992; Nei, 1975). The basic.stats function in the R package, *hierftstat* (Goudet, 2005) was used to calculate H_S, H_O and F_{IS}. Allelic richness was calculated by rarefaction based on the genotypes of individuals from each site-time period combination using the allelic.richness function in *hierftstat*. Confidence intervals for each estimate were generated using 10,000 bootstrap replicates of loci with replacement in the R package *boots* (Canty and Ripley, 2012).

Results 3.4.

I generated 1.1. billion reads across 94 samples, of which 79 were included in this project (one pre-fire sample from site 107 period was destroyed during shipping). Initial processing of all individuals resulted in 3.3 million ddRAD loci and 356,823 polymorphic sites. The average depth of coverage was 9.25X, with 12.55% missing sites. After filtering and the removal of individuals from other projects, the final dataset consisted of 33,566 SNPs. Kinship coefficients were > 0.125. Thus, no individuals were identified as full or half-siblings (Manichaikul *et al*., 2010) and all 79 samples were retained in the dataset.

Expected heterozygosity (H_s) ranged from 0.144 to 0.166 before the fire and from 0.146 to 0.190 following the fire (Figure 5A). H_s significantly increased from the pre-fire to the post-fire time periods at sites 96 and 102. No other sites exhibited significant differences in H_s between time periods (Figure 5A). In contrast, observed heterozygosity (H_o) shifted from 0.109 in the pre-fire period to 0.107 in post-fire period (Figure 5B). Sites 102 and 115 exhibited increases in H_o, whereas sites 104, 105, and 107 exhibited decreases in H_o (Figure 5B).

Values of F_{IS} were well above zero for all sites in both time periods. Mean F_{IS} increased from $F_{IS} = 0.238$ in the pre-fire period to $F_{IS} = 0.270$ in the post-fire period, with four of the five burnt sites and one out of three unburnt sites experiencing significant increases in F_{IS} (Figure 5C). These changes corresponded to changes in both H_s (sites 96 and 102) or H_o (sites 104, 105, 106 107, 115) depending on site.

Allelic richness varied among sites in the pre-fire period (AR = 1.141 to 1.161), and in the post-fire period (AR = 1.137 to 1.180). Changes in allelic richness mirrored those for H_s, with significant increases in allelic richness from the pre-fire to the post-fire time periods at sites 96 and 102 and no change at the other sites (Figure 5D).

