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INTERACTIVE EFFECTS OF WILDFIRE AND DISTURBANCE HISTORY ON AMPHIBIANS AND THEIR PARASITES

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Dissertation

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Interactive effects of wildfire and disturbance history on amphibians and their parasites

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Climate-driven changes in wildfire and other disturbance regimes are expected to affect populations and communities worldwide. Understanding how these changes will affect native species is critical for future conservation efforts, especially on managed forests. Using data from several wildfires that burned between 1988 and 2003 in and next to Glacier National Park, Montana, I examined how fire affected the distribution, abundance, and infection status of 3 native amphibians. In Chapter 1, I used long-term data on wetland occupancy to show the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*) were resistant to change during the first 6 years after wildfire, but declined over longer time periods in areas of high-severity fire. In contrast, boreal toad (*Anaxyrus boreas*) occupancy increased greatly during the 3 years after wildfire burned low-elevation forests, followed by a gradual decline. In Chapter 2, I measured how the interaction of stand-replacement wildfire and forest management affected amphibian abundance and 2 nematodes that infect amphibians. Population size of salamanders was negatively related to fire severity, with stronger effects on populations that were isolated or in managed forests. These effects were not evident in the abundance of the nematode *Cosmocercoides variabilis*. Population size of spotted frogs increased weakly with burn extent in managed and protected forests, a pattern that was reflected in the greater infection intensity of the mutualistic nematode *Gyrinicola batrachiensis*. In Chapter 3, I investigated how environmental variation and habitat use affects the probability that boreal toads had chytridiomycosis, a disease linked with amphibian declines worldwide. Probability of infection was lower for toads captured terrestrially than aquatically, and was lower for toads captured in recently burned habitats compared with unburned habitats. Simulations showed that spatial variation in infection, like that related to habitat use in a heterogeneous landscape, could significantly reduce the risk of metapopulation decline. Collectively, my results underscore the importance of measuring individual-, population-, and community-level responses across a range of disturbances and in both managed and protected forests. These results will provide scientists and land managers a greater understanding of the long-term effects of wildfire on local amphibians and other native species.

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TABLE OF CONTENTS

TABLES AND FIGURES

Chapter 1

Chapter 2

Chapter 3

INTRODUCTION AND OVERVIEW

Disturbance is one of the primary ecological forces shaping biological communities. Despite its ubiquity, most early ecologists viewed disturbance as a temporary interruption of the orderly progression towards a stable community (e.g., Cowles 1899, Clements 1936). The role of disturbance as a fundamental driver of community structure and function was not widely recognized until the latter half of the 20th Century, when the influence of local disturbances on vegetation dynamics and recognition of the importance of scale were incorporated into concepts such as the intermediate disturbance hypothesis, ecosystem ecology, and patch dynamics (Cooper 1913, Watt 1947, Skellam 1951, Likens et al. 1970, Grime 1973, Pickett and White 1985). It is now a basic tenet of ecology that natural disturbances—through effects on vegetation structure or habitat, species interactions, and changes in vital rates—are critical for promoting and maintaining biological diversity (Connell 1978, Sousa 1984, Pickett and White 1985). Through these same mechanisms, however, disturbance can have negative and often unpredictable consequences, especially if the frequency or severity of disturbances is outside the range of conditions with which native species evolved.

Defined broadly, disturbance is "a discrete event that damages or kills residents on a site" (Platt and Connell 2003). This definition includes events that occur at small spatial scales, such as the toppling of a tree or damming of a stream by beaver, to events like wildfires and hurricanes that can encompass large areas and multiple populations. In western North America and many ecosystems across the world, wildfire was historically the most important natural disturbance, where it served a critical role in maintaining varied habitat conditions that supported diverse communities (DeBano et al. 1989, Hessburg and Agee 2003). Many of the clearest examples of benefits of fire come from studies of birds, which can respond quickly to post-fire changes in vegetation structure (Hutto 1995, Smucker et al. 2005). Fire can restore population size, gene flow, and metapopulation structure of reptiles surrounded by unsuitable habitat (Webb et al. 2005, Templeton et al. 2011), and it can decrease disease transmission by reducing abundance of vectors (Fyumagwa et al. 2007). Patchy habitat structure that results from fire can also facilitate the coexistence of competitors (Andersen et al. 2007).

Many of the beneficial effects of fire are documented from systems where natural disturbance regimes still resemble those of pre-European settlement, or where fire is used as a management tool to restore habitat in fire-suppressed areas. However, wildfire can cause population declines or extirpations—especially in fragmented systems or where habitat has been lost, but also in intact landscapes where the historic fire regime has not been altered (Propst et al. 1992, Smucker et al. 2005, Hossack and Pilliod 2011). Determining how species respond to wildfire in both managed and intact, protected landscapes is essential to forming effective conservation strategies. This knowledge will be especially important given expected climate-related increases in the frequency and severity of weather anomalies and natural disturbances, as well as increases in the emergence and spread of infectious diseases (Daszak et al. 2000, IPCC 2007). Understanding the relationships among disturbances has become a critical issue for conservation, especially for moisture- and temperature-sensitive species like amphibians that are often responsive to changes, and served as the primary motivation for my dissertation research.

Wildfires vary widely in their size and severity, and in most cases, direct mortality from fire is not likely to be a threat to amphibian populations (Russell et al. 1999). As a result, long time-series of data or sampling across several wildfires of different ages are often required to isolate changes from background variation (Foster et al. 1998, Kelly et al. 2011). In Chapter 1, I used 11 years of occupancy data from wetlands associated with 6 wildfires that burned in Glacier National Park, Montana, between 1988 and 2003 to evaluate predictions about how fire extent, fire severity, and interactions between wildfire and wetland isolation or forest structure affected the distribution of breeding populations. The occupancy data were collected up to 4 years before an area burned and up to 21 years after wildfire, providing a measure of short- and long-term responses. Both the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*) were resistant to change during the first 6 years after wildfire, but declined over longer time periods in areas of high severity fire. In contrast, occupancy of the boreal toad (*Anaxyrus boreas*) increased greatly in the 3 years after wildfire burned low-elevation forests, which was then followed by a gradual decline back to pre-fire levels. I found no change in occupancy in high elevation forests, where toads were abundant before wildfire.

Most research on amphibian populations and wildfire in the Northern Rockies has been conducted in protected landscapes like national parks or wilderness. To gain a broad understanding, however, it is critical to assess how populations are affected on both managed and protected landscapes. The majority of forests in the Northern Rockies are managed for timber and have extensive road networks, which can reduce population size, distribution, or connectivity of amphibians and other species (Naughton et al. 2000, Marsh and Beckman 2004, Ewers et al. 2007). Although the combined effect of stand-replacement wildfire and forest management on amphibians has not been examined, factors that reduce fitness and population growth in amphibians may be exacerbated in managed forests that burn (Beschta et al. 2004, Lindenmayer and Noss 2006). Changes in amphibian abundance could also have important implications for dependent organisms like parasites, which can be directly or indirectly affected by disturbance through changes in their own vital rates, changes in host abundance, or changes to the transmission process (Hudson et al. 2002, McCallum 2008).

In Chapter 2, I measured how the combination of stand-replacement wildfire and forest management affects amphibian abundance and 2 nematodes that commonly infect amphibians. To determine whether effects differed between protected and managed landscapes, I compared population sizes of long-toed salamanders, Columbia spotted frogs, and infection prevalence and intensity by nematodes from burned and unburned wetlands in Glacier National Park and neighboring managed forests burned by the same stand-replacement wildfires in 1988, 2001, and 2003. Population sizes of long-toed salamanders decreased as a function of increasing fire severity, with stronger negative effects for populations that were isolated or in managed forests. These negative effects were not evident in the distribution or infection intensity of the nematode *Cosmocercoides variabilis* in salamanders. In contrast, population sizes of frogs increased weakly with fire extent in both managed and protected forests. Infection intensity of the mutualistic nematode *Gyrinicola batrachiensis* in spotted frog larvae was strongly correlated with host density in wetlands, and thus was higher in burned wetlands than in unburned wetlands.

Chapter 2 presents strong independent and comparative measurements of the effects of wildfire on abundance of amphibians in managed and protected forests, as well the subsequent implication for their nematodes. Additionally, research on effects of disturbance on amphibian populations has typically used changes in distribution or indices of abundance as the response metric. Occupancy studies (like in Chapter 1) are the most practical way to make valid inferences across long time periods and large spatial scales. However, estimates of abundance or population size provide more insight into extinction risk, especially if local extinction is rare or is limited primarily to small populations (Baguette 2004).

Environmental heterogeneity caused by natural disturbances like wildfire could also modify prevalence and implications of disease. In Chapter 3, I investigated how environmental variation and habitat use by boreal toads affects the probability that they were infected by the aquatic fungus *Batrachochytrium dendrobatidis* (Bd), and the potential implication of variation in infection across a network or populations. Bd causes chytridiomycosis, a recently emerged disease that has been linked to amphibian declines globally (Berger et al. 1998, Bosch et al. 2001, Muths et al. 2003). The effects of disease in communities are complex and difficult to predict (Lafferty and Holt 2003). But how disturbance and individual habitat use interact to affect infection could have important implications for conservation, because of the broad expectations for increases in emerging infectious diseases and disturbances to have strong, negative on wildlife populations (e.g., Daszak et al. 2000, McKenzie et al. 2004).

To determine how Bd infection varied in relation to habitat use, landscape heterogeneity caused by wildfire, and demographic group (female vs. males and juveniles), I sampled boreal toads for disease across Glacier National Park during 4 summers. Probability of infection was lower for toads captured terrestrially than aquatically, and was lower for toads captured in recently burned habitats than in unburned habitats. Based on this variation and documented effects of infection on survival of boreal toads elsewhere in the region (Pilliod et al. 2010b), I used matrix model simulations to examine how spatial variation in disease prevalence among populations might affect metapopulation dynamics under different infection and dispersal scenarios. These simulations showed that spatial variation in infection, like that related to habitat use in a heterogeneous landscape, could significantly reduce the risk of metapopulation decline.

Results from this study provide a more thorough assessment of long-term responses of amphibians to wildfire than previous efforts in western North America. Although changes may be rapid and short-lived or time-lagged and persistent, some species increase after wildfire and some species decrease after wildfire, as expected in a dynamic ecosystem shaped by large disturbances (Dunham et al. 2003, McKenzie et al. 2004). Measuring these responses in protected landscapes with intact disturbance regimes is critical for forming expectations about how species should respond in managed landscapes. However, the negative effects of wildfire I documented suggest that future increases in fire severity could have negative implications for amphibians and associated species like parasites, especially on managed forests. Collectively, my results underscore the importance of measuring individual-, population-, and community-level responses across a range of disturbances in both managed and protected landscapes. These results provide scientists and land managers a greater understanding of the long-term implications of wildfire on local amphibians and other native species and highlight the importance of maintaining natural disturbance regimes and diverse habitats.

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CHAPTER 1

RAPID INCREASES AND SLOW DECLINES: VARIATION IN AMPHIBIAN OCCUPANCY ACROSS A WILDFIRE CHRONOSEQUENCE

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Abstract. Global climate change is expected to modify disturbance regimes worldwide, including increasing the frequency and severity of wildfires in western North America. Aquatic and semi-aquatic species like amphibians may be particularly sensitive to these changes because stand-replacement wildfires tend to occur during extended droughts, potentially compounding threats to individuals and populations. We still have limited understanding of the implications of these wildfires for amphibians, because the few published studies have been short-term and often only encompass 1 fire. Since 1988, several stand-replacement wildfires have burned in Glacier National Park (Montana, USA), where we have conducted long-term monitoring of wetland amphibians. This increased wildfire activity allowed us to measure responses of 3 amphibian species across fires of varying size, severity, and age in a small geographic area of similar biogeography and management. We used data from wetlands associated with 6 wildfires that burned between 1988 and 2003 to evaluate predictions about how burn extent, burn severity, and interactions between wildfire and wetland isolation or forest structure affected the distribution of breeding populations. To measure responses, we used models that accounted for imperfect detection to estimate pre-fire occupancy (0-4 years before fire) to occupancy 1-21 years after an area burned. We also estimated wetland occupancy separately for different post-fire recovery periods (e.g., 1–6 years and 7–21 years) to allow for expected non-linear, temporal changes. For the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*), the best-supported models predicted that occupancy was not affected by wildfire during the first 6 years following fire, but occupancy decreased sharply during post-fire years 7–21 in accordance with the amount of high severity burn near wetlands, a pattern consistent with reduced recruitment into local populations. There was no effect of wetland isolation for either species. Occupancy of the boreal toad (*Anaxyrus boreas*) increased greatly in the 3 years after wildfire burned low elevation forests, followed by a gradual decline to near pre-fire levels during years 7–21 after wildfire. However, we found no change in occupancy in high elevation forests, where toads were abundant before wildfire. Our results show that accounting for detection, the magnitude of change, and time lags is critical to understanding population dynamics of amphibians after large disturbances like wildfire. Our results are also important for understanding the potential threat of increases in wildfire frequency or severity to amphibians and other native species in the region.

INTRODUCTION

The frequency and severity of many disturbances have already increased or are expected to increase with global climate change and a growing human population (Dale et al. 2001, IPCC 2007), and these modified disturbance regimes will likely have broad effects on biodiversity (McKenzie et al. 2004, Scholze et al. 2006). How species respond to disturbance can depend upon the type and magnitude of disturbance, the amount and configuration of remaining habitats, and life-history characteristics that influence resistance and resilience (Keith et al. 2008, Prugh et al. 2008, Kuussaari et al. 2009). For example, the multiple life-history strategies of some fishes can help facilitate population recovery after large disturbance events, but recovery is slowed in isolated or fragmented habitats where colonization from neighboring populations is limited (Dunham et al. 2003, Burton 2005). Species' and community responses to disturbance and changing climate can also be counter to expectations (e.g., Ferraz et al. 2007, Rood et al. 2007, Ozgul et al. 2010), highlighting the need for greater knowledge of how disturbance affects species across a broad range of life history strategies and in both protected and fragmented landscapes.

The recent increase in wildfire activity in many ecosystems worldwide underscores the need for greater understanding of its effects on native species. This need is especially urgent for aquatic and moisture-sensitive species, like amphibians, because large wildfires tend to occur during periods of extended drought (Westerling et al. 2006, Morgan et al. 2008), when these species may already be challenged by environmental conditions (Pechmann et al. 1991, Lake 2003, Ruetz et al. 2005). Direct mortality from fire is not likely to be the primary threat to populations (Russell et al. 1999), but multiple disturbance-related mechanisms may interact synergistically after wildfire to reduce vital rates. For example, lack of water can cause skipped breeding opportunities and eventual extirpation of isolated populations (Corn and Fogleman 1984, Church et al. 2007), and early drying of water bodies can trigger accelerated development of larvae at the expense of juvenile size and immune function (Semlitsch et al. 1988, Gervasi and Foufopoulos 2008). Additionally, individuals that disperse away from disturbed areas, like burned or logged forests, increase their risk of desiccation and predation (Semlitsch et al. 2008, Hossack et al. 2009, Rittenhouse et al. 2009). These reduced vital rates can result in changes to the distribution of populations, although there can be also substantial lags between the time of a disturbance or loss of habitats and when those changes are manifested (Ligon and Stacey 1996, Brooks et al. 1999). As a result, it is important to measure patterns across several wildfires and with long time series of data, because the short-term studies that have been done likely represent an incomplete assessment of the effects of wildfire on amphibian populations.

Since 1988, several large wildfires have burned in Glacier National Park (NP), Montana, USA. Many of these wildfires burned areas where we were already monitoring wetland occupancy of the long-toed salamander (*Ambystoma macrodactylum*), Columbia spotted frog (*Rana luteiventris*), and boreal toad (*Anaxyrus boreas*). All 3 species breed primarily in temporary wetlands in our study area, but habits of juveniles and adults differ among species. Like most ambystomatid (mole) salamanders, long-toed salamanders spend the majority of their lives underground and are thought to be limited primarily to the area surrounding breeding sites (Rittenhouse and Semlitsch 2007). The Columbia spotted frog (hereafter, the spotted frog) is highly aquatic and moves among distinct breeding and foraging habitats in the spring and summer before migrating to permanent water bodies for hibernation (Werner et al. 2004). The boreal toad hibernates terrestrially, reducing its dependence on permanent water bodies compared with the spotted frog, and typically occurs at lower densities than the long-toed salamander and spotted frog (Werner et al. 2004).

We used our long-term monitoring data on these 3 species to evaluate support for predictions about how the distribution of breeding populations would be affected by the extent and severity of wildfire, time since fire, and the interaction between wildfire and population isolation. Specifically, we predicted the largely fossorial long-toed salamander would decline gradually after fire, especially in areas that burned with high severity and had few wetlands, and that declines would not be evident based on changes in occupancy for several years after fire. Like many other wetland-breeding salamanders, the long-toed salamander is sensitive to forest disturbances that modify habitats (Naughton et al. 2000, Semlitsch et al. 2009). We predicted no effect of wildfire on occupancy of the spotted frog except where populations were most isolated. Most spotted frog populations in our study area are small and experience high annual turnover (Hossack and Corn 2007). If dispersal is risky in a burned landscape, isolated populations of both the long-toed salamander and spotted frog may be more likely to go extinct compared with those closer to other sources of colonists (e.g., Brown and Kodric-Brown 1977). Finally, we expected a post-fire increase in occupancy by the boreal toad, but only in low-elevation forests. In Glacier NP, the boreal toad is rare in dense forests at low elevations but common in subalpine forests and tundra meadows at high elevations (Hossack et al. 2006), and often responds positively to disturbances that modify habitats (Crisafulli et al. 2005, Pearl and Bowerman 2006, Deguise and Richardson 2009). Collectively, these long-term response data are critical for forming accurate assessments of how current and future fire regimes might affect the distribution and population dynamics of wetland-associated amphibians.

METHODS

Study Area

Our research focused on 6 stand-replacement wildfires that occurred on the west side of Glacier National Park between 1988 and 2003 (Table 1, Figure 1). Three of the wildfires occurred during 2003, a year with historic dry conditions and an early fire season, ultimately resulting in the most area burned in the park since at least 1655 (Pederson et al. 2006). Four wildfires occurred primarily in low-elevation areas (Red Bench, Moose, Robert, and Middle Fork fires; wetland elevations: 982–1464 m), burning dense forests dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*) that were historically replaced by fire every ~140–340 years (Barrett et al. 1991). Two wildfires were at high elevation (McDonald Creek and Trapper Creek fires; wetland elevations: 1867–2133 m), in areas of open forests of subalpine fir (*Abies lasiocarpa*), Douglas fir, and Engelmann spruce (*Picea engalmannii*) established *ca.* 1735 (Barrett 1988).

Sampling design

To measure how amphibian occupancy changes in response to wildfires, we surveyed wetlands within each of the 6 wildfire perimeters and reference wetlands outside of each wildfire perimeter. Prior to 2002, the areas we surveyed each year were part of a long-term monitoring program and were selected without respect to wildfire boundaries (Corn et al. 2005). After the 2001 Moose fire and subsequent 2003 wildfires burned areas where we had data on amphibian occupancy (Table 1), we increased sampling effort of wetlands within and adjacent to each wildfire to measure changes in occupancy. To provide a longer-term perspective on changes in amphibian occupancy after wildfire, we also surveyed wetlands in and adjacent to areas burned by 1988 and 1998 wildfires (Table 1).

Logistical and environmental constraints limited sampling efforts in some years, so that we did not sample wetlands associated with all wildfires in all years. But each year we sampled wetlands associated with a particular wildfire, we surveyed both unburned reference and burned wetlands to provide a representative measure of occupancy. Reference wetlands had not burned since at least 1967; most had not burned in >80 years prior to our surveys. If we found previously-undetected wetlands in either unburned or burned forest, we added them to our survey list and included the data in the analysis even if we did not have pre-fire data.

