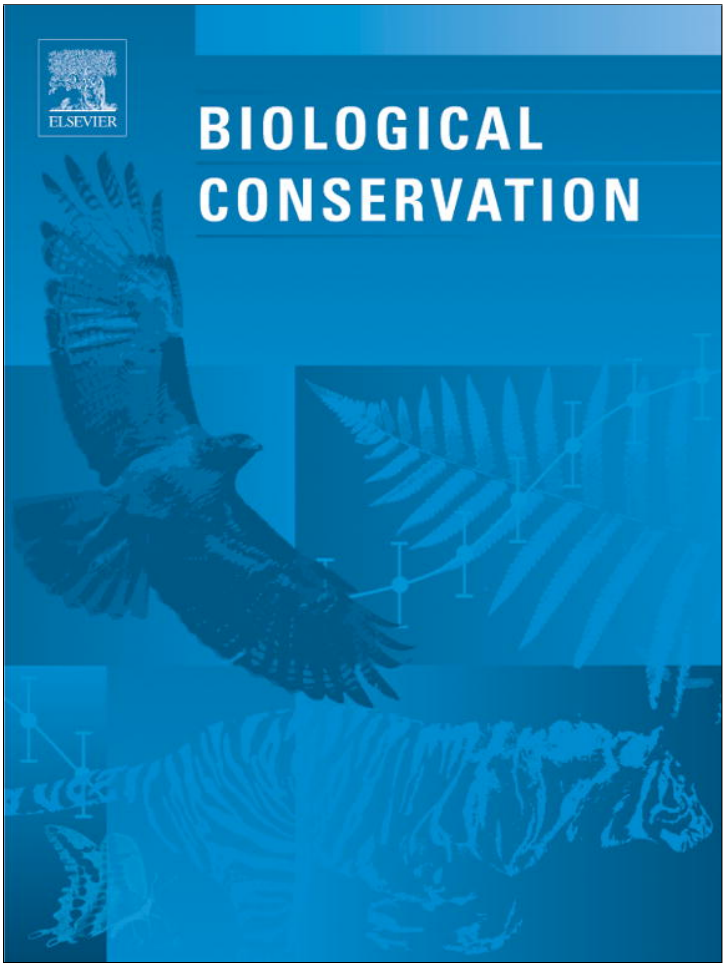
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Disease in a dynamic landscape: Host behavior and wildfire reduce amphibian chytrid infection

Blake R. Hossack [a,b,*], Winsor H. Lowe [c], Joy L. Ware [d], Paul Stephen Corn [a]

[a] *U.S. Geological Survey, Northern Rocky Mountain Science Center, Aldo Leopold Wilderness Research Institute, 790 East Beckwith Avenue, Missoula, MT 59801, USA*
[b] *Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*
[c] *Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA*
[d] *Department of Pathology, Virginia Commonwealth University, Richmond, VA 23298, USA*

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ABSTRACT

Disturbances are often expected to magnify effects of disease, but these effects may depend on the ecology, behavior, and life history of both hosts and pathogens. In many ecosystems, wildfire is the dominant natural disturbance and thus could directly or indirectly affect dynamics of many diseases. To determine how probability of infection by the aquatic fungus *Batrachochytrium dendrobatidis* (Bd) varies relative to habitat use by individuals, wildfire, and host characteristics, we sampled 404 boreal toads (*Anaxyrus boreas boreas*) across Glacier National Park, Montana (USA). Bd causes chytridiomycosis, an emerging infectious disease linked with widespread amphibian declines, including the boreal toad. Probability of infection was similar for females and the combined group of males and juveniles. However, only 9% of terrestrial toads were infected compared to >30% of aquatic toads, and toads captured in recently burned areas were half as likely to be infected as toads in unburned areas. We suspect these large differences in infection reflect habitat choices by individuals that affect pathogen exposure and persistence, especially in burned forests where warm, arid conditions could limit Bd growth. Our results show that natural disturbances such as wildfire and the resulting diverse habitats can influence infection across large landscapes, potentially maintaining local refuges and host behaviors that facilitate evolution of disease resistance.