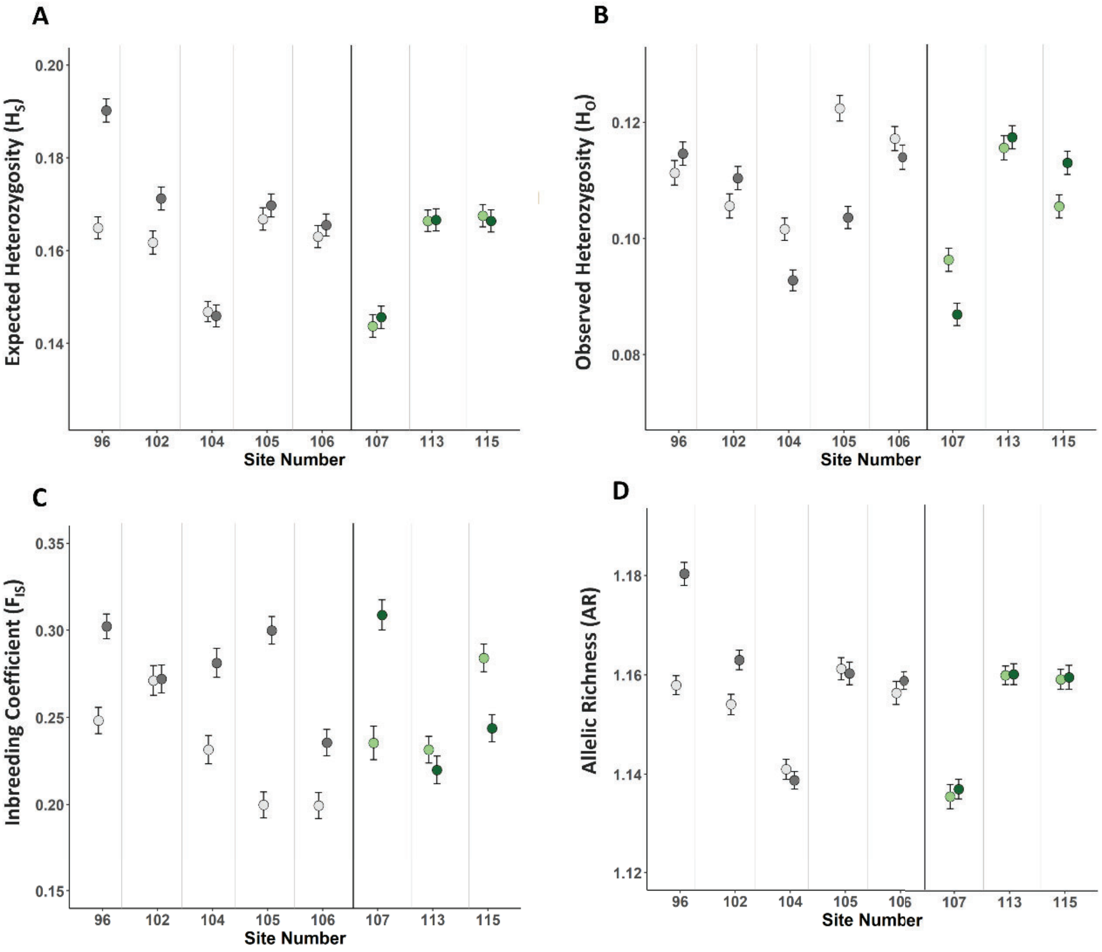


Figure 5. Estimates for (A) expected heterozygosity (H_S), (B) observed heterozygosity (H_O) (C) the inbreeding coefficient (F_{IS}) and (D) allelic richness (AR) for long-toed salamander (*Ambystoma macrodactylum*) populations in Waterton Lakes National park before (2009; light shaded circles) and after (2020; dark shaded circles) the 2017 Kenow wildfire. Sites in burnt and unburnt parts of the park are coloured grey and green respectively. Estimates reflect the average per-SNP value for each metric (N = 33,556). Error bars represent bootstrapped 95% confidence intervals.

3.5. Discussion

I examined changes in genetic diversity in the long-toed salamander following a severe wildfire in southwestern Alberta. Specifically, I compared genetic diversity from tissues collected three years after the Kenow wildfire to baseline estimates from legacy tissues collected eight years before the wildfire at eight sites in Waterton Lakes National Park. Although I found significant changes between time periods in one or more measures of genetic diversity for most sites, changes were observed in both burnt and unburnt parts of the park and are thus difficult to directly attribute to the wildfire. I discuss the implications of these results for our understanding of the effects of severe wildfire on amphibian populations.

3.5.1. Changes in genetic diversity between time points

The most striking pattern observed in the present study was the increase in F_{IS} between time points for most sites in the burn zone. F_{IS} is typically used as a measure of inbreeding within a population (Wright, 1951), and specifically measures the discrepancy between observed and expected heterozygosity. Thus, an increase in F_{IS} reflects a decrease in observed heterozygosity relative to expected heterozygosity. For sites 104, 105, 107, expected heterozygosity remained unchanged and changes in F_{IS} were driven by decreases in observed heterozygosity. Decreases in observed heterozygosity may in turn point to inbreeding, reflecting either population declines and/or reduced connectivity. Thus, at least some populations in the burnt region show negative population trends.

However, an increase in inbreeding does not appear to explain the increase in F_{IS} for site 96 in the burn zone. In this case, observed heterozygosity remained unchanged between time points and the increase in F_{IS} reflected an increase in expected heterozygosity. Site 102 in the burnt region also saw an increase in expected heterozygosity (in this case matched by an increase in observed heterozygosity and not resulting in a change in F_{IS}). Notably, allelic richness increased for both sites as well. Taken together, these results are most consistent with an influx of migrants to these sites since the original sample was taken (*e.g.* Laporte *et al*., 2016). In contrast to the other sites in the burnt region, which are high elevation sites, sites 96 and 102 are low elevation sites in river valleys. In other areas, such low elevation populations tend to be well connected (Giordano *et al*., 2007; Tallmon *et al*., 2000), and thus sites 96 and 102 may have had more opportunities for gene flow than other sites in the burn zone. Changes to the terrestrial environment associated with the wildfire may have enhanced this connectivity. For example, juvenile long-toed salamanders (*i.e.* the dispersing class) travel more quickly over structurally simple substrates (Lee-Yaw *et al*., 2015). Thus, it is possible that the initial absence of dense vegetation following the wildfire and resulting simplified terrestrial landscape facilitated increased migration between some sites.