Wetland sampling

We used dip-net surveys of wetlands to determine occupancy for the 3 focal species. Surveys were conducted by searching the perimeter and shallow areas (≤ 0.5 m depth) of each wetland, sweeping through vegetation and along the substrate to capture amphibian larvae (Corn et al. 2005). We timed wetland surveys to coincide with the approximate 6–8 wk period during which we expected larvae to be present, and we considered a wetland occupied only if we detected embryos, larvae, or recently metamorphosed juveniles. With the exception of 2001, most wetlands were sampled twice per year so we could use detection probabilities to produce unbiased estimates of occupancy (MacKenzie et al. 2006).

During each visit to a wetland, we recorded habitat characteristics that we expected could affect occupancy or detection of amphibians, including approximate wetland size (ha), maximum depth (< 1 m, 1– 2 m, > 2 m), extent of emergent vegetation, and percent of each wetland ≤ 0.5 m deep (Corn et al. 2005). Wetlands ranged in size from 0.01 ha to 15.6 ha (median = 0.10 ha) and most were < 1 m maximum depth. Most of these wetlands fill from snowmelt and rain in the spring, support extensive emergent vegetation (primarily *Carex* spp.), and dry by mid-August. Wildfires in Glacier NP typically occur after most seasonal wetlands have dried.

GIS Analyses

We used a geographic information system (ArcGIS 9.2) to measure landscape characteristics that we expected to influence the presence of amphibian populations. All characteristics were measured from 500-m buffers formed around the perimeter of each wetland. Wildfire information was calculated using 30-m burn severity data from the Monitoring Trends in Burn Severity project (http://mtbs.gov/index.html). We defined areas that burned with high severity as those pixels with differenced Normalized Burn Ratio (dNBR) values ≥ 550, which represents the midpoint of the moderate–high severity burn category that Key and Benson (2006) defined for several wildfires in Glacier National Park. The dNBR is based on changes in vegetation between pre-fire and post-fire Landsat imagery. We measured area of emergent wetlands and freshwater ponds in the 500 m buffers using a National Wetlands Inventory dataset (http://www.fws.gov/wetlands/data).

Statistical analyses

To measure changes in amphibian occupancy relative to the timing of wildfire, we organized data according to years before and after the wildfire to which wetlands were associated. For example, for wetlands associated with the 2003 Robert fire, surveys conducted in 1999 were coded as 4 years pre-fire, surveys conducted immediately before the fire were coded as 0 years pre-fire, and surveys conducted in 2009 were coded as 6 years post-fire. This coding scheme resulted in 5 seasons of pre-fire data and 17 seasons of post-fire data, corresponding to 4 years before to 21 years after a wildfire occurred (Figure 2). This hybrid space-for-time approach allowed us to model occupancy as a function of wildfire and time-since-fire simultaneously across data sets from each of the 6 wildfires.

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

Prior to estimating how wildfire affected occupancy, we used a used a multi-stage approach to find the best model for each species that accounted for variation in detection and occupancy, independent of a wildfire effect. Our goal was to account for "nuisance" spatial, temporal, and habitat-related variation in detection probability and occupancy so that it would not bias our inferences about effects of wildfire. We found the best detection model for each species by evaluating the effect of wetland size (normalized), percent of vegetative cover in each wetland, maximum wetland depth, and percent of each wetland that was ≤ 0.5 m deep while occupancy was held constant. We expected detection would be higher in wetlands with more shallow areas and lower in large wetlands and in those with deeper water or more vegetation. Also, we made the *a priori* decision to include a wildfire effect in all models to account for any bias in detection related to burn status.

After we found the combination of detection covariates that minimized AIC for each species (Burnham and Anderson 2002), we evaluated the effects of the same habitat covariates plus wetland elevation on the probability of wetland occupancy. Elevation was coded as low (982–1464 m) or high (1867–2133 m) to account for elevation-related variation in habitat. For each species, we added all habitat covariates to the best detection model and eliminated variables with small effect sizes until we identified the most parsimonious combination of covariates. This process resulted in a basic habitat model that we used as the starting point to measure support for hypotheses about the effects of wildfire and wetland isolation on amphibian populations.

We expected that occupancy of the long-toed salamander and spotted frog would be positively related to the proximity of suitable habitat that could host other populations. Therefore, we included area of wetland habitat (normalized) within 500 m of each surveyed wetland as an occupancy covariate in all models, except in the basic habitat model described above and in an intercepts-only model. Based on 11 years of surveying wetlands in Glacier National Park and previous descriptions of toad responses to wildfire and other disturbances (Crisafulli et al. 2005, Pearl and Bowerman 2006, Hossack and Corn 2007), we had no reason to expect isolation would affect the response by toads to wildfire, and thus did not estimate its effect.

We used a before-after-control-impact (BACI) design to evaluate changes in amphibian occupancy that were attributable to wildfire (Underwood 1992). For long-toed salamanders and spotted frogs, we started with the best detection and non-fire occupancy model and added a location term that described whether a wetland was inside or outside of a fire perimeter and a time effect that corresponded to the number of seasons before or after a wildfire. This model served as a control to measure the temporal changes in occupancy. Using this same model structure, we then added a location × time term (pre-fire vs. post-fire; hereafter "burn effect") that measured the effect of wildfire on occupancy. To determine whether the effect of wildfire on occupancy differed according to isolation, we fit a subsequent model with a burn effect × isolation interaction term. We used this same model structure to estimate occupancy as a function of the amount of severely burned forest within 500 m of wetlands, resulting in 4 BACI models based on changes in mean pre-fire (1–5 seasons) and post-fire (1–21 seasons) occupancy that included additive and interactive effects of isolation.

After fitting models based on mean pre- and post-fire occupancy for the long-toed salamander and spotted frog, we used the same models to estimate post-fire occupancy separately for 2 categories of post-fire recovery: 1–6 years after wildfire and 7–21 years after wildfire. These separate post-fire estimates allowed for detection of non-linear responses over time, like those that may be expected from a gradual decline or a temporary decline-and–recover response (Whelan et al. 2002). We chose these time periods because 6 years after fire represents the longest continuous time series of data for any fire in our dataset (the 2003 Robert fire), and because it encompasses at least 1 generation for each species.

We used a similar modeling approach to estimate occupancy of boreal toads as a function of wildfire, except we did not include isolation effects in any models. Instead, based on prior knowledge of the study system, we expected different population responses between open forests at high elevations and dense forests at low elevations, similar to responses by many bird species that vary according to forest structure before wildfire (e.g., Kotliar et al. 2002). To measure responses at different elevations, we included burn effect × elevation and burn severity × elevation interactions. Previous analyses also indicated transient changes in occupancy by toads after wildfire that were driven by change s in colonization and extinction (Hossack and Corn

2007). To more accurately capture these brief so , we estimated occupancy separately for post-fire seasons 1–3, 4–6, and 7–21 in addition to the basic pre-fire vs. post-fire BACI models that we fit for the long-toed salamanders and spotted frog.

In total, we fit 12 models for each of the 3 species, which included 2 models that measured temporal and spatial variation in occupancy independent of a fire effect, 8 models that compared changes in occupancy after wildfire, a basic habitat model, and an intercepts-only model. All models were parameterized so that effect of wildfire (including interaction terms) was estimated with its own intercept and slope for each time period. We measured support for models using differences in the Akaike Information Criterion (AIC) and model weights (w_i), which represent the probability that a particular model is the best for a set of data and fitted models (Burnham and Anderson 2002).

RESULTS

In the basic habitat model that was used as the starting point for estimating effects of wildfire, occupancy of long-toed salamanders was negatively related to elevation and positively related to increasing amounts of wetland vegetation (Table 2). Detection probability for long-toed salamanders increased from 0.82 (SE = 0.03) before wildfire to 0.89 (0.01) after wildfire, but it increased equally in unburned and burned wetlands (Table 2). The 5 models we fitted with 3 time periods received almost all of the model support, indicating occupancy differed between pre- and post-fire periods, as well as between the 2 recovery periods 1–6 years after fire and 7–21 years after fire. The best model for salamanders predicted that occupancy did not differ with regards to burn severity during the first 6 years following fire, but it decreased during post-fire years 7–21 in accordance with the amount of high severity burn near wetlands (Table 3, Figure

3a). Models that described salamander occupancy as simply a function of time and space (no fire effect) or that described variation in occupancy as a function of wildfire extent received moderate support (Table 3). Models that included interactions between fire effects and wetland isolation received little support (Table 3), likely because isolation by itself had little effect on occupancy (Table 2).

Occupancy of the spotted frog increased as a function of wetland size and vegetation, and was lower in high elevation wetlands than in low elevation wetlands (Table 2). Detection probability was a function of wetland size and increased from 0.77 (0.05) before wildfire to 0.88 (0.02) after wildfire. The post-fire increase in detection was larger in wetlands that burned (Table 2). The top-ranked model for the spotted frog was clearly the best of the set and described occupancy as an interaction between time since fire and burn severity, with separate estimates during years 1–6 and 7–21 after fire (Table 4). Occupancy did not differ with regards to burn severity during the first 6 years after wildfire, but it decreased as a function of the amount of high severity burn near wetlands 7–21 years after fire (Figure 3b). The second-ranked model for this data set predicted stable occupancy in unburned sites, but predicted a small increase for burned sites 1–6 years after wildfire before decreasing during 7–21 yrs after fire, similar to the burn severity model. We also found evidence of a weak, additive effect of wetland isolation, which predicted greater occupancy in areas with less wetland habitat (Table 2, Table 4).

Occupancy of boreal toads increased as a function of elevation, wetland size, and amount of vegetation (Table 2). Detection was high across the study period, but it decreased from 0.95 (05) to 0.90 (0.02) after wildfire because detection probability decreased in wetlands that burned (Table 2). The model that described occupancy as an interaction between burn extent and elevation received overwhelming support as the best model (Table 5). At low elevations, occupancy increased greatly in the 3 years after fire, followed by a gradual decline during years 4–6 and 7–21 after wildfire (Figure 4a). In contrast, toads occupied most high-elevation wetlands regardless of wildfire (Figure 4b). Occupancy in these wetlands declined in both burned and unburned wetlands over time, with weak evidence that the declines were greater in burned wetlands.

DISCUSSION

By comparing time series of occupancy data for 268 wetlands that from 4 years before wildfire to 21 years after wildfire, we were able to measure how wildfire and the severity with which it burned, patch quality, and wetland isolation affected the distribution of breeding populations of 3 species of amphibians. Accounting for detection error improved our ability to draw inferences related to the effects of wildfire, especially because detection for the spotted frog and boreal toad covaried with wildfire but in opposite directions. Our results show that changes to the distribution of breeding populations range from rapid increases in occupancy by the boreal toad shortly after an area burns, to time-lagged declines in occupancy by the long-toed salamander and spotted frog. Overall, these results show that accounting for detection, burn severity, and time lags is critical to understanding the potential current and future threat of wildfire to populations.

Inference about the importance of wildfire to occupancy of the long-toed salamander was weaker than for the spotted frog, but breeding populations of both species were less likely to occupy wetlands where burn severity was high. Notably, this severity effect was not evident until > 6 years after disturbance. Declines and local extinctions after disturbance may take several years to be detectable (e.g., Ligon and Stacey 1996, Findlay and Bourdages 2000), making sampling designs based on disturbance chronosequences an effective method to measure timing of declines and recoveries (DeWalt et al. 2003, Kelly et al. 2011). Because wetlands burned by the oldest fire (1988 Red Bench fire) were surrounded by the highest mean severity, it is difficult to separate the effect of time-since-fire and burn severity. However, for both species, occupancy was similar in unburned wetlands and wetlands surrounded by little high-severity burn during years 1–6 and 7–21 after wildfire. Furthermore, the mean severity around wetlands within the 2003 Trapper Creek fire was similar to that of wetlands surrounded by the 1988 Red Bench fire. Many wetlands within the perimeter of the 2003 Robert fire also burned more severely than those surrounded by the 1988 fire. Sampling wetlands associated with 6 wildfires from a small geographic area of similar biogeography and uniform management also provided a level of spatial and temporal replication that is uncommon in studies of wildlife responses to wildfire. Thus, it seems unlikely that lower occupancy in areas of high burn severity resulted from differences in habitat quality among areas.

The slow response by the long-toed salamander and spotted frog indicates reductions in occupancy were more likely from changes in vital rates rather than immediate extirpation of populations. Reduced colonization rates in disturbed or fragmented habitats can also cause time-lagged declines (Brown and Kodric-Brown 1977), but our data indicate habitat quality was more important that than wetland isolation, regardless of burn severity. Occupancy of the long-toed salamander was unrelated to wetland isolation, perhaps because the density of wetlands in our study area was high and salamanders occupied most potential breeding sites. Counter to our expectations, probability of occupancy by the spotted frog increased with isolation in both unburned and burned areas. It is possible that measures of wetland isolation at 500 m, like those we used, are less useful for detecting effects of isolation than measures at larger spatial scales.

However, this lack of a relationship with isolation is consistent with other several studies of amphibians and other species with spatially-structured populations in intact landscapes, where turnover in occupancy is less common than in fragmented landscapes (Marsh and Trenham 2001, Baguette 2004). This positive relationship between occupancy and wetland isolation for the spotted frog is also consistent with the conspecific attraction hypothesis, which posits that females are more attracted to large breeding congregations, and males should abandon wetlands with few conspecifics if a large congregation is nearby (Ray et al. 1991, Schmidt and Pellet 2005).

Lower occupancy over time in areas of high severity burn regardless of wetland isolation matched our prediction for the long-toed salamander, but was opposite of our prediction for the spotted frog. The spotted frog and many other anurans are more common at wetlands with open canopies (Werner and Glennemeier 1999, Pearl et al. 2007a); thus, we expected a neutral or even positive response by spotted frogs to wildfire except in areas where populations were most isolated. Our second-ranked model for the spotted frog predicted a small increase in occupancy in burned wetlands 1–6 years after wildfire, but like the top-ranked burn severity model, it also predicted a large decline in occupancy in burned wetlands 7–21 years after wildfire compared to unburned wetlands. These results suggest areas burned by high severity wildfires could be ecological traps (Schlaepfer et al. 2002), where post-fire conditions are attractive to adult frogs but represent poor habitat for juveniles.

The negative effect of wildfire on occupancy of the long-toed salamander and spotted frog differs from a previous study that found no change in occupancy for these species between the 3 years before and 3 years after the 2001 Moose fire (Table 1; Hossack and Corn 2007). Importantly, we did not estimate the effect of burn severity near wetlands in the previous study.

Among burned sites in our current study, total area that burned and the area burned with high severity weak correlation (Spearman's r = 0.27), indicating that one measure is not a substitute for the other. Severity represents post-fire changes in vegetation and is more likely to reflect modifications to habitat and microclimate than simple measures of burn extent (Key and Benson 2006, Guscio et al. 2008, Hossack et al. 2009). Declines or losses of amphibian populations after wildfire have been linked most strongly to high severity fire and related post-fire changes, especially for salamanders and in managed or fragmented landscapes (Major 2005, Rochester et al. 2010, Hossack and Pilliod 2011). Similarly, severe wildfire and drought in eucalypt forests have been associated with persistent declines of small, ground-dwelling mammals and some birds, with different forms and timing of responses among species (Whelan et al. 2002, Recher et al. 2009, Kelly et al. 2011).

Mechanisms that drive population change of amphibians after habitat disturbance are still not well understood. However, several recent experiments have shown removal of forest canopy and woody debris can reduce dispersal, survival, and other vital rates of juvenile amphibians (Semlitsch et al. 2009, Popescu and Hunter 2011). In areas of low quality habitat, juveniles crowd into the few high quality habitats and experience strong density-dependent mortality (Patrick et al. 2008). Similar mechanisms could operate in areas of severe fire that lose woody debris and other cover (Guscio et al. 2008), and population growth of both the long-toed salamander and spotted frog is expected to be highly sensitive to reductions in juvenile survival (Biek et al. 2002, Vonesh and Cruz 2002). If survival of adults is also reduced, population growth would likely decline even more quickly, potentially increasing local extinction rates and resulting in the lower occupancy rates we observed in areas that burned with high severity.

In contrast to occupancy patterns of the long-toed salamander and spotted frog, the response of the boreal toad was rapid and positive. Occupancy of the boreal toad increased greatly during the first 3 years after wildfire in low-elevation forests and then decreased to near pre-fire levels 7–21 years after wildfire. This post-fire increase was driven by colonization of several previously unoccupied wetlands the first year after wildfire, a pattern that has been documented for the boreal toad after other disturbances (Crisafulli et al. 2005, Pearl and Bowerman 2006). More than 20 years after extensive wildfires in Yellowstone National Park (Wyoming, USA), boreal toad populations near burned forests had greater genetic connectivity than populations farther from burned areas, suggesting a similar pattern of increased colonization after wildfire (Murphy et al. 2010). Also, some endangered toads in Europe are more abundant in areas with frequent disturbances that maintain a mix of habitats in different successional stages (Denton et al. 1997, Tockner et al. 2006, Warren and Büttner 2008). We do not know what triggers the response of the boreal toad to disturbance, the source of colonists, and why occupancy declines rapidly after an initial post-fire colonization phase. However, this pattern resembles the facilitation and decline response typical of some birds and other species that increase in abundance after a temporary change in resources and can have a lasting effect on population structure and genetics (Whelan et al. 2002, Smucker et al. 2005, Schrey et al. 2011).

Although the boreal toad and some other amphibians can respond positively to many forms of disturbance, the response is context specific and cannot be generalized too broadly, as evidenced by the lack of change in occupancy by toads after wildfire at high elevations in our study area. We suspect the null response by the boreal toad to wildfire at high elevations reflects the reflect the extent of change effected by wildfire in low- and high-elevation forests. Most low-elevation wetlands in our study areas were embedded in dense forests, whereas wetlands in high-elevation forests were more likely to be in sparse forest or open meadows that experience less relative change in canopy cover and solar insolation after wildfire. Similarly, responses of many birds to wildfire varies with forest structure before wildfire and the magnitude of change caused by fire (Kotliar et al. 2002). Toads also bred in most high-elevation wetlands in our study area before wildfire, reducing the capacity for an increase in occupancy.

The different responses we documented to wildfire extent and burn severity created distinct temporal and spatial patterns in amphibian occupancy. We found additional evidence that disturbance can benefit some amphibians, depending upon forest structure before wildfire. Along with other species that respond positively to wildfire, these results reinforce the importance of maintaining natural disturbance regimes for diverse communities (Russell et al. 1999, Smucker et al. 2005). We also found strong evidence of time-lagged declines in occupancy of the long-toed salamander and spotted frog, but only in areas that burned with high severity. Native species in the region evolved in dynamic ecosystems shaped by large disturbances (Dunham et al. 2003, McKenzie et al. 2004). Temporary declines after large disturbances should be expected for many species, and measuring patterns of decline and eventual recovery in protected landscapes is critical for forming expectations about how species should respond to these disturbances.

More importantly, our data highlight the potential negative effects from expected changes to climate-associated disturbance regimes, even to species considered relatively resistant to disturbance, like the long-toed salamander and spotted frog (Hossack and Corn 2007). The consequences of changing disturbance regimes will likely be even more important outside of protected landscapes, where populations or connectivity may already be reduced (Naughton et al. 2000, Dunham et al. 2003, Burton 2005). Extending our results outside of protected landscapes will be critical for development of models to predict where and under what conditions wildfire might be a significant threat to populations and to help prioritize targeted conservation efforts.