1. 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 (Mbora and McPeek, 2009; McCallum, 2008). Environmental variation and how individuals are exposed to this variation could modify disease risk through several mechanisms. For example, disturbances (e.g., fragmentation) or unusual climate events (e.g., drought) can magnify the effects of disease by increasing the density of hosts and subsequent transmission rates (Anderson and May, 1978; Arneberg et al., 1998), changing community structure (Poteet, 2006; Van Buskirk and Ostfeld, 1998), or affecting the condition of hosts or pathogens (Jokela et al., 2005; Jolles et al., 2005). 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 host populations (Lafferty and Holt, 2003). Greater knowledge of how disease varies among habitats and individuals is critical to predicting its effects on host fitness and population growth.

Pathogens are one of the primary causes of amphibian decline worldwide (Wake and Vredenburg, 2008). Many of these declines have been attributed to chytridiomycosis, a recently-emerged disease caused by the aquatic fungus *Batrachochytrium dendrobatidis* (Bd) (Berger et al., 1998; Bosch et al., 2001; Muths et al., 2003). In the Rocky Mountain region (USA), Bd has been linked with the possible extirpation of boreal toad (*Anaxyrus boreas boreas*) populations, and enzootic infection of extant populations reduces survival of adults (Muths et al., 2003; Pilliod et al., 2010). There is growing evidence that environmental variation may affect prevalence of Bd infection among populations (Adams et al., 2010; Becker and Zamudio, 2011; Hossack et al., 2010; Kriger and Hero, 2007; Murray et al., 2009), but there has been less emphasis on how habitat use by individuals within populations affects the probability of infection. For amphibian species that use a variety of habitats, this variation may alter the individual- and population-level implications of chytridiomycosis by limiting infection rates or promoting

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* Corresponding author at: U.S. Geological Survey, Northern Rocky Mountain Science Center, Aldo Leopold Wilderness Research Institute, 790 East Beckwith Avenue, Missoula, MT 59801, USA. Tel.: +1 406 542 3245; fax: +1 406 542 4196.

E-mail addresses: blake_hossack@usgs.gov (B.R. Hossack), winsor.lowe@mso.umt.edu (W.H. Lowe), jware@mcvh-vcu.edu (J.L. Ware), steve_corn@usgs.gov (P.S. Corn).

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host recovery (Briggs et al., 2010; Pilliod et al., 2010; Puschendorf et al., 2011).

The environmental limitations of Bd suggest that how individuals use their environment could mediate exposure or the ability to resist or tolerate infection. Not surprisingly, highly aquatic amphibians that experience greater exposure to Bd often more likely to be infected than less aquatic species (Longcore et al., 2007; Rowley, 2006). Ecological and physiological mechanisms can also affect disease prevalence of females compared to males. Females of many amphibians are less aquatic than males or juveniles (Bartelt et al., 2004; Grayson and Wilbur, 2009; Tinsley, 1989), which may reduce the frequency of disease-transmitting encounters, especially during breeding season when males linger at breeding sites and mount each other frequently (Wells, 1977). Females may also have stronger immune systems or invest more resources in immunity than males (Stoehr and Kokko, 2006; Zuk and McKean, 1996). 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 in amphibians (Biek et al., 2002; Trenham and Shaffer, 2005).

Temperature is also a critical factor in many host–pathogen interactions. Most pathogens have optimal growth temperatures below that of their hosts; thus, warm microhabitats may slow pathogen growth (Kluger et al., 1975; Piotrowski et al., 2004). Growth of Bd declines above ~24 °C (Longcore et al., 1999; Piotrowski et al., 2004), which is below the optimum growth or performance temperature of boreal toads and some other anurans (Hillman et al., 2009; Lillywhite et al., 1973). At the same time, warm temperatures can enhance a host's immune response, providing a complementary mechanism to limit pathogen growth (Ribas et al., 2009; Xiao et al., 2011). Many invertebrates and vertebrates induce behavioral fever after infection by a pathogen, increasing their survival or other correlates of fitness (Elliot et al., 2002; Kluger et al., 1975; Richards-Zawacki, 2010). For example, in a laboratory experiment, boreal toads infected with Bd were more likely to induce fever than uninfected toads, and infected toads that induced fever had higher survival than those that did not induce fever (Murphy et al., 2011). Prior exposure to Bd also increased survival of boreal toads compared with naive hosts, but only when infected hosts used dry microenvironments (Murphy et al., 2011). Evidence of resistance to re-infection indicates that hosts can acquire immunity (Ramsey et al., 2010), and a recent discovery that the major histocompatibility complex (MHC) is linked with susceptibility to Bd provides a potential mechanism for evolving resistance (Savage and Zamudio, 2011).