In unburnt parts of the park, there were also changes in F_{IS} for some sites. Specifically, F_{IS} increased for site 107, and decreased for site 115. In both cases, expected heterozygosity remained unchanged and the changes in F_{IS} were entirely driven by changes to observed heterozygosity, with site 107 experiencing a decrease in observed heterozygosity, and site 115 experiencing an increase in observed heterozygosity. Although the number of sites examined was small, variation in patterns in the unburnt region of the park, which serves as a type of control in the present study, highlight that the genetics of these populations are dynamic. Thus, the wildfire is unlikely to fully explain changes observed in the burnt region.

3.5.2. Implications for understanding the effects of wildfire on amphibian populations

My study represents one of few studies that have examined the impacts of wildfire on genetic diversity in amphibian populations. Robertson *et al.* (2018) found that allelic richness and effective population sizes increased with increasing wildfire frequency and severity of the most recent wildfire in a species of hylid frog (*Hyla femoralis*) in Florida, although these trends were not significant. Furthermore, they noted that the 17 sites in their study were effectively panmictic before and after the wildfire (Robertson *et al*., 2018). The authors suggested that these patterns indicated that this species either experienced greater recruitment or increased immigration following wildfire events (Robertson *et al*., 2018). By contrast, Potvin *et al*. (2017) compared pre- and post-fire estimates of genetic diversity for two species of hylid frogs (*Litoria ewingii* and *L. paraewingi*) from 11 locations affected by a very severe wildfire in southeastern Australia. They found consistent declines in allelic richness, effective population sizes, and increases in inbreeding for both species up to two years following the wildfire (Potvin *et al.*, 2017). They also found that population connectivity was reduced following the wildfire (Potvin *et al.*, 2017). The population-specific changes in genetic diversity observed presently for the long-toed salamander suggest that the impact of wildfire on amphibian populations may be population-specific in some cases, with site-specific environmental characteristics and other demographic processes contributing to changes in genetic diversity over periods coinciding with fire events.

3.5.3. Limitations and future directions

My results represent a first-step in assessing the effects of the Kenow wildfire on genetic diversity in long-toed salamanders in Waterton. However, several limitations of this study make my findings preliminary. First, I acknowledge that with just two time points that were several years on either side of the wildfire (*i.e.* eight years pre-fire, three years post-fire), it is difficult to directly attribute any observed changes in genetic diversity within populations in the burnt region to the wildfire. In particular, some of the observed changes may have predated the occurrence of the wildfire. However, the inclusion of sites both inside and outside the burnt region in the present study at least allows me to partially disentangle the effects of the wildfire from time (*i.e.* had I observed consistent changes in the burn zone that were not matched in unburnt parts of the park, that would have been compelling evidence of a strong impact of the wildfire). In this regard, having a larger number of sites would have facilitated greater generalization of trends in impacted and unimpacted parts of the park alike. In addition to the sites presented here, I collected pre- and post-fire samples from an additional 15 sites from across the park. Sequencing of these samples is currently underway, and it will therefore be possible to expand upon my results in the near future. Additional sites and samples will also facilitate other analyses, including exploration of general changes in population connectivity and differentiation over time (*e.g.* Robertson *et al*., 2018).