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Table 1. Wildfires in Glacier National Park, Montana (USA), sampled to measure changes in wetland occupancy by amphibians. High severity indicates the mean (range, in parentheses) area (for burned wetlands only) that burned with high severity within 500 m around the perimeter of wetlands.

Wildfire	Fire size (ha)	Wetlands surveyed (reference/burned)	High severity (%)	Years sampled
1988 Red Bench	14584	11/21	51.3 (4.9 – 83.8)	2001–2005, 2008–2009
1998 McDonald Creek	3544	6/9	28.9 (2.0 – 80.2)	2001–2002, 2004–2009
2001 Moose	28574	41/42	17.5 (0.01 – 70.4)	1999–2006, 2008–2009
2003 Middle Fork	4855	4/9	0.40 (0.0 – 1.5)	2001, 2004–2009
2003 Robert	21908	17/92	38.9 (0.4 – 98.9)	1999–2009
2003 Trapper Creek	7446	6/10	46.9 (1.7 – 78.7)	2001–2002, 2004–2009

Table 2. Model-averaged occupancy and detection parameters (unconditional SE) for covariates used to measure the effect of wildfire on the distribution of 3 amphibian species. The detection parameters "Before" and "After" refer to detection before and after wildfire occurred. "Burned" is the difference in detection between burned and unburned wetlands. Isolation is the amount of wetland habitat within 500 m of each sampled wetland. For the boreal toad, a model that included an interaction with the elevation covariate received all the model weight, which precluded averaging the main effect. The elevation parameter below is the average estimate from other models with the same time structure as the best model.

	Occupancy ($\hat{\Psi}$)				Detection ($\hat{p}$)			
Species	Elevation	Area	Vegetation	Isolation	Before	After	Burned	Area
long-toed salamander	-1.99 (0.27)	—	2.19 (0.34)	0.04 (0.10)	1.50 (0.21)	2.06 (0.14)	-0.05 (0.21)	—
Columbia spotted frog	-1.33 (0.46)	4.32 (0.56)	1.92 (0.35)	-0.21 (0.09)	1.04 (0.29)	1.02 (0.23)	0.82 (0.27)	-0.51 (0.12)
boreal toad	4.28 (0.39)	0.66 (0.20)	0.62 (0.51)	—	3.03 (1.12)	3.61 (0.73)	-1.42 (0.77)	—

Table 3. Models used to estimate the effects of wildfire on wetland occupancy (Ψ) by breeding populations of the long-toed salamander (*Ambystoma macrodactylum*), after accounting for the effects of wetland elevation, vegetation, and wetland isolation. Isolation is the area of wetlands within 500 m of the sampled site. Models were structured so occupancy was estimated as time-constant (1 time period [Time]) or varying over time periods before and after wildfire occurred: 2 time periods (4–0 yrs before and 1-21 yrs after), or 3 time periods (4–0 yrs before,1–6 yrs after, and 7–21 yrs after). "Location" indicates whether a wetland was inside or outside of a wildfire perimeter, including before a wildfire occurred. The covariates "Burned" and "Severity" estimate the change in occupancy that resulted after wildfire. Severity is the percent of area within 500 m of wetlands that burned with high severity. Models are ranked according to ΔAIC and model weights (w_i).

Model	Time	-2log(*L*)	k	ΔAIC	w_i
Ψ (Elevation, Vegetation, Isolation, Severity)	3	2186.96	12	0.00	0.57
Ψ (Elevation, Vegetation, Isolation, Location)	3	2193.29	10	2.33	0.18
Ψ (Elevation, Vegetation, Isolation, Burned)	3	2189.35	12	2.39	0.17
Ψ (Elevation, Vegetation, Isolation, Severity, Isolation × Severity)	3	2191.09	13	6.13	0.03
Ψ (Elevation, Vegetation, Isolation, Burned, Isolation × Burned)	3	2191.48	13	6.52	0.02
Ψ (Elevation, Vegetation)	1	2206.18	6	7.22	0.02
Ψ (Elevation, Vegetation, Isolation, Severity, Isolation × Severity)	2	2199.12	11	10.16	0.00
Ψ (Elevation, Vegetation, Isolation, Severity)	2	2201.31	10	10.35	0.00
Ψ (Elevation, Vegetation, Isolation, Burned)	2	2203.64	10	12.68	0.00
Ψ (Elevation, Vegetation, Isolation, Location)	2	2205.85	9	12.89	0.00
Ψ (Elevation, Vegetation, Isolation, Burned, Isolation × Burned)	2	2204.59	11	15.63	0.00
Ψ (.)	1	2489.53	2	282.57	0.00

*We used the same detection structure (*p*) for all models (*p*[Location, before vs. after wildfire]) except for the intercepts-only model, where *p*(.).

Key: -2log(*L*), -2 log-likelihood; k, number of model parameters; AIC, Akaike Information Criterion; ΔAIC, difference in the Akaike Information Criterion (AIC) between a particular model and the top-ranked model.

Table 4. Models used to estimate the effects of wildfire on wetland occupancy (Ψ) by breeding populations of the Columbia spotted frog (*Rana luteiventris*), after accounting for the effects of wetland elevation, size (Area), vegetation, and wetland isolation. Isolation is the area of wetlands within 500 m of the sampled site. Models were structured so occupancy was estimated as time-constant (1 time period [Time]) or varying over time periods before and after wildfire occurred: 2 time periods (4–0 yrs before and 1-21 yrs after), or 3 time periods (4–0 yrs before,1–6 yrs after, and 7–21 yrs after). "Location" indicates whether a wetland was inside or outside of a wildfire perimeter, including before a wildfire occurred. The covariates "Burned" and "Severity" estimate the change in occupancy that resulted after wildfire. Severity is the percent of area within 500 m of wetlands that burned with high severity. Models are ranked according to ΔAIC and model weights (w_i).

Model	Time	-2log(*L*)	k	ΔAIC	w_i
Ψ (Elevation, Area, Vegetation, Isolation, Severity)	3	1783.52	14	0.00	0.96
Ψ (Elevation, Area, Vegetation, Isolation, Burned)	3	1790.59	14	7.07	0.03
Ψ (Elevation, Area, Vegetation, Isolation, Severity, Isolation × Severity)	3	1791.66	15	10.14	0.01
Ψ (Elevation, Area, Vegetation, Isolation, Burned, Isolation × Burned)	3	1792.71	15	11.19	0.00
Ψ (Elevation, Area, Vegetation, Isolation, Severity)	2	1801.19	12	13.67	0.00
Ψ (Elevation, Area, Vegetation, B/A, Isolation, Location)	3	1801.98	12	14.46	0.00
Ψ (Elevation, Area, Vegetation, Isolation, Burned, Isolation × Burned)	2	1804.39	13	18.87	0.00
Ψ (Elevation, Area, Vegetation, Isolation, Severity, Isolation × Severity)	2	1806.13	13	20.61	0.00
Ψ (Elevation, Area, Vegetation)	1	1816.23	8	20.71	0.00
Ψ (Elevation, Area, Vegetation, Isolation, Burned)	2	1808.73	12	21.21	0.00
Ψ (Elevation, Area, Vegetation, B/A, Location, Isolation)	2	1812.46	11	22.94	0.00
Ψ (.)	1	2052.91	2	245.39	0.00

*We used the same detection structure (*p*) for all models (*p*[Area, Location, before vs. after wildfire]) except for the intercepts-only model, where *p*(.).

Key: *T*, number of time periods for which we estimated occupancy; -2log(*L*), -2 log-likelihood; k, number of model parameters; AIC, Akaike Information Criterion; ΔAIC, difference in the Akaike Information Criterion (AIC) between a particular model and the top-ranked model.

Table 5. Models used to estimate the effects of wildfire on wetland occupancy (Ψ) by breeding populations of the boreal toad (*Anaxyrus boreas*), after accounting for the effects of wetland elevation, size (Area), and vegetation. Models were structured so occupancy was estimated as time-constant (1 time period [Time]) or varying over time periods before and after wildfire occurred: 2 time periods (4–0 yrs before and 1-21 yrs after), or 4 time periods (4–0 yrs before, 1–3 yrs, 4–6 yrs, and 7–21 yrs after). “Location” indicates whether a wetland was inside or outside of a wildfire perimeter, including before a wildfire occurred. The covariates “Burned” and “Severity” estimate the change in occupancy that resulted after wildfire. Severity is the percent of area within 500 m of wetlands that burned with high severity. Models are ranked according to ΔAIC and model weights (w_i).

Model	Time	-2log(L)	k	ΔAIC	w_i
Ψ (Elevation, Area, Vegetation, Burned, Elevation × Burned)	4	891.17	14	0.00	0.99
Ψ (Elevation, Area, Vegetation, Severity)	4	901.11	14	9.94	0.01
Ψ (Elevation, Area, Vegetation, Severity, Elevation × Severity)	4	902.49	14	11.32	0.00
Ψ (Elevation, Area, Vegetation, Burned, Elevation × Burned)	2	914.36	10	15.19	0.00
Ψ (Elevation, Area, Vegetation, Location)	4	913.22	11	16.05	0.00
Ψ (Elevation, Area, Vegetation, Burned)	4	907.80	14	16.63	0.00
Ψ (Elevation, Area, Vegetation, Severity)	2	932.42	10	33.25	0.00
Ψ (Elevation, Area, Vegetation, Severity, Elevation × Severity)	2	933.43	10	34.26	0.00
Ψ (Elevation, Area, Vegetation, Location)	2	938.62	9	37.45	0.00
Ψ (Elevation, Area, Vegetation, Burned)	2	937.22	10	38.05	0.00
Ψ (Elevation, Area, Vegetation)	1	968.90	6	61.73	0.00
Ψ (.)	1	1279.91	2	364.74	0.00

*We used the same detection structure (p) for all models (p[Location, before vs. after wildfire]) except for the intercepts-only model, where p(.).

Key: T, number of time periods for which we estimated occupancy; -2log(L), -2 log-likelihood; k, number of model parameters; AIC, Akaike Information Criterion; ΔAIC, difference in the Akaike Information Criterion (AIC) between a particular model and the top-ranked model.

FIGURE LEGENDS

Figure 1. Location of 85 unburned wetlands (white circles) and 183 burned wetlands (black circles) associated with 6 wildfires that burned in Glacier National Park, Montana (USA), between 1988 and 2003. Wetlands were surveyed for amphibians between 1999 and 2009. Areas in yellow indicate the perimeter of wildfires. Brown indicates areas of high-severity burn.

Figure 2. Number of sites surveyed in Glacier National Park between 1999 and 2009 relative to the number of years before (-4–0) and after (1–21) wildfire occurred. Sites coded “0” were surveyed prior to a wildfire burning that same season.

Figure 3. Estimated occupancy (± 1 approximate SE) of the long-toed salamander (*Ambystoma macrodactylum)* and Columbia spotted frog (*Rana luteiventris*) relative to amount of area within 500 m of wetlands that burned with high severity (*x*-axis) and time since wildfire. In each graph, open bars represent occupancy during the first 6 years after wildfire and gray bars represent occupancy during years 7–21 after wildfire.

Figure 4. Estimated occupancy (± 1 approximate SE) of the boreal toads (*Anaxyrus boreas*) in unburned (empty bars) and burned wetlands (filled bars) at low elevation (<1465 m) and high elevation (>1866 m) during the 5 summers years before wildfire and 1–21 years after wildfire (yrs. 1-3, 4-6, 7-21; *x*-axis).

Figure 1.

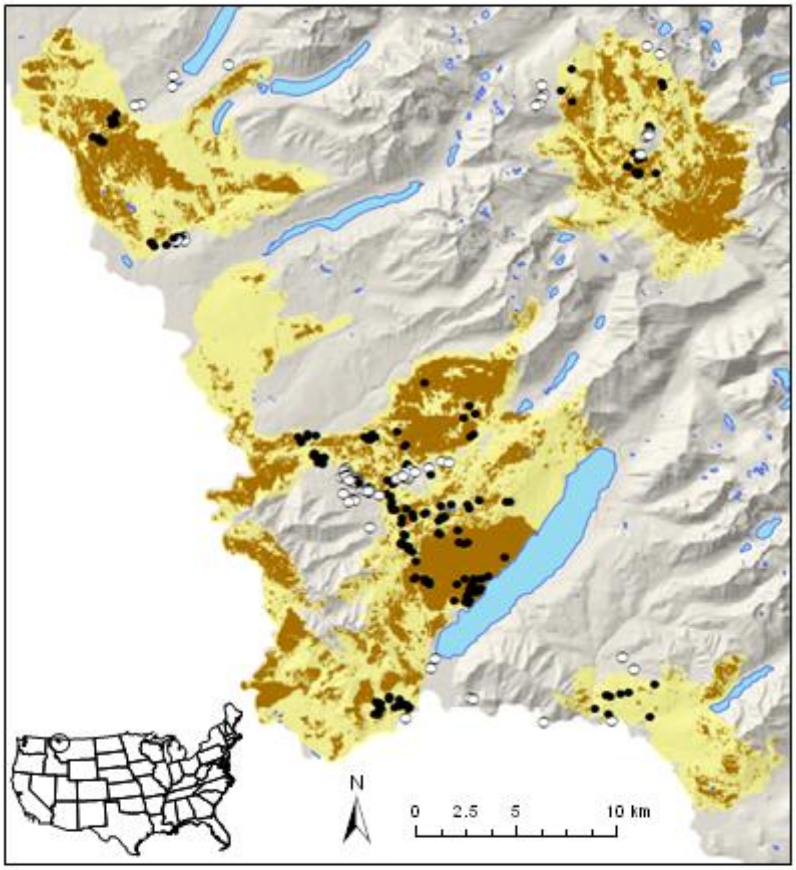


Figure 2.

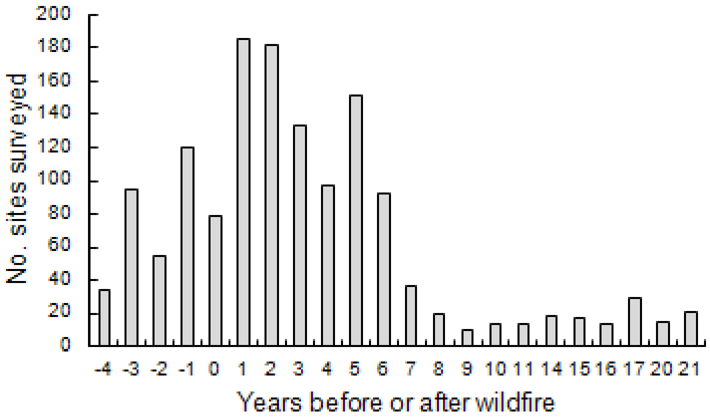


Figure 3.

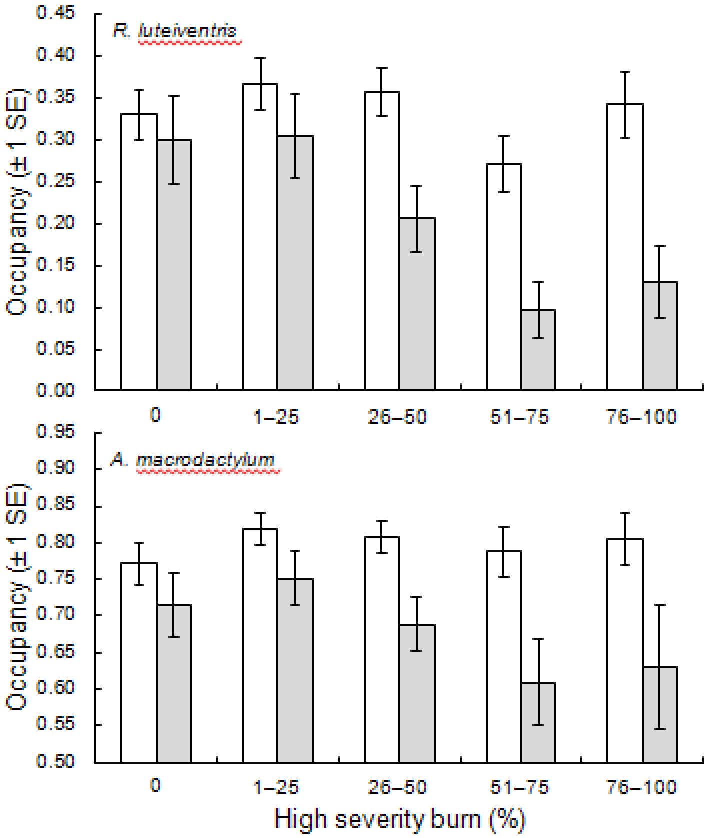
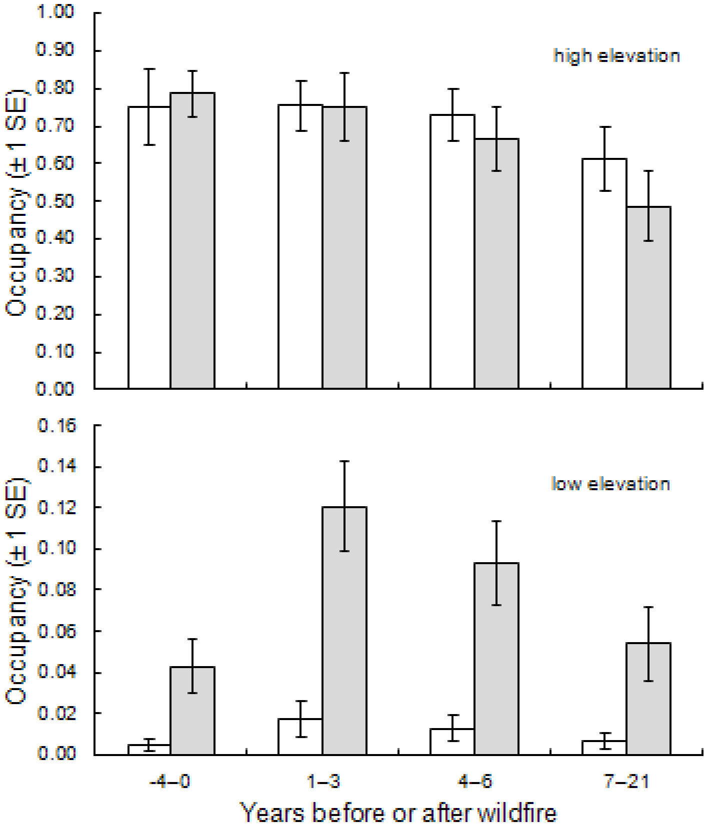

R. luteiventris
0.45
0.40
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
Occupancy (± 1 SE)
0
1–25
26–50
51–75
76–100
A. macrodactylum
0.95
0.90
0.85
0.80
0.75
0.70
0.65
0.60
0.55
0.50
Occupancy (± 1 SE)
0
1–25
26–50
51–75
76–100
High severity burn (%)

Figure 4.