In western North America and many other ecosystems, wildfire is the dominant natural disturbance and is critical for structuring habitats for a wide variety of species, including altering host–parasites interactions (Fyumagwa et al., 2007; Hutto, 1995; Whelan et al., 2002). Through its effects on host abundance and microclimate, we expected wildfire could also affect the distribution and dynamics of Bd. Loss of litter and duff on the forest floor and greater amounts of solar radiation reaching the soil surface can result in persistent increases in soil temperatures for several years after wildfire in northern forests (Bissett and Parkinson, 1980; Kasischke and Johnstone, 2005; Zhuang et al., 2002). Compared with unburned forest, terrestrial habitats in recently burned forest are warmer and provide more opportunities for boreal toads to achieve preferred temperatures (27–29 °C; Lillywhite et al., 1973) that could limit growth of Bd (Hossack et al., 2009). Alternatively, harsher terrestrial conditions after wildfire could force animals to become more aquatic, potentially increasing their exposure to Bd. Although variation in Bd infection has been linked to differences in forest structure (Becker and Zamudio, 2011; Van Sluys and Hero, 2009), we do not know how natural disturbances like wildfire influence the dynamics of this pathogen. This question is especially important given the expected climate- and management-related changes in wildfire regimes occurring throughout the world (IPCC, 2007; Westerling et al., 2006).

To determine how habitat use, landscape variation caused by wildfire, and individual host characteristics affect probability of infection by Bd, we sampled 404 boreal toads over four summers across a wide variety of habitats in Glacier National Park (NP), Montana (USA). We predicted that use of terrestrial habitats and recently-burned forests would reduce Bd infection relative to use of aquatic habitats and unburned forest, consistent with differences in exposure and growth conditions for the pathogen. We also predicted reduced probability of infection for female toads compared with males and juveniles, consistent with differences in exposure or immunocompetence. During the last year of the study, we sampled Columbia spotted frogs (*Rana luteiventris*) to provide an independent measure of the association between wildfire and Bd infection. In contrast to majority of previous studies focusing on species- and population-level variation in Bd infection, ours was explicitly designed to assess sources of variation in infection among individuals within a species and thus elucidate both ecological and behavioral mechanisms linked with disease.

2. Materials and methods

2.1. Study system

We sampled all toads ⩾1 year old (i.e., we excluded larval and recently metamorphosed toads) encountered in Glacier NP, Montana, during the late spring and summers of 2004–2005 and 2008–2009. Toads were captured during surveys that were part of an amphibian monitoring program and while hiking among water bodies (Corn et al., 2005). Boreal toads are often terrestrial outside of a discrete breeding season in the spring (Bartelt et al., 2004; Guscio et al., 2008). Our sampling of animals away from discrete population centers or breeding sites differs from most other studies of Bd in aquatic-breeding amphibians, but sampling the full range of habitats used by individuals was required to better understand variation in disease. Including toads in all habitats was also necessary to gain information on females, which are secretive and often skip years between breeding (Muths et al., 2010; Pilliod et al., 2010), yet are critical for population growth. Many toads were captured within the perimeters of nine stand-replacement wildfires that burned mixed-conifer forests between 1998 and 2006 (Fig. 1). These forests were historically replaced by fire every ~140–340 years, and recovery of these forests is slow as a result of the cold, dry conditions in the region (Barrett et al., 1991).

The Columbia spotted frog and the long-toed salamander (*Ambystoma macrodactylum*) are the only other widespread lentic-breeding amphibians in the park and often occupied the same wetlands as boreal toads. The spotted frog is commonly infected with Bd (Muths et al., 2008), but long-toed salamanders are rarely infected (C. Goldberg 2012, University of Idaho, personal communication). Sampled habitats ranged from 950 m to 2164 m in elevation.