Despite the limitations of my study, my results have several implications for long-toed salamander populations in southwestern Alberta. For instance, it is noteworthy that estimates of genetic diversity for populations of long-toed salamanders in Waterton, even before the wildfire, were considerably lower than genome-wide estimates reported for other amphibians. For instance, Nunziata *et al*. (2017), also using ddRAD data generated using *Sph1* and *EcoR1*, reported estimates of observed heterozygosity 52% - 175% higher than values observed here for populations of *A. opacum* and *A. talpoidium* in South Carolina. Likewise, Kosch *et al*. (2019) reported estimates of expected and observed heterozygosity as well as allelic richness in populations of the highly endangered southern corroboree frog (*Pseudophryne corroboree*) that were considerably higher than those reported here. Finally, Kan *et al*. (2021) reported much higher estimates of expected and observed heterozygosity in the endangered Anji salamander (*Hynobius amjiensis*). That the long-toed salamanders studied here have lower levels of genetic diversity than this critically imperilled species is potentially alarming given the importance of genetic diversity for long-term population persistence (Leimu *et al*., 2006; Reed and Frankham, 2003). At the same time, the low levels of genetic diversity reported here are consistent with what has been found for populations of long-toed salamanders elsewhere using microsatellites (Funk *et al*., 1999). Despite these low levels of genetic diversity, my results spanning 12 years and a major disturbance event, suggest that genetic diversity, at least in terms of allelic diversity, has remained relatively stable for most of the populations studied here. Thus, these populations may generally persist at low levels of genetic diversity without subsequent declines in population size, potentially indicating that measures of genetic diversity alone cannot predict population performance (*e.g.* Westbury *et al*., 2018). Nevertheless, low levels of genetic diversity, and a signature of increased inbreeding in some of these populations, may make long-toed salamanders in this region vulnerable to future environmental stressors. Therefore, continued population and genetic monitoring of these populations is encouraged as part of adaptive management strategies in Waterton.

CHAPTER 4: CONCLUSION

4.1. Summary of main findings

Extreme wildfire is projected to increase in frequency and severity over the coming decades. Although there have been research efforts to characterize the impacts of fire on amphibians, there are still relatively few studies that have documented the effects of wildfires of the magnitude predicted for the future (*e.g.* Coogan *et al*., 2019; Westerling *et al*., 2006). Furthermore, few studies quantifying the impacts of wildfire on amphibian populations have explored the response of populations at different levels, limiting our ability to address the population-level processes that drive patterns of response. In this thesis, I characterized the impacts of the Kenow wildfire on populations of amphibian populations in southwestern Alberta, considering both changes to occupancy and genetic diversity.

With respect to occupancy, I found limited evidence for an effect of the Kenow wildfire on overall patterns of breeding pond-occupancy or species richness in Waterton Lakes National Park. Thus, my results suggest that amphibian populations may be fairly resilient to severe wildfire, at least in the short-term. These findings are in line with trends identified in reviews of previous studies exploring the impact of wildfire on occupancy in amphibians (Hossack and Pilliod; Pilloid *et al*., 2003; Chapter 1 of the present thesis). Therefore, wildfires in general, including severe wildfires such as the Kenow wildfire, do not appear to impact the local distribution of amphibian populations, at least not in the short term.

With respect to genetic diversity, I found there were signatures of increased inbreeding at some sites, and evidence of increased genetic diversity at other sites in the burnt region. Thus, the wildfire did not have consistent effects on the genetic diversity for long-toed salamander populations. Together with two other studies looking at how wildfire effects amphibian genetic diversity, and which that found contrasting findings within the same family of frogs (*i.e.* Potvin *et al*., 2017; Robertson *et al*., 2018), my results indicate that we may not be able to draw general conclusions about the impacts of wildfire on genetic diversity in amphibians that apply across species, or even within a species. Therefore, researchers and land managers interested in understanding how wildfire will impact genetic diversity in amphibian populations (and populations of other taxa) should identify putative species traits and environmental conditions that might make some populations more vulnerable than others (Nimmo *et al*., 2022).

Joint examination of my results for the long-toed salamander yields additional insights into the responses of long-toed salamander populations to wildfire. For this species, I found occupancy decreased in the burnt region following the wildfire, although this difference was not significant. At the same time, populations demonstrated different patterns with respect to genetic diversity. Whereas some sites in the burn zone exhibited increases genetic diversity, likely reflecting an influx of alleles through gene flow, others exhibited reduced genetic diversity, likely reflecting reductions in population size following the wildfire. Thus, although most populations weathered the impacts of the Kenow wildfire, some may have been negatively impacted in ways that have implications for the long-term persistence of populations. Therefore, populations may be vulnerable to longer-acting processes or additional environmental stressors as they occur.