Occupancy (± 1 SE)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
high elevation
Occupancy (± 1 SE)
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
low elevation
-4–0
1–3
4–6
7–21
Years before or after wildfire

INTERACTIVE EFFECTS OF WILDFIRE, FOREST MANAGEMENT, AND ISOLATION ON ABUNDANCE OF AMPHIBIANS AND THEIR NEMATODES

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Abstract. Projected increases in wildfire and other climate-driven disturbances will affect populations worldwide. These effects may be magnified by synergisms with human disturbances, such as forest management activities that fragment habitats and alter microclimates. Previous research in the Northern Rockies has documented weak negative effects of wildfire on amphibians, but this research has been restricted primarily to protected landscapes. Furthermore, we know little about how changes in habitat or hosts populations as a result of disturbances like wildfire affect directly-transmitted parasites. Parasites represent a large component of biodiversity and can affect host fitness, host population dynamics, and can modify species interactions. To determine how wildfire affects amphibian populations and their parasites, and whether the effects differ between protected and managed landscapes, we compared population sizes of male long-toed salamanders (*Ambystoma macrodactylum*) and female Columbia spotted frogs (*Rana luteiventris*) in burned and unburned wetlands in Glacier National Park and neighboring managed forests burned by the same stand-replacement wildfires in 1988, 2001, and 2003. We also compared prevalence and infection intensity by a generalist nematode that infected salamanders and a specialist nematode that infected spotted frog larvae. Population sizes of long-toed salamanders decreased with increasing burn severity, with stronger negative effects on populations that were isolated or in managed forests. These negative effects were not evident in the distribution or infection intensity of the generalist nematode *Cosmocercoides variabilis* in salamanders. In contrast, population sizes of frogs increased weakly with burn extent in both managed and protected forests. Infection intensity of the specialist nematode *Gyrinicola batrachiensis* in larvae of the Columbia spotted frog was strongly correlated with host density in wetlands, and thus was higher in burned wetlands than in unburned wetlands. These results show that effects of wildfire on amphibian populations depend upon burn severity, isolation, and prior

land use. Through subsequent effects on the abundance of a specialist parasite, these results also illustrate how large disturbances like wildfire can affect communities across trophic levels.

INTRODUCTION

Climate-driven changes to disturbance regimes are expected to have widespread effects on biological communities. In many areas, including western North America, these changes will likely include altered precipitation regimes, greater intensity of droughts, and increased frequency and severity of wildfires and other disturbances (Westerling et al. 2006, IPCC 2007). In most cases, these changes will occur in working landscapes that have been altered by various forms of management or fragmentation. Consequently, understanding how these climate-related changes will interact with human land use has become a major emphasis for conservation (Laurance and Williamson 2001, Kuussaari et al. 2009), and may be especially important for species like amphibians that are often responsive to habitat change. These changes and their interactions with land use histories could also have large effects on abundance, community structure, or ecological effects of parasites (Gulland et al. 1993, Kutz et al. 2005). Parasites represent a large but often hidden component or biodiversity and often at greater risk of decline after disturbances than are their hosts (Dunn et al. 2009).

Wildfire is an integral component of many ecosystems, where it serves a critical role in maintaining suitable habitat conditions for diverse communities (Hutto 1995, Hessburg and Agee 2003, Means 2006). Although wildfire may have filled a similar role in structuring amphibian habitats and communities in western North America, there are few studies from the cold forests with long fire-return intervals that cover much of the region, including the Northern Rockies (Hossack and Pilliod 2011). Additionally, most forests in the Northern Rockies are managed for timber and have extensive road networks, which can reduce population size, distribution, or connectivity of amphibians and other species (Marsh and Beckman 2004, Ewers et al. 2007). How the combination of stand-replacement wildfire and forest management affects amphibian populations and their parasites in the region is unknown. But factors that reduce fitness and population growth may be exacerbated in burned forests with legacies of timber harvest, including roads, edge effects, and reduced recruitment of large woody debris (Beschta et al. 2004, Lindenmayer and Noss 2006). Although native species evolved with wildfire and have persisted in managed landscapes, the combined effects of wildfire and human disturbances on populations may be additive or synergistic (Laurance and Williamson 2001, Castro et al. 2010).

The effects of wildfire and fragmentation may not be easily predicted from life-history characteristics or from research conducted only in protected landscapes (Ricketts 2001). For example, mobile species that are good colonizers in unfragmented landscapes can be more adversely affected by fragmentation than sedentary species (Funk et al. 2005, Fahrig 2007), and individuals of the same species can have different dispersal abilities in fragmented and unfragmented systems (Ferraz et al. 2007). Burned and fragmented forests may also act as ecological traps for species that are good colonizers and are attracted to early successional habitats, especially if there is a mismatch between habitat suitability of adults and offspring (Schlaepfer et al. 2002).

Changes in amphibian populations in response to wildfire and forest management are also likely to have important implications for their parasites. Parasites can affect host fitness and population dynamics, and by modifying the outcome of species interactions, they can have large effects on ecosystem structure and function (Dobson and Hudson 1986, Lafferty et al. 2006). Disturbances can directly or indirectly affect parasite abundance or richness through changes in vital rates of parasites; through changes in host vital rates, abundance, or activity; or through changes in the transmission process (Hudson et al. 2002, McCallum 2008). Parasites that use intermediate hosts such as snails and amphibians often increase in response to aquatic eutrophication (Johnson et al. 2002, Poteet 2006), but little is known about how land use patterns or disturbances that change host abundance affect directly-transmitted parasites of amphibians (McKenzie 2007). Most helminths like nematodes must complete part of their life cycle outside of a host, exposing them to variation in habitat and microclimate independent of variation in host condition or population dynamics. There is a general expectation that changes in abundance of hosts will affect abundance of their parasites (Dobson and Hudson 1992, Arneberg et al. 1998), but the link between hosts and their parasites may vary according to the ability of parasites to infect multiple hosts versus reliance on a single host (Dobson 2004). However, few studies have evaluated host–parasite relationships—and how that relationship is modified by disturbance—using field estimates of amphibian abundance.

We used a natural experiment to conduct an integrated analysis of the independent and combined effects of wildfire and land-use history on amphibians and their parasites. Specifically, we compared population sizes of the long-toed salamander (*Ambystoma macrodactylum*) and Columbia spotted frog (*Rana luteiventris*) and infection prevalence and intensity by 2 common nematodes in neighboring managed and protected forests that were burned by the same wildfires. Long-toed salamanders spend the majority of their time underground, limiting surface activity primarily to cool seasons (Werner et al. 2004). Despite their sedentary habits, there is substantial inter-population movement by long-toed salamanders (Giordano et al. 2007), and forest harvest has been linked reductions in their abundance (Naughton et al. 2000). Therefore, we predicted population sizes would be reduced by wildfire, especially in areas of high severity fire, and that the effects of wildfire would be greater in managed forests than in protected forests.

The Columbia spotted frog (hereafter, spotted frog) often moves among complementary hibernating, breeding, and foraging habitats (Pilliod et al. 2002). We predicted populations in managed forests would be smaller than in protected forests because fragmentation by roads can impede dispersal and increase mortality of similar species (Carr and Fahrig 2001, Eigenbrod et al. 2008). Overall, we expected a neutral or positive relationship between wildfire and size of spotted frog populations because many ranid frogs are attracted to breeding sites with open canopies, but we also expected the most isolated population might be negatively affected by post-fire changes in habitat, especially in areas with extensive roads.

Through changes in habitat conditions or host abundance, we expected wildfire and forest management would also affect the distribution and abundance of 2 nematode species with contrasting levels of host specificity. The nematode *Cosmocercoides variabilis* hatches and develops into an infective stage in the soil before colonizing a wide range of terrestrial amphibians and reptiles, including the long-toed salamander (Vanderburgh and Anderson 1987). The nematode *Gyrinicola batrachiensis*, which infects only anuran (frog and toad) larvae and cannot persist in its host after it metamorphoses (Adamson 1981), infects multiple species, like *C. variabilis* does, but the spotted frog was the only common host in our study area. Both nematodes are transmitted directly and lack intermediate hosts, and thus we expected their abundance would be correlated with host abundance (Arneberg et al. 1998). However, *C. variabilis* has a free-living life-stage that we hypothesized could be susceptible to disturbance-related changes in microclimate as well as to differences in host abundance. In contrast, transmission of *G. batrachiensis* occurs by ingestion of resting eggs that are resistant to environmental variation (Adamson 1981). Thus, we expected infection prevalence and intensity of infection by *G. batrachiensis* would be controlled by host density alone (Adamson 1981). Changes in abundance of either amphibians or parasites as a result of wildfire, especially if those effects differ between managed and protected forests, could have important implications for species conservation and community structure under future disturbance regimes.

METHODS

Study Area

Our research focused on 3 stand-replacement fires that occurred in the North Fork Valley, Montana: the 1988 Red Bench fire (14584 ha), the 2001 Moose fire (28574 ha), and the 2003 Wedge Canyon fire (21615 ha) (Figure 1). The study area is divided by the North Fork Flathead River, which forms the boundary between Glacier National Park (NP) on the east and a landscape of mixed ownership on the west. The area outside of the park includes Forest Service, state, and private lands that are managed for varied activities, including timber production and recreation. Human residences on private lands include small ranches and homes surrounded by forest and meadows. Forests within the park are not harvested and have fewer roads than in forests on neighboring lands. Hereafter, we refer to land outside of the park as “managed forest” and land inside the park as “protected forest”.

All 3 wildfires started on public lands outside of the park, where they were ignited by lightning during drought conditions. The fires burned in an area covered with dense forests composed primarily of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*). The fire regimes of these forests range from mixed-severity with mean fire-return intervals of < 100 years in some areas of the north, to a stand-replacement fire regime with mean fire-return intervals of 140–340 years in the southern end of the valley (Barrett et al. 1991). Due to the naturally long fire intervals, fire suppression has not greatly altered the natural succession of most forest stands in this area (Barrett 2002).

The study area is densely populated by shallow wetlands in depressions left by receding

Pleistocene glaciers. There are also a few lakes and large wetlands that we excluded from sampling (see below). The wetlands we sampled ranged in size from 0.01 ha to 1.4 ha and only 3 were >1 m maximum depth. Most of these wetlands fill from snowmelt and rain in the spring, support extensive emergent vegetation, and dry by mid-August. Consequently, most of our study sites were likely dry when the fires occurred. Two wetlands on Forest Service lands were human-created or modified but contained suitable habitat for local amphibians.

Sampling Design

To determine if wildfire and fragmentation from forest management and roads affect amphibian populations and their associated parasites, we randomly selected wetlands based on their burn status (burned vs. unburned) and location (managed vs. protected) to achieve a fully replicated, factorial sampling design represented by 4 classes of wetlands: burned/protected, unburned/ protected, burned/managed, and unburned/managed. We limited our sampling population to small wetlands ≤ 1 km of roads to reduce travel time because we had to access wetlands several times when there was still deep snow cover. We also limited the size of wetlands trapped for salamanders to 1 ha, because we were not confident we could effectively trap larger sites.

After identifying candidate wetlands, we randomly selected 3 burned and 3 unburned wetlands inside and outside of the park for each of the 3 fires (n = 36). For example, for the 2003 Wedge Canyon fire, we selected 3 burned and 3 unburned wetlands in protected forest, and 3 burned and 3 unburned wetlands in managed forest. We also randomly selected alternate wetlands that were used in the few cases that wetlands did not fill with water. We estimated abundance of the long-toad salamander and spotted frog in each of these 36 wetlands.

We selected wetlands for sampling frogs by including the same 36 wetlands where we trapped salamanders, and then adding 2 wetlands in each combination of burn and management status. These additions resulted in 60 wetlands, with 5 per combination of burn status (burned vs. unburned), location (managed vs. protected), and fire (Red Bench, Moose, Wedge Canyon). The spotted frog occupies fewer wetlands than the long-toed salamander in our study area (Corn et al. 2005), necessitating the larger sample size. One of the sites we selected for the 2001 Moose fire was burned by the 2003 Robert Fire instead, near where the 2 fires overlapped, and 1 wetland > 1 ha was included in our sample of wetlands where we searched for spotted frog egg masses.

Amphibian sampling and abundance

We captured salamanders by placing unbaited minnow traps along the margins of wetlands as they started to fill with snowmelt and rain, when salamanders migrate from terrestrial hibernacula to breeding sites. Using the same type of traps, Wilson and Pearman (2000) showed captures rates of adult rough-skinned newts (*Taricha granulosa*)—a species with similar breeding behaviors as the long-toed salamander—was an accurate measure of abundance. We scaled the number of traps to area of open water, with approximately 1 trap every 10 m of open shoreline (range = 2–13 traps). Trapping dates varied widely among wetlands according to topography and insolation, starting as early as 18 March 2010 at the southern end of our study area and ending on 25 April 2010 at the northern end of our study area.

Traps were left overnight and captured salamanders were sedated with tricaine methane sulfonate (MS-222) before being marked with a session-specific toe clip used to construct capture histories. We measured snout-vent length (mm) and weight (g) of the first 25 salamanders captured at each wetland. This trapping method primarily captured male salamanders (>90% of captures), so we excluded females from the population estimates. After the final trapping session at each wetland, we euthanized 15 male salamanders or 25% of the total number of individuals captured (whichever was less) with an overdose of MS-222 and froze them for necropsies.

We estimated population size of salamanders using closed population estimators in program MARK (White and Burnham 1999). Before fitting models, we tested for population closure using program CloseTest and pooled captures as needed by combining trap sessions (e.g., by combining captures from the first 2 sessions; Stanley and Jon 2005). This pooling resulted in between 2 and 5 capture sessions used to estimate population size. We fit the data to models that assumed constant capture probability (M_0) and models that allowed for temporal heterogeneity in captures (M_t), and used AICc weights to generate model-averaged estimates of population size of male salamanders for each wetland.

At 9 of the 36 wetlands we trapped, we captured too few salamanders to estimate population size or could not satisfy the closure assumption of the models. For these wetlands, we estimated population size using a linear regression model based on data from the other 27 wetlands by regressing the population estimate from MARK against peak number of captures at each wetland. We log-transformed both variables prior to the regression to make the relationship linear and kept the predicted values in the log-transformed format for all subsequent analyses. Other measures of trapping effort, such as number of traps deployed or number of trap nights, did not improve the fit of the regression model.

We estimated population size of breeding female spotted frogs by counting egg masses at wetlands. Spotted frogs lay 1 egg mass, providing an accurate way to track size of the breeding population (Licht 1975). We conducted egg mass surveys by walking the entire shoreline and other shallow areas of each wetland on every visit. Spotted frog egg masses float at the water's surface and are typically laid communally near shore, making them easy to detect. We marked individual masses by inserting a colored toothpick into the center of each egg mass. We also placed a flag pin at each location with eggs and labeled it with the date and count of egg masses. Marking the masses and flagging their locations reduced counting errors because egg masses become more difficult to distinguish as they age.

We conducted between 3 and 10 surveys at each wetland (mean = 5.7) during the breeding season. We visited a wetland at least once per week until the count of masses did not change for 2 consecutive visits and there was no change in counts in neighboring wetlands. Egg masses were first detected on 19 April 2011. We continued surveys through 27 May, although we did not detect new masses after 20 May. We returned to breeding sites later in the summer (6 to 11 July) to collect up to 15 spotted frog larvae from throughout each wetland (to avoid sampling siblings). Larvae were euthanized with MS-222 and stored in 10% formalin until they were necropsied for nematodes.

Nematode sampling

We examined the external surface, buccal cavity, body cavity, lungs, and digestive tract of 3–15 long-toed salamanders from 30 wetlands (373 total) under a dissecting scope to measure infection prevalence and intensity by *C. variabilis*. To measure infection prevalence and intensity by *G. batriachiensis*, we excised the entire digestive tract of 2–15 spotted frog larvae from 22 wetlands (205 total), removed the digestive contents, and counted the nematodes under a dissecting scope. All nematodes were stored in 70% ethanol and identified using characteristics described in Vanderburgh and Anderson (1987) and Adamson (1981).

There is uncertainty about the identity of some *Cosmocercoides* in amphibians. *Cosmocercoides variabilis* is a common parasite of amphibians and reptiles (Vanderburgh and Anderson 1987), but it is possible some amphibians may also become infected by *C. dukae* after ingesting infected gastropods (Baker 1978). However, isozymes and cross-transmission experiments showed that *Cosmocercoides* in anurans and gastropods were distinct, suggesting *C. dukae* found in amphibians are accidental infections and are likely temporary (Vanderburgh and Anderson 1987). Also, we did not find any male worms in our samples, which are preferred for species identification. We refer to nematodes we found in salamanders as *C. variabilis*, but acknowledge that some could have been *C. dukae*.

GIS Analyses

We used a geographic information system (ArcGIS 9.2) to measure landscape characteristics within 2-km buffers surrounding wetlands that we expected to be correlated with population sizes of amphibians and nematodes. Within each buffer, we calculated the extent of burned area, the area that burned with high severity, length of roads, area of ponds and emergent wetlands, mean canopy cover, and mean topographic slope. Fire information was calculated using 30 m burn severity data from the Monitoring Trends in Burn Severity project (MTBS; http://mtbs.gov/index.html). We defined areas that burned with high severity as pixels with differenced Normalized Burn Ratio (dNBR) values ≥ 550, which represents the midpoint of the moderate-high severity burn category that Key and Benson (2006) defined for several wildfires in Glacier NP. The dNBR is based on changes in vegetation between pre-fire and post-fire Landsat imagery. Length of roads was calculated from a database for Flathead County (http://nris.mt.gov/gis/). Area of emergent wetlands and freshwater ponds was measured using the National Wetlands Inventory dataset (http://www.fws.gov/wetlands/data/). We estimated mean canopy cover for forested vegetation only (i.e., we excluded riparian areas, meadows, and water) within each buffer using LANDFIRE data (http://www.landfire.gov/). Mean topographic slope was calculated from a 10 m digital elevation model for the study area (http://nris.mt.gov/gis/).

Statistical Analyses

Amphibian populations.—Before evaluating our research hypotheses, we first sought to account for background variation in amphibian abundance unrelated to wildfire or management effects. Specifically, we expected topographic slope and area of wetlands in the surrounding landscape to be important predictors for both the long-toed salamander and spotted frog. The slope and wetland variables also account for natural differences between managed and protected forest, because the former included areas with greater topographic variation and had less wetland area (Table 1). Slope and wetland area were also strongly, negatively correlated, because steeper areas are less likely to have ponded water. To describe the covariation between topography and wetlands, we used principal components analysis to reduce them into a single variable that we used as a measure of population isolation, which we included as a covariate in all linear models. The first principal component accounted for 85% of the covariation between slope and wetlands. Positive values of the principal component represented areas of high slope and few wetlands (i.e., greater isolation).

We evaluated 15 models that included additive and interactive effects of isolation, length of roads, forest management (managed vs. protected), percent of area burned (burn extent), and percent of area burned severely to describe variation in amphibian abundance. We hypothesized the effects of fire would be greater in steeper areas or where there were fewer neighboring wetlands. Steeper areas impose greater energetic costs for movement and should increase effective isolation (e.g., Ricketts 2001). More wetlands in the surrounding area could facilitate movement and provide a source of colonists to rescue local populations (Brown and Kodric-Brown 1977). We expected roads would be associated with smaller population sizes because they can inhibit movement of amphibians, they create strong edge effects that alter the local habitat and microclimate, and because they are often associated with forest management activities such as logging that can reduce population sizes (Gibbs 1998, Naughton et al. 2000, Marsh and Beckman 2004).

We included the management term to account for differences in timber harvest between areas, but it is also reflects differences in road density and fragmentation by private residences and ranches. Because management and roads were correlated, we did not include both terms in the same model. Given the mixed ownership of the study area, there is no data source that provides consistent, accurate information on harvest history. Canopy cover is generally reflective of timber harvest over large areas (Houlahan and Findlay 2003), but it was highly correlated with both percent of area burned (r = -0.73) and percent of area burned severely (r = -0.86) in our study area and thus was not included in any models. We evaluated both burn extent and burn severity because severity is more specifically related to consumption of vegetation and subsequent heating and exposure of soils (Key and Benson 2006). Burn severity is often highly variable, however, and the cumulative effect of the net area burned may be more important in some cases or at broader spatial scales.

We originally fit these 15 models to data measured from both 500 m and 2 km wetland buffers. For both species, however, results from the 2 spatial scales were nearly identical and data measured from 2 km wetland buffers explained more variation in population sizes. As a result, we do not show or discuss results from models based on 500 m buffers.