4.2. Limitations and future directions

Results from my thesis add to the literature suggesting that amphibian populations are largely unimpacted by wildfire, even wildfires of the magnitude studied here. However, I acknowledge some limitations to this study. First, the limited number of sites available for analysis precluded me from examining trends in different ecoregions (*i.e.* parkland, montane, and subalpine) or incorporating other environmental variables (*e.g.* elevation, wetland characteristics, *etc*.) that might influence the response of populations to wildfire. Furthermore, the temporal sampling of tissues for Chapter 3 did not preclude the possibility that the changes I reported here took place before the occurrence of the Kenow wildfire, reflecting the impact of other ecological and evolutionary processes. I also note that the data included in this thesis only extends to four years post-fire, which limits my ability to speak to longer-term impacts of this event on amphibian populations. Other studies have found that the impacts of a wildfire event may not be evident until several years have passed (*e.g.* Hossack and Honeycutt, 2017; Hossack *et al*., 2013b). Thus, I encourage Parks Canada to consider extending these monitoring programs to incorporate sites along additional environmental gradients, and to continue to monitor these populations to detect any subsequent post-fire changes (e.g.Wood *et al*., 2022).

4.3. Overall conclusion

Overall, my results, based on the analysis of two datasets spanning the occurrence the Kenow wildfire, suggest that severe wildfire does not necessarily pose an immediate threat to amphibian populations and communities. Nevertheless, some of the trends identified here suggest that additional monitoring would be prudent to rule out longer-term impacts on these specific populations.

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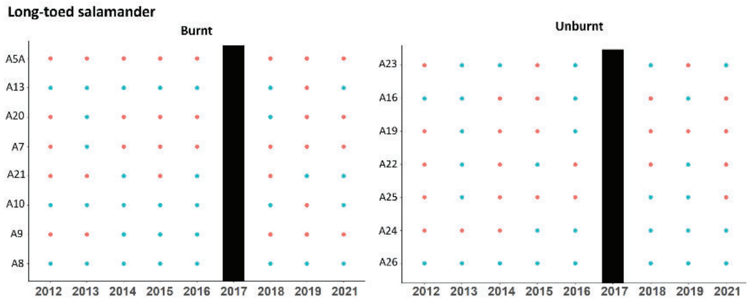
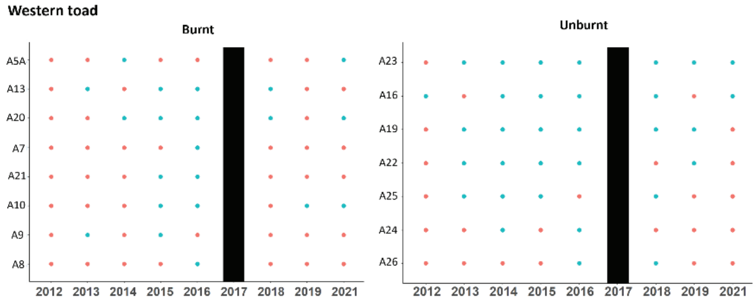
Appendix

Table S1. See the corresponding spreadsheet file. Site details and visit history of the amphibian monitoring program in Waterton Lakes National Park (see Notes tab for additional information). The first column refers to the site code. The second column refers to the position of each site relative the perimeter of the burn. The third column refers to the ecoregion for each site. The following columns refer to the year and visit number of that year (*e.g.* v1.08 refers to the first visit of 2008, v2.08 the second visit of 2008, *etc*.). The entries refer to the month (1-12) that the visit took place in. Most visits were in the fifth month of the year (*i.e.* May). A zero represents no visit occurring for that site. Changes in shading indicate formal adjustments made by the Park to the number or identity of sites visited and/or number of visits per year or timing of visits (as indicated by the visit history cell values).

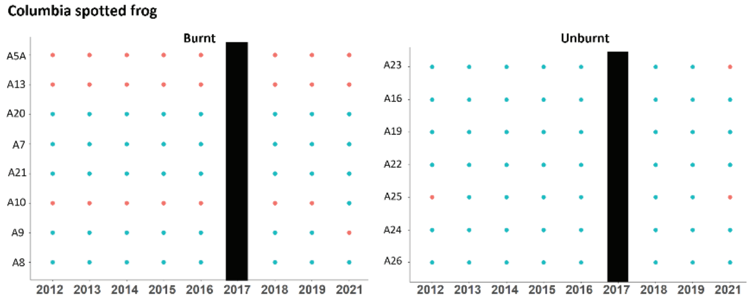
a)



b)



c)



d)