To model salamander abundance (on the log scale), we used generalized linear models with a normal distribution and identity link (PROC GENMOD, SAS 9.2). Counts of spotted frog egg masses were modeled using generalized linear models with a negative binomial distribution and log link, because the counts were over-dispersed (mean = 5.23, variance = 108.45). We included area of the sampled wetland (log transformed) as an offset variable for the population models because larger wetlands tended to host larger populations, especially for salamanders. In preliminary analyses, we also evaluated the ability of wetland depth, vegetative cover, and other wetland characteristics to explain variation in population size of salamanders and spotted frogs; none were useful predictors for either species. For these and subsequent analyses, we ranked models in each respective set using AICc and model weights to evaluate support for our hypotheses (Burnham and Anderson 2002). Model weights represent the probability that a particular model is the best for the given data set.

Prior to the analyses, we tested the population data for evidence of spatial autocorrelation using a distance-weighted matrix to calculate Moran's I (PROC VARIOGRAM). Moran's I measures how values are correlated based on distance, with 0 representing no correlation and -1 or +1 indicating perfect negative or positive correlation, respectively (Moran 1950). We did not find evidence of significant autocorrelation for either the long-toed salamander (I = 0.10, $P = 0.27$) or spotted frog data (I = 0.12, $P = 0.16$).

Nematodes.— We used different analytical approaches to compare abundance of nematodes in salamanders and spotted frogs. The nematode in salamanders (*C. variabilis*) has a free –living stage that could be sensitive to environmental variation, but this parasite should also be sensitive to variation in host abundance (Dobson and Hudson 1992). To estimate the probability and intensity of infection by *C. variabilis*, we used generalized linear mixed models (PROC GLIMMIX) estimated with Laplace maximum likelihood methods and empirical standard errors. We used the same 15 models that we used to model variation in salamander abundance, but considered wetlands and individuals as random factors. We modeled within-wetland covariance using the compound symmetry structure, which assumes equal correlation among individuals in a wetland. Infection probability was modeled using the binomial distribution and a logit link. We used the gamma distribution with a log link to model infection intensity, because intensity was under-dispersed (mean = 1.84, variance = 1.45). We considered both snout-vent length and the scaled mass index (Peig and Green 2009) of salamanders as offsets to account for potential relationships between size or condition and infection, but neither improved the fit of the models.

We did not expect landscape disturbances would directly affect the distribution or infection intensity of *G. batrachiensis* in spotted frog larvae. This nematode produces resting eggs that must survive outside of a host (Adamson 1981), but we had no reason to expect egg survival varied among wetlands. Also, *G. batrachiensis* does not infect salamanders and only 2 wetlands contained larvae of an alternative host (boreal toad, *Anaxyrus boreas*; B. Hossack, unpublished data). Thus, we expected variation in *G. batrachiensis* would primarily reflect the density of spotted frog larvae. For this analysis, we fit a single model for each of infection prevalence and intensity based on burn status of each wetland (i.e., burned vs. unburned). We used burn status because it provided a better fit to the data than quantitative measures of fire effects (e.g., percent of area burned), given the reduced set of wetlands where we collected frog larvae and range of burn severity at these wetlands.

We estimated the probability of infection and infection intensity by *G. batrachiensis* in spotted frog larvae according to burn status using the same random effects model as for *C. variabilis* in salamanders, except we modeled infection intensity using the negative binomial distribution and a log link because the count of *G. batrachiensis* was overdispersed (mean = 19.78, variance = 459.51). We excluded data from 1 wetland where most spotted frog larvae appeared sick and many had empty or atrophied guts. These larvae generally were not infected by *G. batrachiensis*, perhaps because they were not feeding or because their gut provided unsuitable habitat for the nematodes. Larvae in this same wetland have experienced occasional die-offs in previous years (B. Hossack, personal observation).

RESULTS

Amphibian populations.—Estimated population sizes for long-toed salamanders from program MARK ranged from 8 to 4220, with a mean population size of 599 (SE = 126). At the 9 wetlands where we captured too few salamanders to estimate population size or could not satisfy the closure assumption of the models, estimated population size from linear regression based on peak captures ranged from 2 salamanders at a wetland where we never had any captures, to 690 at a wetland where we captured 245 male salamanders.

The model with the interaction between isolation and burn extent received the most support and predicted a negative effect of wildfire in areas with greater burn extent and in steep areas with few wetlands (Table 2, Figure 2). There was only a weak effect of isolation in areas that burned with moderate extent (e.g., 50% of 2 km buffer) and in areas that experienced little wildfire, population sizes were larger in more isolated wetlands. The model that included an isolation × burn severity interaction received less support but predicted a similar response to that of the isolation × burn extent model, with increasingly negative effects of high severity burn for isolated populations (Table 2).

There was also substantial support for the models that described additive or interactive effects of burn severity and forest management or length of roads (Table 2). Collectively, there was more support for effects of burn severity ($\Sigma w_i = 0.70$) than for burn extent ($\Sigma w_i = 0.30$), even though the latter was in the top-ranked model. All severity models described a strong, negative effect of high severity burn on salamander populations. Road density had a negative effect on population size of salamanders in addition to the effect of burn severity (Figure 3), and the effect of high severity burn was stronger in managed forests than in protected forests (Figure 4).

To evaluate the influence of the 9 populations for which we had to estimate population size using linear regression, we conducted a sensitivity analysis by refitting all of the models using only population estimates generated from program MARK. The only significant change from using the smaller dataset was reduced support for the isolation × burn extent model ($w = 0.02$ instead of $w = 0.27$ for the full dataset). This change resulted because some of the wetlands where we could not estimate population size in MARK were also the most isolated and occurred in thoroughly burned areas. For example, the only wetland where we did not capture salamanders was in an area where 99% of the surrounding area burned. This site also had the fewest neighboring wetlands and highest mean topographic slope.

We detected spotted frog egg masses at 26 of 60 wetlands, with the number of egg masses ranging from 1 to 57. Seventeen of the 26 breeding sites were burned. In contrast to salamanders, counts of spotted frog egg masses were weakly, positively correlated with burn extent near wetlands (Figure 5). No model clearly fit the data the best, but the model with burn extent received the most support, followed by the models with the interaction between burn extent and isolation (Table 3). The isolation × burn extent term indicated that wildfire had a negative effect on isolated populations; however, the estimate did not differ from 0. None of the other models explained additional variation in population size relative to the top model.

Nematodes.—We found the nematode *C. variabilis* in 39% of salamanders. Infection intensity ranged from 1 to 7 worms (mean = 1.84). All nematodes were juveniles or females and were found in the intestine or (rarely) the body cavity. We found no evidence that the probability or intensity of infection was related to wildfire, management effects, or isolation of populations. The basic model that included only population isolation received the most support for both the prevalence and intensity data sets (models not shown). However, the effect of isolation did not differ from 0 for either infection prevalence or intensity. The covariance parameter for the random intercepts (i.e., different wetlands) also did not differ from 0 for either set of models, indicating differences in host density or other factors that varied among wetlands had little effect on infection.

We found *G. batrachiensis* in 66% of spotted frog larvae and in 75% of breeding sites. Of infected larvae, intensity ranged from 1 to 107 worms. We found no difference in probability of infection of larvae between unburned and burned wetlands (b = 0.26, SE = 0.79). However, infection intensity was greater in larvae collected from burned wetlands (least-squares mean = 21.71, SE = 1.23) compared with unburned wetlands (least-squares mean = 13.18, SE = 1.16). Burned wetlands had more than twice the density of spotted frog egg masses as unburned wetlands (mean of 69 vs. 33 masses ha^{-1}, respectively). Mean infection intensity by *G. batrachiensis* was strongly correlated (log-log r = 0.66) with the density of spotted frog egg masses in wetlands, which we considered a surrogate for host density (Figure 6).

DISCUSSION

Given the expected increases in drought and conditions that foster wildfire in many forested ecosystems, along with increases in insect-related tree mortality and the use of forest harvest to mitigate wildfire hazards, it is important to understand how interactions among disturbances will affect native species at all trophic levels (IPCC 2007, Reinhardt et al. 2008, Bentz et al. 2010). Our results show that projected changes to disturbance regimes in western North America could affect abundance of amphibians and their parasites, depending upon the extent and severity of wildfire, isolation from other populations, and host specificity. Additionally, these implications may differ between managed and protected forests.

We found strong evidence that salamander populations were smaller in areas that burned with high severity. Burn extent was also negatively related to salamander abundance, but less so than burn severity. Burn severity likely was more important than extent because it represents post-fire changes in vegetation structure that provides protective cover and modifies the microclimate of ground-dwelling organisms (Key and Benson 2006). This negative relationship with burn severity is consistent with results from an 11-year study of wetland occupancy by breeding populations of the long-toed salamander in Glacier NP wetlands, in which wetlands in areas of high severity wildfire were less likely to be occupied > 6 years after they burned (Chapter 1). There have been few population estimates for adult ambystomatid salamanders, especially across multiple populations and a large study area like ours, but they provided more information on the relationship with burn severity than measures of occupancy.

Connectivity among populations is critical for population persistence and recovery after declines, especially in disturbed or fragmented landscapes (Thomas and Jones 1993, Ricketts 2001). For example, high connectivity in stream systems reduces probability of decline or local extinction for fishes during drought or after wildfire (Fagan et al. 2002, Neville et al. 2009), and the presence of neighboring water bodies reduces extinction probability of amphibians in montane catchments with introduced fish (Pilliod et al. 2010a). Similarly, the effects of wildfire on long-toed salamanders increased with population isolation, indicating isolated populations were less resistant or resilient to the effects of wildfire. However, isolation was negatively associated with population size only in areas where >50% of the area within 2 km of wetlands burned. The positive correlation we found between wetland isolation and population size has been documented previously for mole salamanders and could result from focusing breeding efforts when there are few alternative breeding sites (Veysey et al. 2011). This interaction suggests isolated populations will also be the most vulnerable to future increases in frequency or severity of wildfire, and underscores the importance of maintaining suitable habitat between breeding habitats to facilitate colonization and recovery after disturbances.

We suspect the increased vulnerability of isolated populations in steep, burned areas reflects the direct effect of wildfire on habitat and resulting costs of dispersal. Loss of tree canopy results in reduced movement and increased desiccation and mortality of other ambystomatid salamanders (Rothermel and Luhring 2005). Amphibians are also less likely to disperse into forested habitats with strong edges or open canopies (Todd et al. 2009, Popescu and Hunter 2011), characteristics that are more common in burned forest than in unburned forest (Guscio et al. 2008). A previous study in Glacier NP showed soil temperatures averaged 3°C higher in severely burned areas compared to neighboring unburned forest, and surface temperatures were frequently higher than those preferred by most salamanders (Hossack et al. 2009). After a severe wildfire in New Mexico, temperatures in microhabitats of the Jemez Mountain salamander (*Plethodon neomexicanus*) often exceeded the thermal preference for the species, and occasionally exceeded its critical thermal maximum (Cummer and Painter 2007). The lower cover and higher temperatures in burned forests could limit surface and foraging activity or increase desiccation and mortality during dispersal for long-toed salamanders, ultimately reducing population connectivity and size.

Projected increases in frequency and severity of wildfires will present many challenges for conservation. These challenges will be greater if the effects of wildfire and other disturbances are additive or even synergistic (e.g., Laurance and Williamson 2001, Castro et al. 2010), like those we found indicating the negative effects of high-severity wildfire on long-toed salamanders were magnified on managed forests fragmented by roads and development. By themselves, forest management and roads were weakly related to population size of salamanders. The lack of a management effect was surprising, because timber harvest has been associated with reduced abundance of long-toed salamanders elsewhere in western Montana (Naughton et al. 2000). But in areas that burned with high severity, the effect of fire increased in areas with high road densities and on managed forests. These additive and synergistic effects could result from post-fire salvage logging, but because of the mixed private and public ownership of the study area and the age of the oldest fire, we do not have data to evaluate this hypothesis.

In contrast to the data for long-toed salamanders, we did not find negative effects of wildfire, forest management, or fragmentation by roads on population size of spotted frogs. We expected population size to be negatively associated with road density because spotted frogs and other vagile anurans are more likely to encounter roads, increasing the risk of mortality or reducing dispersal (Funk et al. 2005, Eigenbrod et al. 2008). Instead, we found a weak, positive association between burn extent and population size that was similar in managed and protected forests. Spotted frogs prefer exposed wetlands for breeding and foraging and thus may be attracted to disturbed areas with open canopies (Pilliod et al. 2010a). Some ranid frogs have suffered population losses or persistent declines after large wildfires, particularly in the US Southwest (Hossack and Pilliod 2011). However, those species typically occupied stream habitats that are more likely to experience significant post-fire changes in habitat than the temporary wetlands we sampled, which quickly recover to pre-fire conditions. Notably, in a long-term occupancy study across a series of wildfires inside Glacier NP, the distribution of spotted frog populations was negatively associated with burn severity in wetlands that burned 7–21 years before they were surveyed (Chapter 1). Burn severity was not an important predictor for variation in population size in the wetlands we sampled here, but over time, persistent reductions in recruitment or dispersal away from the most severely burned areas could reduce population growth.

Although we found huge variation in abundance of salamanders that was strongly associated with wildfire, isolation, and forest management, infection prevalence and intensity by the generalist nematode *C. variabilis* was not related to these habitat characteristics or to variation in salamander abundance among wetlands. We expected abundance of *C. variabilis* would vary spatially because it has a free-living stage that could be directly affected by variation in habitat and because the long-toed salamander is the most abundant host in the area (Dobson and Hudson 1992; B. Hossack, unpublished data). Remarkably, abundance of *C. variabilis* did not differ among populations. We suspect the ability of *C. variabilis* to infect multiple species of amphibians and reptiles—most of which probably do not decline in abundance in response to wildfire or forest management—may have buffered it from high variation in salamander abundance (Dobson 2004). *C. variabilis* can also be more abundant in these other, less sedentary host species because they are more likely to encounter infectious stages of the nematode (e.g., Yoder and Coggins 2007).

Unlike *C. variabilis*, the gut nematode *G. batrachiensis* is almost completely dependent upon the spotted frog in our study area, where the only other potential host bred occurred in < 3% of wetlands. The close relationship between *G. batrachiensis* and the spotted frog was evident by the 60% greater infection intensity in burned wetlands compared with unburned wetlands, which mirrored differences in host density. Infection by *G. batrachiensis* can accelerate development of American bullfrog (*Lithobates catesbeiana*) larvae, with no sacrifice in size at metamorphosis (Pryor and Bjorndal 2005). Developmental rate and size-at-metamorphosis are both strong predictors of fitness for amphibians, especially in temporary wetlands like we sampled (Semlitsch et al. 1988). Thus, greater infection intensity in spotted frogs in burned wetlands compared with unburned wetlands could increase host fitness. Despite the greater infection intensity in burned wetlands, however, there was no effect of wildfire or other covariates on infection prevalence, suggesting the conditions that allow *G. batrachiensis* to become established or persist in an individual and conditions that control infection intensity may be independent.

By estimating sizes of amphibian populations in burned and unburned wetlands in both managed and protected forests, we found strong, negative effects of wildfire on long-toed salamanders, especially on isolated populations in managed forests. These synergistic effects could increase the threat of wildfire to salamanders and other species that are sensitive to post-wildfire changes in habitat or microclimate, especially if expected increases in wildfire frequency and severity are realized (Westerling et al. 2006, IPCC 2007). Despite these strong effects on population size of salamanders, infection by *C. variabilis* seemed insulated from the effects of disturbance or host abundance, likely because it is capable of infecting many host species in the area that are less sensitive to disturbance than salamanders. However, the positive association between wildfire, spotted frogs, and the specialist nematode *G. batrachiensis* reinforces the important role of wildfire in structuring populations and communities. The close relationship between abundance of spotted frogs and infection intensity by *G. batrachiensis* also illustrates the hidden loss of biodiversity that has likely resulted from the global decline of amphibians (and other hosts) on parasites, especially in areas where host diversity is low or where host–parasite relationships are specific (Dunn et al. 2009). Collectively, our results underscore the importance of measuring population- and community-level responses across a range of disturbances and in both managed and protected forests. To form effective conservation strategies, future research should prioritize isolating the mechanisms underlying these population differences, and in particular, how those mechanisms differ between managed and protected forests.

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Table 1. Mean (SD) wetland and landscape characteristics according to forest management (managed vs. protected) of 30 burned and 30 unburned wetlands. All data except wetland size were measured from 2 km buffers around the sampled wetlands. “Surrounding wetlands” refers to area of wetland habitat within the 2 km buffers around sampled wetlands.

Variable	Management	Unburned	Burned
Wetland size (ha)	managed	0.15 (0.25)	0.29 (0.28)
	protected	0.25 (0.36)	0.17 (0.12)
Roads (km)	managed	16.68 (6.19)	15.72 (4.55)
	protected	6.59 (3.55)	5.87 (2.55)
Surrounding wetlands (ha)	managed	10.36 (8.79)	6.91 (2.99)
	protected	24.67 (18.53)	11.59 (7.92)
Topographic slope (%)	managed	7.23 (3.68)	8.29 (5.68)
	protected	4.88 (2.34)	5.58 (1.92)
Burn extent (%)	managed	3.23 (5.63)	85.57 (12.95)
	protected	38.58 (15.22)	73.08 (10.70)
High severity (%)	managed	0.59 (1.87)	30.27 (13.10)
	protected	10.92 (7.13)	25.36 (17.55)

Table 2. Models fitted to estimated population size of male long-toed salamanders in 18 burned and 18 unburned wetlands using fire and landscape information measured from 2 km buffers. Models are ranked according to AICc and model weights (w_i).

Model	-2log(*L*)	AICc	w_i
Isolation + % Burned + % Burned × Isolation	121.80	133.80	0.27
Isolation + % Severe + Roads	122.29	134.29	0.21
Isolation + % Severe + Management +% Severe × Management	119.64	134.54	0.19
Isolation + % Severe + Roads +% Severe × Roads	119.99	134.88	0.16
Isolation + % Severe + % Severe × Isolation	124.43	136.43	0.07
Isolation + % Severe	128.55	137.77	0.04
Isolation + % Severe + Management	125.97	137.97	0.03
Isolation + % Burned + Management + % Burned × Management	123.45	138.34	0.03
Isolation + % Burned + Roads	130.67	142.67	<0.01
Isolation + % Burned	133.57	142.86	<0.01
Isolation + % Burned + Management	131.78	143.78	<0.01
Isolation + % Burned + Roads + % Burned × Roads	130.58	145.47	<0.01
Isolation	146.83	153.58	<0.01
Isolation + Roads	146.50	155.79	<0.01
Isolation + Management	146.82	156.11	<0.01

Table 3. Models fitted to counts of Columbia spotted frog egg masses in 30 burned and 30 unburned wetlands using fire and landscape information measured from 2 km buffers. Models are ranked according to AICc and model weights (w_i).