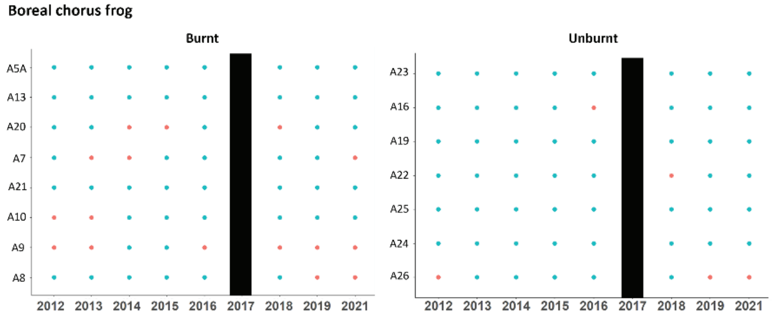


Figure S1. Detection histories of a) long-toed salamanders (*Ambystoma macrodactylum*), b) western toads (*Anaxyrus boreas*), c) Columbia spotted frogs (*Rana luteiventris*), and boreal chorus frogs (*Pseudacris maculata*) for 15 core monitoring sites in Waterton Lakes National Park surveyed from 2012 to 2021. Blue dots indicate that the species was detected at least once that year, whereas red dots indicate no detections in that year.

Table S2. Relative performance of occupancy models (intercept-only) used to determine whether Julian date, or Julian date and elevation would be used to model the effects of the wildfire on occupancy. The set of covariates that performed best based on AICc in this procedure were used when constructing the subsequent occupancy models.

Species	**Model**	**(Q)AICc[1]**	**Δ(Q)AICc[1]**	**Relative likelihood**	**(Q)AICc[1] weight**
Boreal chorus frog	**Date**	**617.82**	**0.00**	**1.00**	**0.56**
	Date + Elevation	618.30	0.48	0.79	0.44
Columbia spotted frog	Date	259.48	6.10	0.05	0.05
	Date + Elevation	**253.38**	**0.00**	**1.00**	**0.95**
Western toad	**Date**	**562.35**	**0.00**	**1.00**	**0.76**
	Date + Elevation	564.64	2.29	0.32	0.24
Long-toed salamander	Date	585.60	5.70	0.05	0.05
	Date + Elevation	**579.90**	**0.00**	**1.00**	**0.95**

[1] Data for the Columbia spotted frogs were overdispersed, and therefore QAICc is presented for this species

Table S3. Probability of false absence (P_{fa}) for those amphibian breeding ponds in Waterton Lakes National in which a particular species was seen before the 2017 Kenow wildfire but was not seen in the three years of monitoring following the fire. Three different estimates of P_{fa} were calculated depending on how probability of detection (*P*) was calculated (see main text for details).

			P_{fa}		
Species	**Site**	**Region**	**Site-specific *P***	**Nearest - neighbour grouped *P***	**Four nearest - neighbours grouped *P***
Long-toed salamander	A9	burnt	< 0.001	< 0.001	< 0.001
Long-toed salamander	A19	unburnt	< 0.001	< 0.001	< 0.001
Western toad	A9	burnt	0.28	0.32	0.001
Western toad	A21	burnt	0.13	0.21	0.32
Western toad	A24	unburnt	0.014	0.13	<0.001
Boreal chorus frog	A9	burnt	0.19	0.005	< 0.001

Table S4. Occupancy (Ψ) estimates for four amphibian species in Waterton from 2008 to 2021 based the subset of 30 sites that were visited before and after the 2017 Kenow wildfire.