Model	-2log(L)	AICc	w_i
Isolation + % Burned	243.32	252.05	0.37
Isolation + % Burned + % Burned × Isolation	243.09	254.20	0.13
Isolation + % Burned + Roads	243.26	254.37	0.12
Isolation + % Burned + Management	243.31	254.42	0.11
Isolation + % Burned + Management + % Burned × Management	241.67	255.25	0.08
Isolation + % Burned + Roads + % Burned × Roads	242.58	256.17	0.05
Isolation + % Severe	248.41	257.14	0.03
Isolation	251.31	257.74	0.02
Isolation + % Severe + Roads + % Severe × Roads	244.28	257.87	0.02
Isolation + % Severe + Management + % Severe × Management	244.36	257.95	0.02
Isolation + % Severe + Roads	247.57	258.68	0.01
Isolation + % Severe + Management	247.70	258.81	0.01
Isolation + Roads	250.49	259.22	0.01
Isolation + % Severe + % Severe × Isolation	248.18	259.29	0.01
Isolation + Management	250.99	259.71	<0.01

FIGURE LEGENDS

Figure 1. Location of 60 wetlands sampled for long-toed salamanders (*Ambystoma macrodactylum*) and Columbia spotted frogs (*Rana luteiventris*) in the North Fork Flathead Valley, Montana, and 4 stand-replacement wildfires that have burned since 1988. Circles indicate the 36 wetlands sampled for both salamanders and frogs; squares indicate the 24 wetlands sampled only for spotted frogs. Wetlands within the perimeter of a wildfire are designated by solid symbols. The North Fork Flathead River forms the boundary between protected forests inside Glacier National Park and managed forest outside of the park.

Figure 2. Mean effect (±95% CI) of isolation on population size of male long-toed salamanders given 10%, 50%, and 90% burn extent in 2 km buffers around breeding wetlands. Isolation was measured as the covariation between topographic slope and wetland area, with high values representing steep areas with few wetlands.

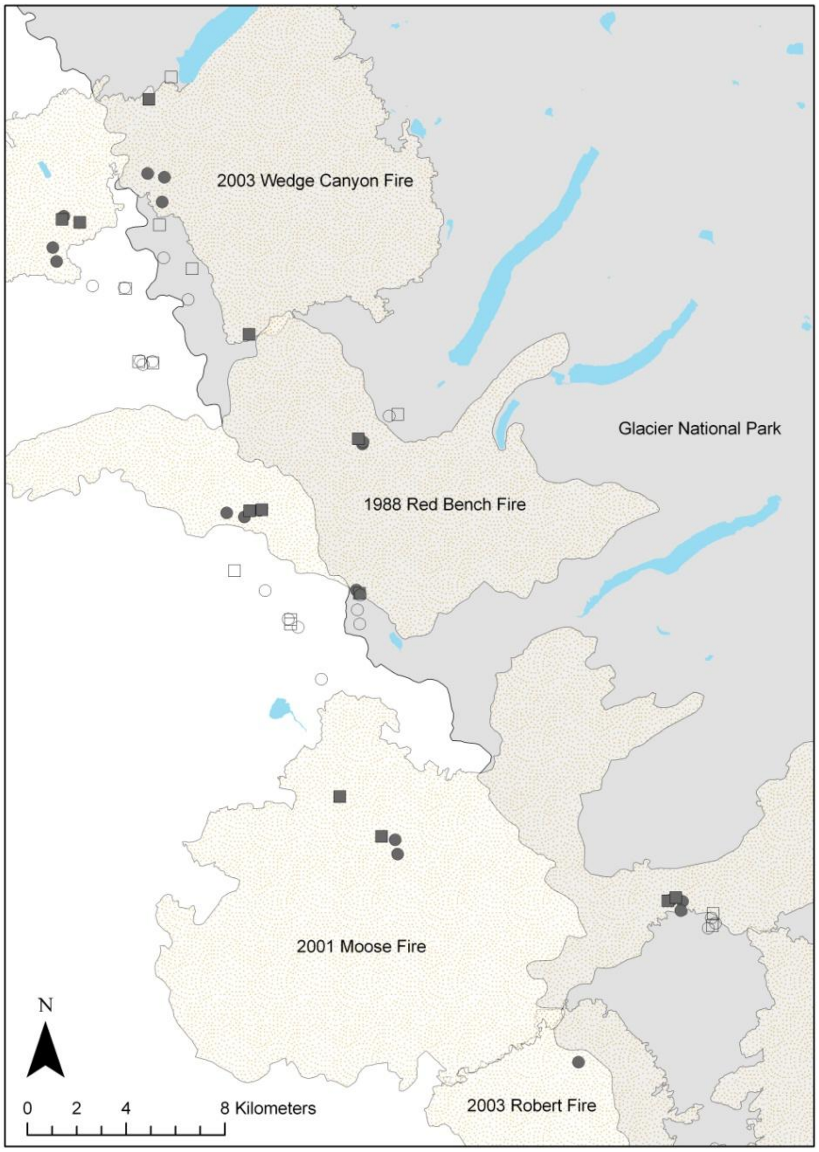
Figure 3. Mean effect (±95% CI) of length of roads within 2 km of breeding wetlands on population size of male long-toed salamanders, after accounting for the effect of variation in high severity burn.

Figure 4. Mean effect (±95% CI) of amount of 2 km wetland buffer that burned with high severity on population size of male long-toed salamanders in managed vs. protected forest.

Figure 5. Mean predicted count (± 95% CI) of Columbia spotted frog egg masses according to burn extent in the 2 km area around wetlands.

Figure 6. Relationship between infection density of Columbia spotted frog egg masses (host density) in wetlands and infection intensity in spotted frog larvae.

Figure 1.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Glacier National Park
1988 Red Bench Fire
2001 Moose Fire
2003 Robert Fire
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Figure 2.

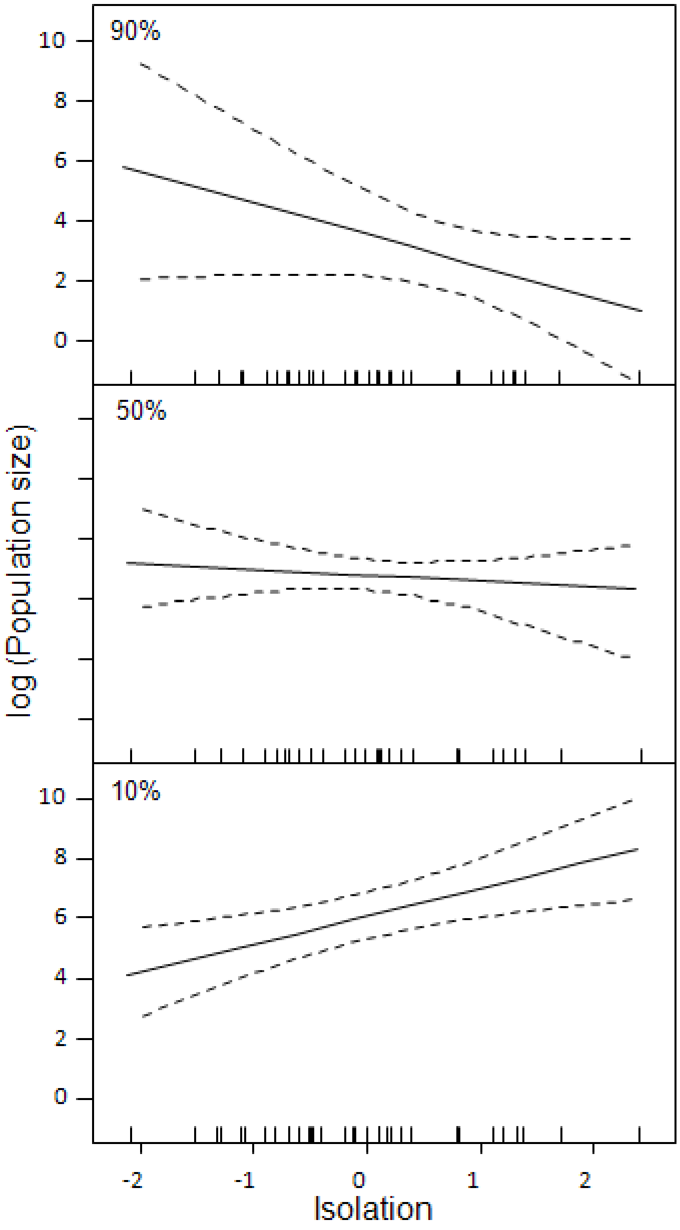


Figure 3.

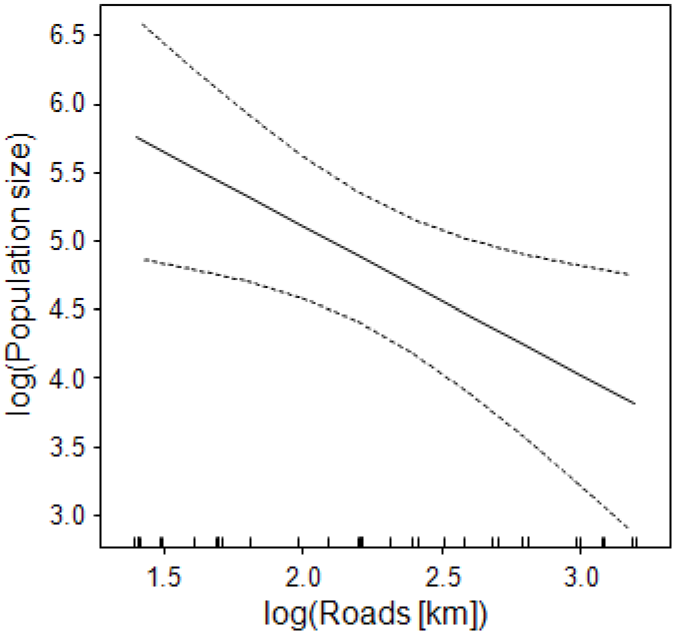


Figure 4.

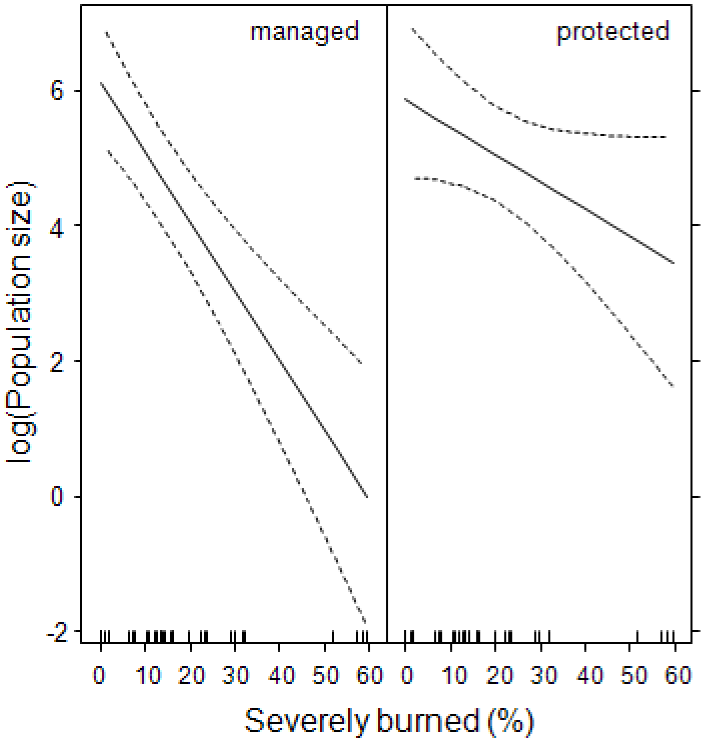


Figure 5.

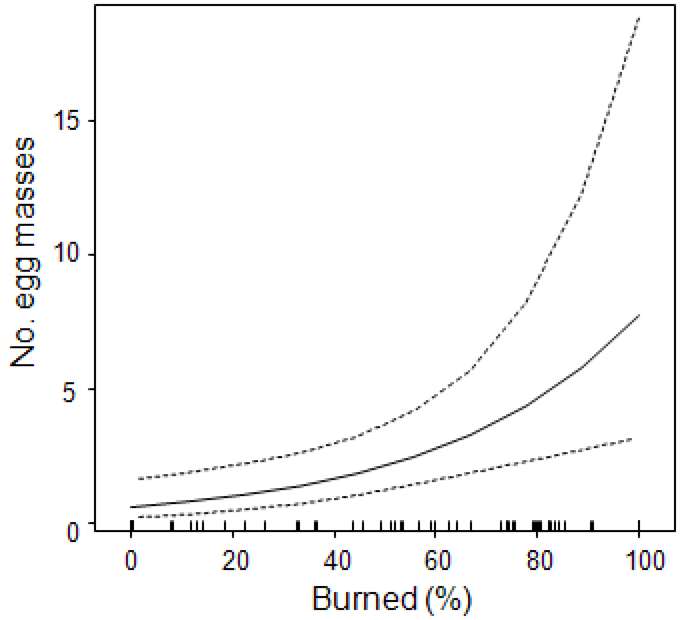
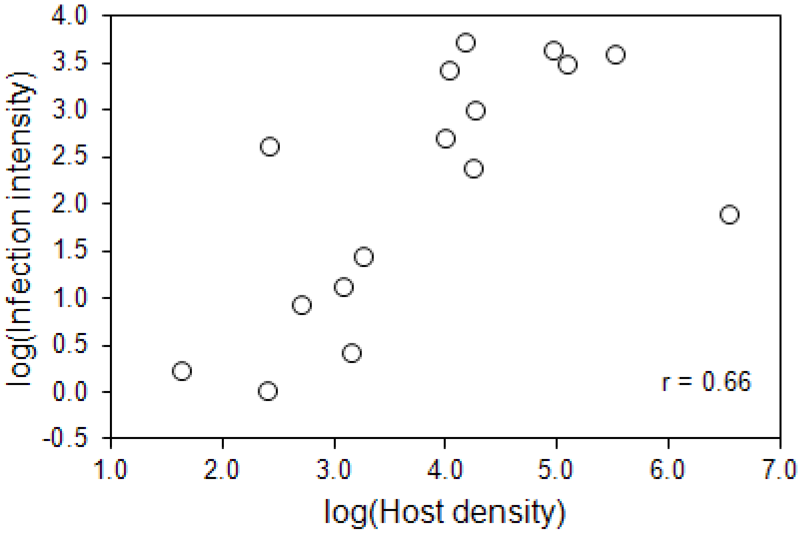


Figure 6.



HOST BEHAVIOR AND NATURAL DISTURBANCES REDUCE DISEASE RISK: POPULATION IMPLICATIONS OF VARIATION IN CHYTRIDIOMYCOSIS

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Abstract. Disturbances are generally expected to magnify the negative effects of disease on hosts; however, these expectations depend on the ecology of the hosts and pathogens, mechanisms of disease transmission, and how disease affects populations. To determine how infection by the aquatic fungus *Batrachochytrium dendrobatidis* (Bd) varies in relation to environmental heterogeneity caused by recent wildfires and use by hosts of aquatic vs. terrestrial habitats, we sampled 404 juvenile and adult boreal toads (*Anaxyrus boreas*) across Glacier National Park, Montana (USA), during 4 years. Bd causes chytridiomycosis, an emerging infectious disease that has been associated with amphibian declines globally. After accounting for capture environment, infection probability for females and the combined group of males and juveniles was similar. Only 9% of toads captured terrestrially were infected, compared to >30% of toads captured in wetlands, and toads captured in recently burned areas were half as likely to be infected as toads in unburned areas. We suspect the large differences in infection prevalence among habitats reflect habitat choices by toads that affect exposure to the pathogen, as well as the increased ability of terrestrial animals to clear infections in arid environments that are less conducive to pathogen growth. To determine how the observed variation in disease prevalence could affect metapopulation dynamics under different infection and dispersal scenarios, we used demographic simulations based on documented effects of Bd on toad survival. Our simulations showed that spatial variation in infection related to habitat use and landscape characteristics can significantly reduce the risk of metapopulation decline over a 10-year period. More broadly, our results show that maintenance of natural disturbance regimes and diverse habitats can strongly influence disease prevalence and population-level effects across broad landscapes.

INTRODUCTION

Despite growing recognition of the role of diseases in the population dynamics of wild animals (Brown et al. 1995, Jolles et al. 2005), how environmental variation and individual habitat use affect host–pathogen interactions is not well understood (McCallum 2008, Mbora and McPeek 2009). Environmental variation and individual exposure to this variation could modify disease risk through several mechanisms. For example, perturbations such as disturbance (e.g., fragmentation) or unusual climate events (e.g., drought) can magnify the effects of disease by increasing the density of hosts and transmission rates (Anderson and May 1978), by changing community structure (Van Buskirk and Ostfeld 1998, Poteet 2006), or by affecting the condition of hosts or pathogens (Jokela et al. 2005, Jolles et al. 2005, Becker and Zamudio 2011). However, these predictions may be context-specific, depending upon the ecology of the hosts and pathogens, how disease transmission occurs, and the effects of disease on the host population (Lafferty and Holt 2003). Greater knowledge of how disease varies among habitats and individuals, and the implications of such variation, are important for making predictions about the effects of disease on populations.

Disease is one of the primary causes of amphibian decline worldwide (Wake and Vredenburg 2008). Many of these declines have been attributed to chytridiomycosis, a widespread, recently emerged disease caused by the aquatic fungus *Batrachochytrium dendrobatidis* (Bd) (Berger et al. 1998, Bosch et al. 2001, Muths et al. 2003). Bd infects keratinized tissues and is transmitted by flagellated zoospores in water or by contact with infected individuals (Longcore et al. 1999, Nichols et al. 2001). There is growing evidence that environmental variation may affect prevalence of Bd infection among populations (Kriger and Hero 2007, Adams et al. 2010, Hossack et al. 2010, Becker and Zamudio 2011), but there has been less emphasis on how habitat use by individuals affects disease prevalence and its potential implication for population dynamics. Variation in aquatic diseases has been linked to habitat conditions such as water permanence, elevation, habitat fragmentation, and differences in host communities (Johnson et al. 2002, Urban 2006, Kriger and Hero 2007, Muths et al. 2008). For amphibian species that use a variety of habitats, this variation may alter the population-level implications of chytridiomycosis by limiting infection rates or promoting host recovery (Briggs et al. 2010, Pilliod et al. 2010b, Puschendorf et al. 2011).

The environmental limitations of Bd suggest that how individuals use their environment could mediate disease exposure or the ability of individuals to recover from infection. Not surprisingly, highly aquatic amphibians that experience greater exposure to Bd often have greater prevalence of infection than more terrestrial species (Longcore et al. 2007, Rowley and Alford 2007). Ecological and physiological mechanisms may also affect disease prevalence of females compared to males. Females of many amphibians are less aquatic than males or juveniles (Tinsley 1989, Bartelt et al. 2004, Grayson and Wilbur 2009), which may reduce the frequency of disease-transmitting encounters, especially during breeding season when males linger at breeding sites and may mount each other frequently (Wells 1977). Females also may have stronger immune systems or invest more resources into immunity than males (Zuk and McKean 1996, Stoehr and Kokko 2006). These differences in exposure or susceptibility to disease could be especially significant because female survival is often the most important vital rate for driving population growth of temperate amphibians (Biek et al. 2002, Trenham and Shaffer 2005). More generally, variation in disease prevalence among individuals and demographic classes could produce very different vital rates and population dynamics in the host species.

Temperature is also a critical factor in host–pathogen interactions. Most pathogens have optimal temperatures below that of their hosts, and elevated body temperature can increase the ability of hosts to combat infection (Kluger et al. 1975, Elliot et al. 2002, Ribas et al. 2009). For example, induction of behavioral fever by locusts (*Schistocerca gregaria*) infected by a fungus increased survival time and allowed them to reproduce, increasing their fitness relative to locusts that were not able to induce fever (Elliot et al. 2002). In a laboratory experiment, boreal toads (*Anaxyrus boreas*) infected with Bd were more likely to select warm temperatures and induce fever than uninfected toads, and infected toads with access to a heat gradient had higher survival than infected toads without access to a heat source (Murphy et al. 2011). More generally, the innate immune system plays a large role in resistance to chytridiomycosis (Ribas et al. 2009), underscoring the importance of environmental variation to the outcome of infection. Notably, toads (family Bufonidae) and some other anurans often respond positively to disturbances and favor open habitats (Denton et al. 1997, Hossack and Corn 2007, Warren and Büttner 2008), suggesting that disturbances that increase landscape variation could affect the prevalence and population-level implications of disease.

To determine how Bd infection varies in relation to habitat use, landscape heterogeneity caused by wildfires, and demographic group, we sampled 404 boreal toads during 4 years in Glacier National Park, Montana, USA. During the last year, we also sampled Columbia spotted frogs (*Rana luteiventris*) to provide an independent measure of the association between habitat characteristics and Bd infection. We subsequently incorporated published estimates of the effect of chytridiomycosis on survival of boreal toads into matrix model simulations to examine how spatial variation in disease prevalence among populations might affect metapopulation dynamics under different infection and dispersal scenarios.

STUDY AREA

We sampled all toads ≥ 1 year old encountered in Glacier National Park, Montana, during the late spring and summers of 2004–2005 and 2008–2009. Toads were captured during surveys of wetlands that were part of an amphibian monitoring program (Corn et al. 2005). The majority of surveyed water bodies were wetlands < 0.5 ha and < 1.0 m deep. These wetlands typically fill from snowmelt in late spring, support extensive emergent vegetation, and dry by late summer. Other wetlands included permanent beaver ponds, forest ponds, and small cirque lakes. Sampled habitats ranged from 950 m to 2164 m in elevation. The Columbia spotted frog and the long-toed salamander (*Ambystoma macrodactylum*) are the only other widespread lentic-breeding amphibians in the park, and commonly occupy the same wetlands as boreal toads.

Many toads were captured within the perimeters of 9 wildfires that burned between 1998 and 2006, including 5 wildfires that burned in 2003 (Figure 1). All wildfires were stand-replacement burns that occurred in forests dominated by Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and western redcedar (*Thuja plicata*).

DISEASE SAMPLING

Boreal Toads

We sampled each toad for Bd by thoroughly swabbing the pelvic patch and the undersides of legs and feet with a sterile swab, using standardized, clean procedures (Muths et al. 2008). Each swab was stored in a sealed vial with ethanol or was air-dried and then placed into a sealed vial and refrigerated until analysis for presence of Bd DNA using a PCR assay (Annis et al. 2004).

After sampling for Bd, we recorded whether the toad was collected within the perimeter of a recent wildfire and assigned each toad to a demographic group (juvenile, female, or male) and measured its snout-vent length (SVL). Distinguishing large juveniles from small females can be difficult because neither vocalizes or has secondary sexual characteristics; consequently, we considered all toads ≤ 60 mm SVL to be juveniles. Above 60 mm SVL, males have reliable secondary sexual characteristics (BRH, personal observation). We recorded sampling date, capture environment (aquatic vs. terrestrial), geographic coordinates, and distance from a wetland for each toad. Toads within 10 m of a lentic water body were considered aquatic, because many had obviously just departed from the water or were basking next to a water body. If a wetland was not visible from the capture point, we measured the distance to the nearest known lentic water in a geographic information system using a National Wetlands Inventory database (http://www.fws.gov/wetlands). We did not consider proximity of streams because Bd is rare or absent in local streams (Hossack et al. 2010).

Columbia Spotted Frogs

We used similar techniques to sample 98 Columbia spotted frogs during summer 2009, except we focused our efforts in and adjacent to areas that have burned since 1998 rather than park-wide. Our primary goal in including spotted frogs was to provide an independent test of the relationship between wildfire and prevalence of Bd, because preliminary analyses suggested an association between recent fire and infection prevalence in toads. Specifically, we used the frogs to determine whether conditions in wetlands surrounded by burned forest limit Bd populations. Columbia spotted frogs are much more aquatic than boreal toads, which should increase their exposure to Bd (e.g., Longcore et al. 2007).

STATISTICAL ANALYSES

Boreal Toads

We estimated the mean prevalence of infection on toads in relation to demographic group (juvenile, female, or male), capture environment (aquatic or terrestrial), and whether or not they were captured in an area burned since 1998 using generalized estimating equations (GEE; PROC GENMOD in SAS 9.2). These models account for the expected correlation among observations from the same water body (Hanley et al. 2003). We grouped toads captured in or ≤ 10 m from the shore of the same water body into 1 site and assumed all toads at a site were equally likely to be infected.

Before estimating the effects of interest, we sought to account for as much nuisance variation as possible. Specifically, infection prevalence often covaries with season and elevation (Muths et al. 2008, Adams et al. 2010). Because we were not explicitly interested in this variation, we first fit a set of models that included individual and interactive effects of sample date, year, and linear and quadratic functions of elevation to determine which nuisance parameters described the most variation in the response data. The model with year and the linear effect of elevation provided the best fit and was used as the basis for all subsequent models.

We estimated the effects of capture environment and demographic group because we expected both to affect Bd exposure and therefore influence disease status. We hypothesized capture environment (aquatic vs. terrestrial) would affect disease status because individuals captured in or near wetlands likely experienced greater, or at least more recent, exposure to Bd than individuals captured away from wetlands. We expected the warmer temperatures in recently burned forests might reduce infection prevalence relative to toads in unburned forest. Finally, we hypothesized the more aquatic tendencies of males would increase their exposure to Bd relative to females. We did not consider the effect of community structure because in previous analyses we found no relationship between infection of toads and the presence of breeding populations of the Columbia spotted frog or long-toed salamander (BRH, unpublished analysis).

We also fit models with demographic group × capture environment and fire × capture environment interactions. A demographic group × capture environment interaction would be important if differences in how individuals use habitats, such as frequency of use of aquatic versus terrestrial habitats according to age or sex, affected exposure and prevalence of disease. Similarly, the capture environment × fire interaction would be important if disease prevalence in burned and unburned areas was mediated by use of terrestrial or aquatic habitats. We did not consider a demographic group × fire interaction because we captured too few females in burned habitats.

We ranked models using QIC_u, an analog to Akaike's information criterion (AIC) (Pan 2001). QIC_u includes a penalty of 2 for each covariate, like AIC, but it also incorporates the correlation among observations into the penalty term. We calculated model weights (w_i), the likelihood that a model is the best for the given dataset, to measure support for each model and used them to calculate model-weighted probabilities of infection for each main effect (Burnham and Anderson 2002). After initially fitting all of the models, we combined the juveniles and males into 1 group and re-ran the models. The estimated probability of infection for these 2 groups was always nearly identical, and combining them resulted in more parsimonious models and more precise estimates.

Columbia Spotted Frogs

We used similar methods for the analysis of infection of Columbia spotted frogs, except we were interested solely in isolating the effect of wildfire on infection status, because we sampled frogs during the last years of the survey to determine whether conditions in wetlands surrounded by burned forests limited Bd populations. To estimate the effect of wildfire on infection of Columbia spotted frogs, we started with a basic model that included sample date and elevation to describe nuisance variation, then added terms for frog size (snout-vent length) and burn status of the water body where each frog was captured. We used frog size rather than sex and developmental stage because we sampled only 5 juveniles and preliminary analyses indicated no differences in infection between sexes. We did not consider the effect of capture environment because only 1 frog was captured away from a water body. Support for an effect of wildfire or body size was assessed using model weights and estimated probability of infection as described above.

Implications of Variation in Disease Prevalence

To estimate how spatial variation in disease prevalence might affect population dynamics, we used matrix projection models to compare population growth and probability of decline for hypothetical metapopulations comprised of 4 breeding ponds. In the first scenario, 30% of toads at each of 4 breeding ponds were infected by Bd. This metapopulation was compared to one in which disease prevalence was 0%, 20%, 40%, or 60% at the 4 breeding populations. In the second scenario, we compared a metapopulation in which disease prevalence was 40% at each of 4 breeding ponds to a metapopulation in which disease prevalence was 10%, 30%, 50%, or 70% at the 4 breeding populations. In both scenarios, the mean infection prevalence of the 2 metapopulations was the same (30% or 40%), allowing us to assess the importance of spatial variation in disease prevalence independently of differences in mean infection. We chose these infection levels because one was similar to the mean of our field samples (described below) and the other represents a realistic alternative.

We used stage-based, transition matrix models to project population growth of toad populations in RAMAS Metapop (Akçakaya 2005). We used the same vital rates and transition probabilities from the post-birth pulse model that Biek et al. (2002) used to conduct a sensitivity analysis of the boreal toad, except we incorporated estimates of survival from a 6-year capture-recapture study of 3 populations (1 was disease-free) that estimated the effect of chytridiomycosis on survival of boreal toads (Pilliod et al. 2010b; see Appendix Tables 1 and 2 for vital rates). Each matrix model had 3 stages: pre-juveniles (embryos, tadpoles, and overwintering metamorphs), juveniles, and adult males. We used a male-based model because there are no estimates of the effects of infection on survival of female toads. We used a single standard deviation matrix based on uninfected toads for all populations, regardless of disease prevalence. Using the same standard deviation matrix likely provided conservative estimates of disease effects, because disease is expected to increase temporal variation in vital rates, which could further reduce population growth (Gaillard et al. 2000).

We incorporated disease effects into matrix elements by weighting the mean survival of the population at each breeding pond by the presumed infection rate. For example, for a population in which 20% of the toads were infected, mean survival was $(0.80 \times 0.732) + (0.20 \times 0.422) = 0.670$, where 0.732 and 0.422 are mean survival estimates for uninfected and infected toads, respectively, and 0.80 and 0.20 are the proportions of the populations in the 2 groups. Application of these rates for each infection level resulted in mean survival rates of breeding populations ranging from 0.515 (70% infection) to 0.732 (0% infection). Pilliod et al. (2010) estimated effects of Bd on survival for 2 toad populations: Black Rock and Lost Trail. We used only the estimates from the Black Rock population because they were similar to Lost Trail, but were much more precise.

We assumed the same disease-related reduction in survival for juvenile toads as for adults. We believe this is a reasonable assumption because the 2 life stages share habitats and because preliminary results indicated similar infection prevalence. We did not incorporate disease effects into the pre-juvenile life stage. Although tadpoles of boreal toads can be infected by Bd in the lab (Blaustein et al. 2005), infection in the wild is rare (Green and Muths 2005, Padgett-Flohr and Goble 2007, Pearl et al. 2007b, Adams et al. 2010). We are unaware of data on infection rates for boreal toad metamorphs, which already have low survival (Biek et al. 2002).

For metapopulations with variable disease prevalence, we modeled dispersal among populations using annual dispersal rates of 1% or 10%. Dispersal was density independent and equally likely by all life stages and among all breeding populations within a metapopulation. Dispersal also did not affect survival relative to non-dispersers; however, dispersers assumed the survival rate of their recipient population. We are unaware of estimated dispersal rates for boreal toads, but the rates we used are similar to those documented for the Fowler's toad (*A. fowleri*) and used in a simulation of population dynamics of the natterjack toad (*Epidalea calamita*) (Smith and Green 2006, Stevens and Baguette 2008), species with similar habitat associations as the boreal toad. We did not simulate dispersal in metapopulations where all populations had the same disease prevalence because varying the dispersal rate had no effect on projections.

We incorporated demographic and environmental stochasticity into each simulation. Demographic stochasticity was estimated by sampling the parameters from a lognormal distribution during each time step (i.e., year; Akçakaya 2005). Environmental stochasticity was modeled by sampling the standard deviation matrix of the matrix elements from a lognormal distribution during each time step (Akçakaya 2005). We assumed 50% correlation in environmental variation among the 4 subpopulations, as would be expected from variation in weather or other factors that would simultaneously affect all populations.

All projections were run using stable population growth (log $\lambda = 0.0$) in the absence of disease or stochasticity. We set growth to log $\lambda = 0.0$ by modifying the pre-juvenile matrix element (Conroy and Brook 2003). The resulting growth rate of uninfected populations then matched the estimated growth rate of the disease-free population of boreal toads in the Colorado population in Pilliod et al. (2010), where mean annual survival of males (0.760) was similar to that of uninfected toads (0.732) in the population we used as the basis of our survival rates. For all simulations, each of the 4 breeding populations in a metapopulation started at stable age distribution with 50 adult males and we simulated exponential growth of 10,000 replicated populations for 10 years. We calculated stochastic growth of metapopulations using maximum likelihood methods and assessed population risk by the probability of metapopulation decline at the end of the 10 year projections.

RESULTS

Boreal Toads

We sampled 404 *A. boreas* across Glacier National Park, of which 29% tested positive for Bd. Of the 404 toads, 69% were captured aquatically, 23% were female, and 43% were captured in an area that had burned since 1998. The model with the main effects of capture environment (aquatic or terrestrial), demographic group (female or male/juvenile), and burn status (burned or unburned) provided the best fit to the data and received 2.5 times more support than the second-ranked model (Table 1). There was little difference in model weights among the next 4 models

(w_i = 0.13–0.17), which all received similar levels of support because they included the covariate for capture environment, the covariate with the largest effect size. Only 9% of toads captured terrestrially were infected, compared to >30% of toads captured in wetlands (Figure 2a). Greater probability of infection for aquatic toads was consistent for both females and males/juveniles (Figure 3a).

Although the effect of fire on infection status of toads received less support than capture environment, its inclusion improved the fit of models and the 95% confidence interval around the coefficient excluded 0. Toads in recently burned areas were only half as likely to be infected as toads in unburned areas (Figure 2b). This fire effect was consistent regardless of capture environment, suggesting that toads in burned areas were less likely to be infected in both aquatic and terrestrial environments compared with toads in unburned habitats, but the estimates for the interaction between capture environment and wildfire did not differ from 0 (Figure 3b).

After controlling for capture environment, the sex or developmental stage of a toad had the smallest effect on probability of infection. The model with the main effect of demographic group provided only a slightly better fit to the data than the base model that included only capture year and elevation (Table 1). Males and juveniles combined were 1.4 times more likely to be infected as females, but the estimates were imprecise (Figure 2c). The higher infection prevalence for males and juveniles was evident only for toads captured aquatically (Figure 3a). Terrestrial toads of both demographic groups had similar infection rates (9%).

Columbia Spotted Frogs

Thirty-two percent of 98 Columbia spotted frogs tested positive for Bd in 2009. The prevalence of infection on Columbia spotted frogs increased slightly with body size (b = 0.04

[SE = 0.02]), but the probability of infection was similar for frogs from burned (0.33 [0.07]) and unburned wetlands (0.28 [0.06]), suggesting that wildfire did not reduce the suitability of wetlands for Bd populations.

Implications of Variation in Disease Prevalence

Stochastic growth rates (log λ_s) of simulated toad metapopulations ranged from a low of -0.101 (± 0.054 [95% CI]) for the metapopulation comprised of 4 populations each with 40% infection prevalence, to a high of -0.059 (± 0.052) for the metapopulation with 1% dispersal rate and a mean of 30% infection prevalence that varied among populations. All metapopulations were predicted to decline over the 10 year projection, which we expected because vital rates were set so populations would experience stable growth only in the absence of disease and stochasticity. Regardless, there were clear differences in projected rates of decline attributable to spatial variation in disease prevalence, and, to a lesser extent, dispersal rate within metapopulations.

Metapopulations with uniform disease prevalence were much more likely to experience a projected 50%–60% decline in number of adult males over 10 years than metapopulations where disease prevalence varied spatially (Figure 4). With a mean infection prevalence of 30%, there was a 64% chance of 50% decline in metapopulation size when all populations had the same prevalence, compared to only 36% chance of the same decline for the metapopulation with variable disease prevalence and 1% annual dispersal. The metapopulation had a 95% chance of 50% decline when all populations had 40% infection prevalence, compared to 81% chance for the metapopulation with variable disease prevalence and 1% annual dispersal.

In metapopulations with spatially variable disease prevalence, increasing dispersal among populations reduced growth rate and increased risk of metapopulation decline (Figure 4). For both simulations, risk of decline was higher for the metapopulation with 10% annual dispersal than for the metapopulation with 1% annual dispersal. However, the risk imposed by increased dispersal among populations with different disease prevalence was still smaller than the risk for metapopulations with the same mean infection but uniform disease prevalence.

DISCUSSION

Our results show that how individuals use habitats in a heterogeneous landscape can have a large effect on their infection status, and that this variation may have important population-level implications. Habitat use by toads at the time of capture was the best predictor of infection status, with aquatic toads averaging 35% infection compared to only 9% infection for terrestrial toads. We suspect this large difference reflects both recent exposure to the aquatic fungus, as well as the enhanced ability of terrestrial animals to clear minor or moderate infections in an arid environment that is less conducive to pathogen growth (Piotrowski et al. 2004, Murphy et al. 2011). Among *Litoria* frogs in Queensland rainforests, species more closely associated with water were more likely to be infected and to have suffered declines consistent with chytridiomycosis (Rowley and Alford 2007), and species that used permanent water bodies for breeding were more likely to be infected than congeners that used temporary water bodies (Kriger and Hero 2007). In our study area, several toads that were tracked using radio telemetry had mild Bd infections when they were first captured in wetlands, but tested negative shortly after shifting to terrestrial habitats (Guscio et al. 2008; BRH and PSC, unpublished data). If the ability to avoid or clear infection is linked with habitat use, variation in habitat composition and how individuals use those habitats could partially ameliorate the effects of disease.

The lower prevalence of disease on toads occupying recently burned areas indicates that landscape disturbances like wildfire may reduce disease risk or prevalence. The effect of wildfire was clearly secondary in importance to use of aquatic versus terrestrial habitats, but all fire-effects models, including the best-supported model (Table 1), predicted a lower occurrence of Bd on toads in burned habitats than in unburned habitats. Furthermore, this fire effect occurred in both aquatic and terrestrial habitats, although the imprecise estimates of infection prevalence prohibit a strong conclusion about the interaction between capture environment and wildfire (Figure 3). The lower prevalence of disease on toads in recently burned areas is consistent with other studies showing that natural and anthropogenic disturbances can modify disease risk or prevalence. For example, expansion of tall grasslands that resulted from fire suppression was linked with an increase in tick density and tick-borne haemolytic disease in African buffalo (*Syncerus caffer*); the disease declined after reintroduction of fire (Fyumagwa et al. 2007). Modification of ponds and fragmentation by roads has lead to an increase in trematodes that infect amphibians and other aquatic hosts (Johnson et al. 2002, Urban 2006). Also, similar to our evidence of lower infection prevalence for toads in burned wetlands, warm water temperatures in ponds with open canopies may limit Bd infection in aquatic newts (Raffel et al. 2010).

We suspect the warmer conditions in burned forests compared with unburned forests may reduce infection either by limiting growth of Bd or by enhancing the immune response of hosts. There is increasing evidence that small, achievable increases in body temperature may confer important survival advantages to hosts infected by Bd. Growth of the fungus declines above approximately 24°C (Longcore et al. 1999, Piotrowski et al. 2004), which is below the optimum growth or performance temperature of boreal toads (Lillywhite et al. 1973) and some other anurans (Hillman et al. 2009). During a chytridiomycosis epidemic, Panamanian golden frogs

(*Atelopus zeteki*) that increased their body temperature via behavioral thermoregulation were less likely to become infected than frogs that did not induce fever (Richards-Zawacki 2010). Terrestrial habitats in recently burned forests in Glacier NP are warmer and provide more opportunities for boreal toads to achieve preferred temperatures than in neighboring unburned forest (Hossack et al. 2009), which may help toads combat infection.

It is uncertain whether Bd infection in free-ranging animals is directly limited by host temperatures, by increased immune response by hosts, or a combination of these factors. Increased survival of infected boreal toads that induced fever was achieved while ambient temperatures remained within the optimum growth range of Bd (Murphy et al. 2011), and some species can clear Bd infection even when housed at optimal growth temperatures for Bd (Bustamante et al. 2010, Márquez et al. 2010). These studies suggest that infection can be inhibited by an increased immune response rather than ambient temperature alone, thus a combination of environmental variation and host behavior may buffer some individuals and populations from the effects of a lethal disease. If Bd is limited by warmer host or ambient temperatures in recently burned areas, the same benefits should be achievable in open habitats like meadows or in forests disturbed by other mechanisms. For example, tropical anuran communities in deforested areas had lower prevalence or intensity of infection by Bd than anurans inhabiting intact forest, possibly as result of less hospitable conditions for the fungus in forest fragments (Van Sluys and Hero 2009, Becker and Zamudio 2011).