Species	**Detection covariates[1]**	**Model**	**Ψ[2] (SE[3])**	***k***	**AICc**	**ΔAICc**	**AICc weight**
Long-toed salamanders	date + elevation	**Intercept**	**0.58 (0.05)**	**3**	**578.68**	**0.00**	**0.58**
		Time	0.61 (0.05), 0.54 (0.07)	4	580.67	1.99	0.22
		Region	0.59 (0.06), 0.57 (0.06)	4	581.30	2.62	0.16
		Fire	0.56 (0.08), 0.65, 0.62 (0.09), 0.43 (0.10)	6	583.79	5.11	0.05
Western toads	date	**Region**	**0.82 (0.08), 0.46 (0.07)**	**3**	**532.38**	**0.00**	**0.84**
		Fire	0.89 (0.09), 0.42(0.08), 0.72 (0.12), 0.53 (0.13)	5	535.79	3.41	0.15
		Intercept	0.63 (0.06)	2	543.96	11.58	0.00
		Time	0.62 (0.06), 0.64 (0.09)	3	546.42	14.04	0.84
Columbia spotted frogs	date + elevation	**Region**	**0.79 (0.05), 0.59 (0.05)**	**4**	**296.35**	**0.00**	**0.42**
		Fire	0.91 (0.05), 0.58 (0.07), 0.62(0.08), 0.60 (0.08)	4	299.03	1.17	0.11
		Intercept	0.68 (0.04)	3	297.58	1.23	0.23
		Time	0.73 (0.04), 0.59 (0.06)	4	299.03	2.68	0.11
Boreal chorus frogs	date	**Intercept**	**0.88 (0.03)**	**2**	**332.71**	**0.00**	**0.51**
		Region	0.93 (0.04), 0.83 (0.05)	3	333.91	1.20	0.28
		Time	0.86 (0.04), 0.93 (0.06)	3	334.69	1.98	0.19
		Fire	0.93 (0.05), 0.80 (0.06), 0.93 (0.08), 0.93 (0.08)	5	338.72	6.01	0.03

[1] The covariates used to estimate the probability of detection for each species were selected using a model selection procedure based on AICc or QAIC (Table S2).

[2] Order of Ψ estimates for the different models:
Time: pre-fire; post-fire
Region: unburnt, burnt
Fire: pre-fire unburnt, pre-fire burnt, post-fire unburnt, post-fire burnt

[3] Standard error was calculated using a non-parametric bootstrapping method.

Table S5. Occupancy (Ψ) estimates for four amphibian species in Waterton from the years 2008 to 2021 excluding site A18, an unburnt site on the otherwise burnt western side of the park.

Species	Detection covariates[1]	Model	Ψ[2] (SE[3])	*k*	AICc	ΔAICc	AICc weight
Long-toed salamanders	date + elevation	**Time**	**0.54 (0.05), 0.50 (0.06)**	**4**	**313.85**	**0.00**	**0.89**
		Intercept	0.56 (0.04)	3	318.59	4.74	0.08
		Region	0.57 (0.06), 0.56 (0.06)	4	321.06	7.21	0.02
		Fire	0.53(0.07), 0.62 (0.07), 0.63 (0.09), 0.43 (0.09)	6	324.72	10.87	0.00
Western toads	date	**Region**	**0.80 (0.07), 0.43 (0.06)**	**3**	**583.42**	**0.00**	**0.82**
		Fire	0.84 (0.08), 0.40 (0.07), 0.71 (0.12), 0.53 (0.13)	5	586.54	3.12	0.17
		Intercept	0.60 (0.05)	2	597.80	14.38	0.00
		Time	0.59 (0.06), 0.63 (0.09)	3	600.00	16.58	0.00
Columbia spotted frogs	date + elevation	**Region**	**0.83 (0.05), 0.66 (0.06)**	**4**	**351.01**	**0.00**	**0.35**
		Intercept	0.75 (0.04)	3	351.03	0.02	0.35
		Fire	0.93 (0.05), 0.63 (0.07), 0.67 (0.08), 0.72 (0.10)	6	352.52	1.51	0.16
		Time	0.78 (0.05), 0.70 (0.06)	4	352.88	1.87	0.14
Boreal chorus frogs	date	**Intercept**	**0.84 (0.03)**	**2**	**352.81**	**0.00**	**0.48**
		Region	0.90 (0.04), 0.80 (0.05)	3	353.83	1.02	0.29
		Time	0.82 (0.04), 0.88 (0.05)	3	354.59	1.78	0.20
		Fire	0.87 (0.06), 0.77 (0.06), 0.93 (0.07), 0.84 (0.07)	5	358.44	5.63	0.03

[1] The covariates used to estimate the probability of detection for each species were selected using a model selection procedure based on AICc or QAIC (Table S2).

[2] Order of Ψ estimates for the different models:
Time: pre-fire; post-fire
Region: unburnt, burnt
Fire: pre-fire unburnt, pre-fire burnt, post-fire unburnt, post-fire burnt

[3] Standard error was calculated using a non-parametric bootstrapping method.