Interactions between disturbance and disease are usually expected to have negative consequences for populations, because the increased density of hosts crowded into fragments of suitable habitat can facilitate disease transmission or reduce host condition and immunological function (Daszak et al. 2000, McCallum 2008). Our study system has a simple amphibian community, with only 2 pond-breeding anurans distributed park-wide. Toads tend to increase in abundance after an area burned, whereas Columbia spotted frogs may increase or decrease, depending upon burn severity and time since fire (Hossack and Corn 2007, Chapters 1 and 2). Therefore, it is unlikely that the lower probability of infection for toads in burned forests results from changes in the transmission process or in host density. Similarly, Bd infection was less common on *Litoria wilcoxii* in open habitats even though host density was higher than in intact forests (Van Sluys and Hero 2009). The comparable Bd prevalence on Columbia spotted frogs from burned and unburned wetlands in our study area further suggests that lower infection probability in burned areas was not a result of changes in wetland characteristics or host community after wildfire.

Counter to our expectation, we found only moderate evidence that prevalence of Bd differed between demographic groups. Males and juveniles were 1.4 times as likely to be infected as females, but they were also twice as likely to be captured aquatically as females. We suspect higher infection prevalence in males and juveniles results from greater exposure to the pathogen than females, rather than differences in immune response or susceptibility to infection. Most males likely try to breed every year and can spend > 1 month at a breeding site (BRH, unpublished data). Males are also more aquatic than females outside of the breeding season (Bartelt et al. 2004). In contrast, females likely do not breed every year in our study area, especially at higher elevations, and do not stay long at wetlands when they do breed (Pilliod et al. 2010b). Our results suggest aquatic females may have a slightly higher prevalence of infection than terrestrial females (Figure 3a). More importantly, terrestrial toads had the same low prevalence of infection (9%) regardless of demographic group (Figure 3b), which suggests leaving the source of pathogen exposure provides similar opportunities to clear infection. These results also highlight the importance of sampling the full range of habitats used by a species to provide a better understanding of disease prevalence and risk.

Our simulations showed that variation in disease prevalence related to habitat use and landscape characteristics can have large effects on expected population growth and risk of decline. Matrix models based on realistic infection prevalence and vital rates for male boreal toads, including documented effects of chytridiomycosis on survival, show that among-population variation in disease prevalence reduces risk of metapopulation decline over 10 years. With a mean Bd prevalence of 30% and 1% annual dispersal rate, a metapopulation composed of 4 populations with equal disease prevalence was nearly twice as likely to experience a 50% decline in size as a metapopulation where infection varied spatially. If infection prevalence was increased to 40%, the benefit of spatial variation in infection prevalence was reduced because decline was more inevitable; however, variation still resulted in a larger population size after 10 years (Figure 4).

Spatial structure and dispersal among populations also has important implications for the spread of disease and population persistence (Hess 1996, McCallum and Dobson 2002). In our simulations, risk of decline was always higher for metapopulations with 10% annual dispersal than for 1% annual dispersal. The lower dispersal rate allowed populations with less disease to maintain more independent dynamics, slowing their rate of decline. With a 10% dispersal rate, more of the offspring that would have otherwise stayed in a disease-free or low-disease environment instead colonized areas with higher disease prevalence and lower survival rates. There are no estimates of dispersal rates by boreal toads, but frequent colonization of new habitats by adults suggests dispersal rates are high (Pearl and Bowerman 2006, Hossack and Corn 2007). In the most detailed study of toad dispersal, inter-population dispersal by Fowler's toads (*A. fowleri*) was estimated at 11% annually and did not differ by life stage (Smith and Green 2005). If dispersal rates for boreal toads are similar, spatial variation in disease prevalence may provide less of a buffer against disease than if populations are more independent unless dispersal is biased towards areas with less disease.

All models are dependent upon the vital rates and assumptions that are used, and the outputs are best used to rank outcomes rather than make specific predictions. Some assumptions we used to model variation in disease—for example, static disease prevalence for 10 years and no changes in vital rates other than survival—are unlikely to be met. Information on infection intensity rather than just infection prevalence would also help in predicting effects on survival (Briggs et al. 2011). Nevertheless, our results suggest that variation in prevalence of Bd among populations, documented in our study and elsewhere (e.g., Kriger and Hero 2007, Muths et al. 2008, Adams et al. 2010), may be crucial to slowing declines. More broadly, our results show that maintaining natural disturbance regimes and diverse habitats can produce significant variation in disease prevalence and projected population growth across large landscapes.

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Table 1. Models used to describe variation in infection of 404 boreal toads (*Anaxyrus boreas*) by the fungus *Batrachochytrium dendrobatidis* relative to capture environment (aquatic or terrestrial), demographic group (female or male/juvenile), and burn status (burned since 1998 or not). Models are ranked according to differences in QIC_u and models weights (w_i). All models included an intercept. For models with interactions, main effects were fitted but are not shown. "k" indicates the number of parameters.

Model	k	ΔQIC_u	w_i
capture environment + demographic group + burn status	8	0.00	0.42
capture environment × demographic group	8	1.88	0.17
capture environment × burn status	8	2.20	0.14
capture environment	8	2.25	0.14
capture environment × demographic group + burn status × demographic group	10	2.36	0.13
burn status	6	21.49	0.00
demographic group	6	32.27	0.00
year + elevation	5	34.99	0.00

FIGURE LEGENDS

Figure 1. Distribution of boreal toads (*Anaxyrus boreas*; circles) and Columbia spotted frogs (*Rana luteiventris*; squares) sampled for the aquatic fungus *Batrachochytrium dendrobatidis* in Glacier National Park, Montana (USA), during 2004–2005 and 2008–2009. Nine wildfires that burned between 1998 and 2006 are shown in gray. For both species, solid symbols indicate individuals that tested positive for Bd and open symbols indicate individuals that tested negative.

Figure 2. Estimated probability of infection of 404 boreal toads (*Anaxryus boreas*) by the aquatic fungus *Batrachochytrium dendrobatidis* according to capture habitat (a), burn status of habitat (b), and demographic group (c).

Figure 3. Estimated probability of infection of boreal toads (*Anaxryus boreas*) by *Batrachochytrium dendrobatidis* according to the interaction between capture habitat (aquatic or terrestrial) and whether or not the toad was in burned forest (a), and the interaction between capture habitats and demographic group (b).

Figure 4. Expected decline of boreal toad (*Anaryxus boreas*) metapopulations with 30% mean infection (a) and 40% mean infection prevalence (b). In each plot, the solid line represents 4 populations with the same infection prevalence, the dash-dot line represents variable infection with 1% annual dispersal, and the dashed line represents variable infection with 10% annual dispersal. Note the different scales on the x-axes for the 2 plots.

Figure 1.

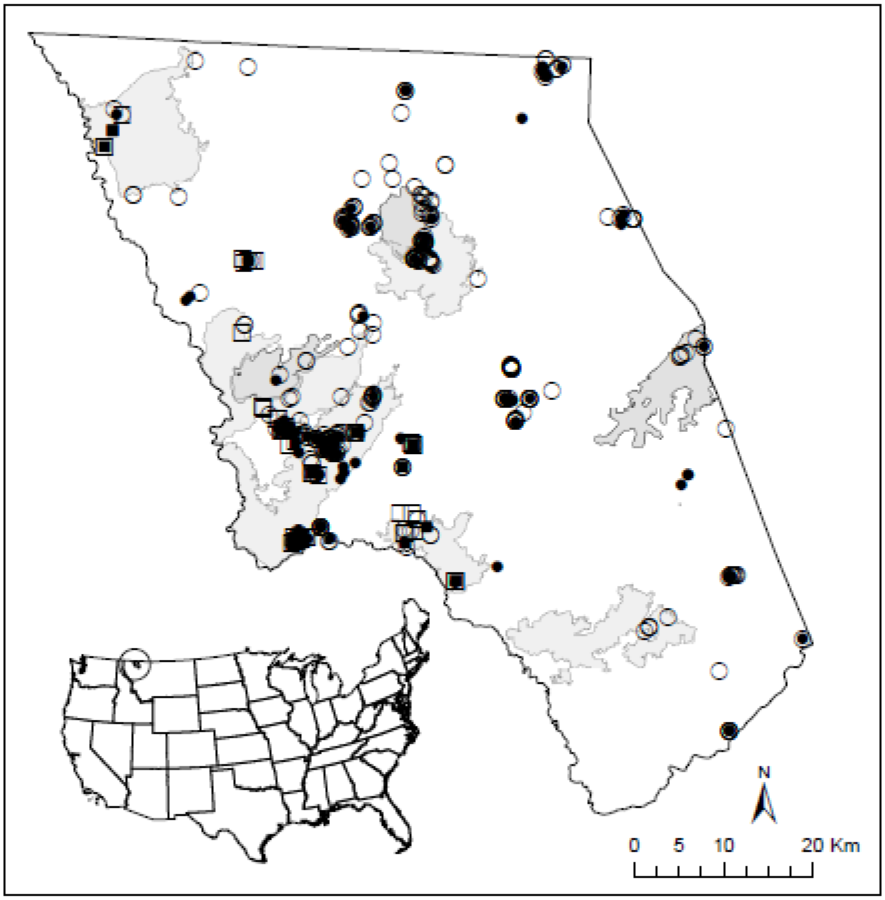


Figure 2.

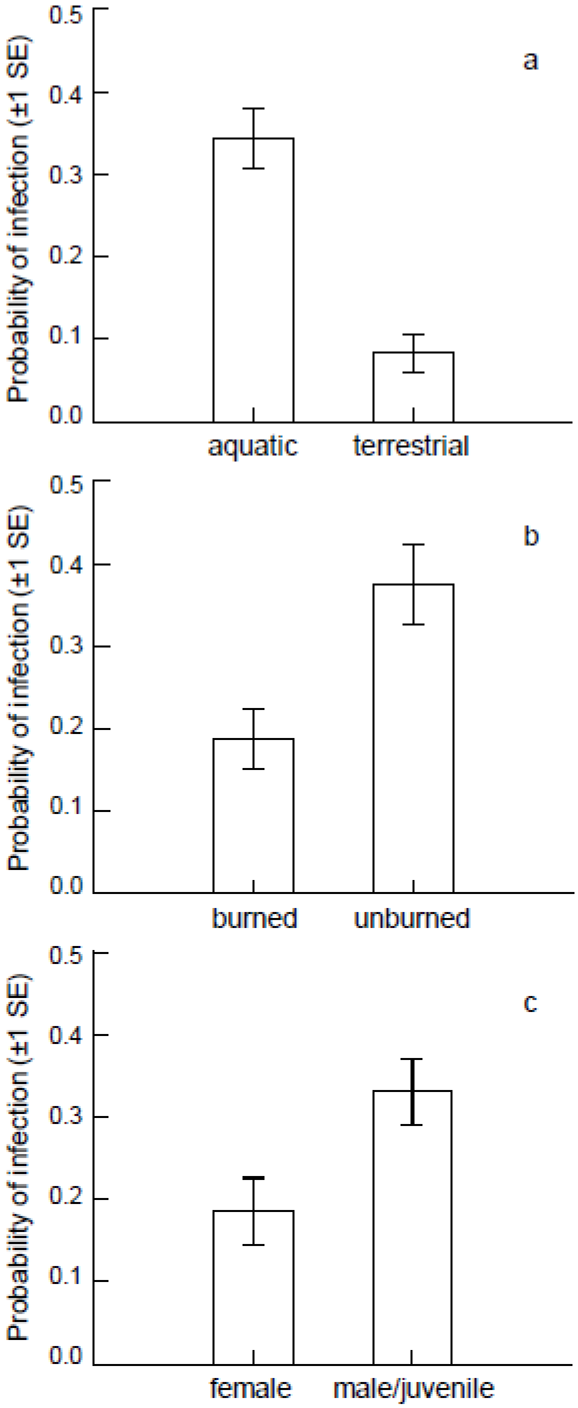

Probability of infection (±1 SE)
0.5
0.4
0.3
0.2
0.1
0.0
a
aquatic
terrestrial
b
burned
unburned
c
female
male/juvenile

Figure 3.

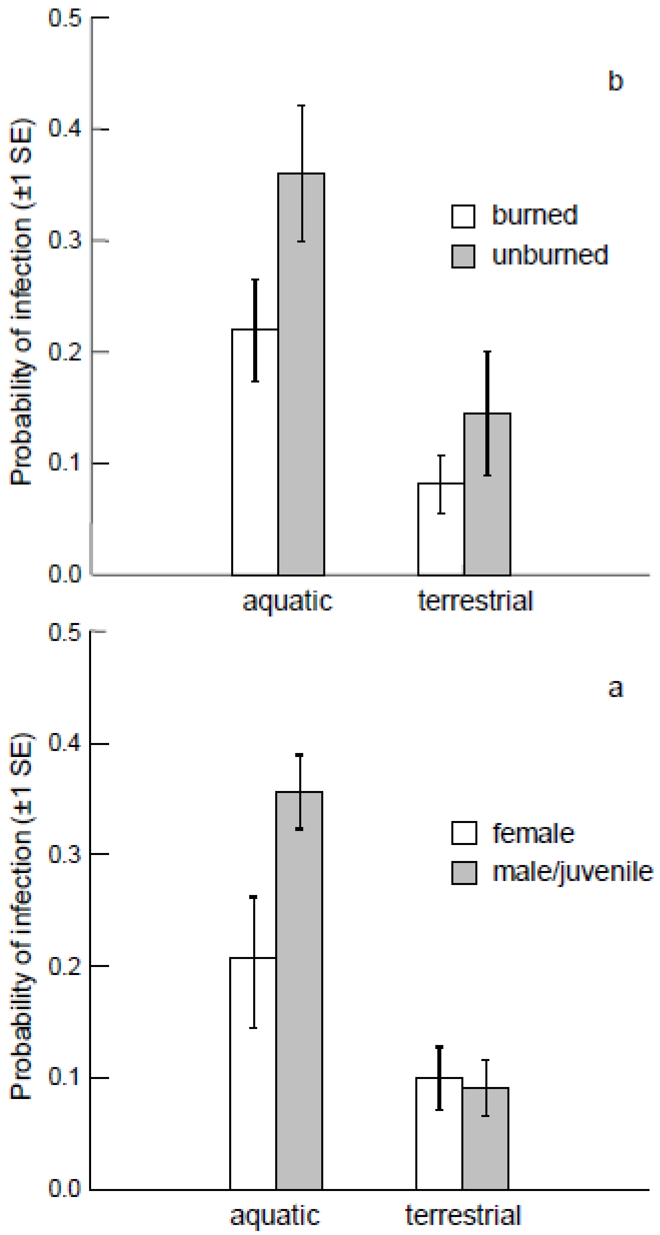
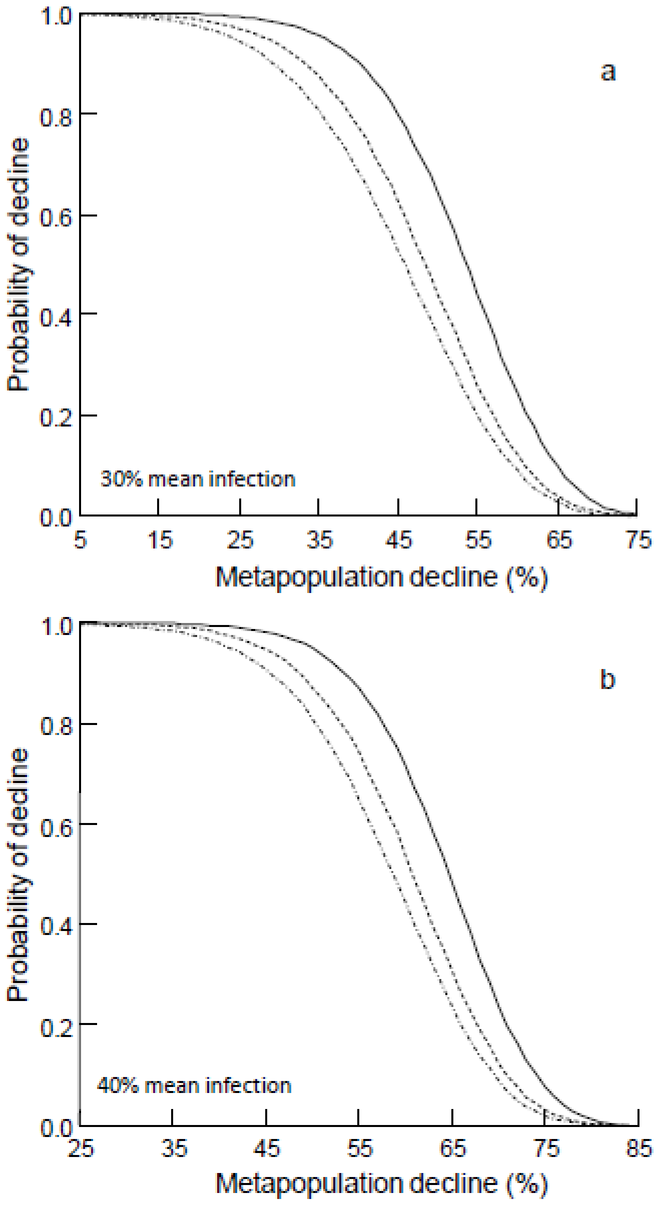

b
Probability of infection (±1 SE)
0.0
0.1
0.2
0.3
0.4
0.5
☐ burned
▨ unburned
aquatic
terrestrial
a
Probability of infection (±1 SE)
0.0
0.1
0.2
0.3
0.4
0.5
☐ female
▨ male/juvenile
aquatic
terrestrial

Figure 4.


a
Probability of decline
1.0
0.8
0.6
0.4
0.2
0.0
30% mean infection
5
15
25
35
45
55
65
75
Metapopulation decline (%)
b
Probability of decline
1.0
0.8
0.6
0.4
0.2
0.0
40% mean infection
25
35
45
55
65
75
85
Metapopulation decline (%)

APPENDIX

Appendix Table 1. Vital rates and transition probabilities used to project population growth of boreal toads (*Anaxyrus boreas*). All vital rates are from Biek et al. (2002) except for adult survival. Adult survival is from Pilliod et al. (2010) and represents survival of uninfected male toads from Black Rock, Wyoming. For the simulations, we modified the product of the pre-juvenile estimates to achieve stable population growth (log $\lambda = 0.0$) in the absence of growth or stochasticity (see text).

Vital Rate	Mean	SD
Embryo survival	0.78	0.36
Larval survival	0.47	0.24
Metamorph survival	0.08	0.06
Juvenile survival	0.26	0.04
Juvenile to juvenile	0.26	0.04
Juvenile to adult	0.014	0.007
Adult survival	0.732	0.07
Probability of mating	0.50	0.25
Clutch size (females)	3532	856
Age at sexual maturity (year)	4–7	—

Appendix Table 2. Survival rates used for adult and juvenile boreal toads (*Anaxyrus boreas*) to estimate the effect of variation in infection by *Batrachochytrium dendrobatidis*. See text for a description of how estimates were derived.

Infection prevalence (%)	Adult survival	Juvenile survival
0	0.732	0.260
10	0.701	0.249
20	0.670	0.238
30	0.639	0.227
40	0.608	0.216
50	0.577	0.205
60	0.546	0.194
70	0.515	0.183