2.2. Disease sampling

We sampled each toad for Bd by thoroughly swabbing the pelvic surface and 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 until analysis for presence of Bd using a PCR assay (Annis et al., 2004). See Hossack et al. (2010) for details on PCR methods. After sampling for Bd, we measured each toad (snout–vent length [SVL]), assigned it to a demographic group (juvenile, female, or male), and recorded

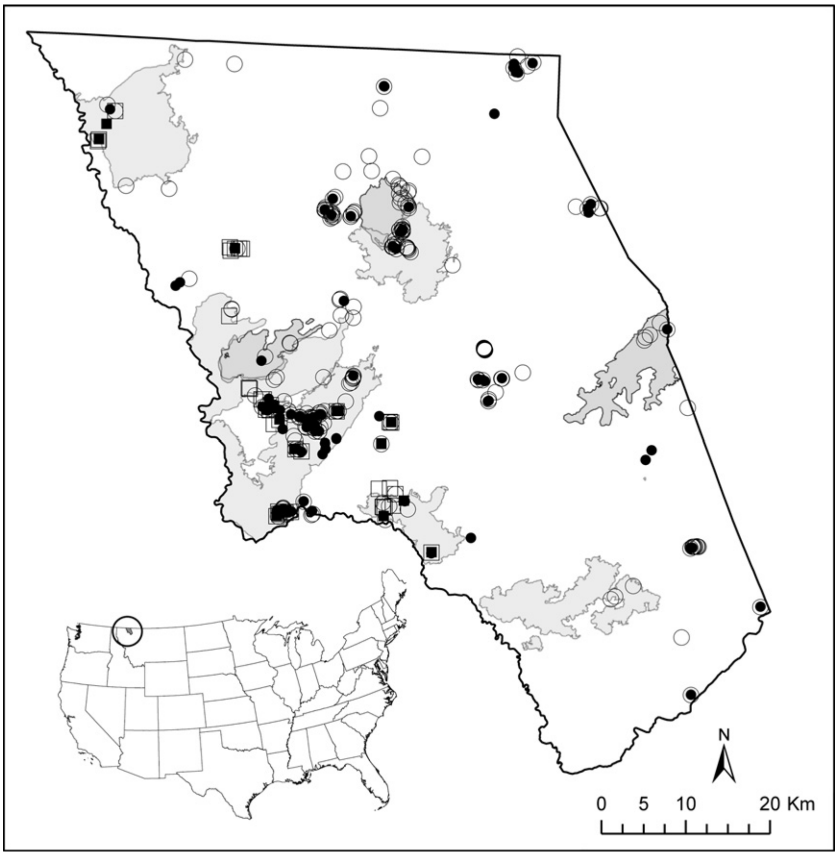

Fig. 1. Distribution of boreal toads (*Anaxyrus boreas*; circles) and Columbia spotted frogs (*Rana luteiventris*; squares) sampled for the aquatic fungus *Batrachochytrium dendrobatidis* in Glacier National Park, Montana (USA), during 2004–2005 and 2008–2009. Nine wildfires that burned between 1998 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.

whether it was collected within the perimeter of a recent wildfire. Distinguishing large juveniles from small females can be difficult because neither vocalizes or has secondary sexual characteristics; therefore, 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 or 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 left the water or were basking next to a water body. We did not consider proximity of streams because Bd is rare or absent in local streams (Hossack et al., 2010).

We used similar techniques to sample 98 Columbia spotted frogs during summer 2009, but we focused our efforts in and adjacent to areas that 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 probability of infection by Bd, because preliminary analyses suggested an association between wildfire and infection prevalence in toads. Specifically, we used the frogs to determine whether conditions in wetlands surrounded by burned forest somehow limited Bd populations. Columbia spotted frogs are much more aquatic than boreal toads, which we expect would increase their exposure to the fungus (e.g., Longcore et al., 2007). The more aquatic habits of Columbia spotted frogs may also result in more consistent exposure to Bd compared with the terrestrial boreal toads.

2.3. Statistical analysis: boreal toads

We used generalized estimating equations (GEEs) to compare probability of infection for boreal toads relative to capture environment (aquatic or terrestrial), demographic group (juvenile, female, or male), and whether or not they were captured in an area burned since 1998 (proc genmod in SAS 9.2). Aside from one wetland in an area burned in 1988, all unburned wetlands had not burned in >75 years. Instead of simply classifying toads as aquatic or terrestrial, we considered using distance from wetland as a covariate. We chose to use the binary covariate because it provided a similar fit to the data and because there are many unmapped wetlands in the park, which would introduce error into the analysis. We accounted for the correlation in infection status of individuals from the same wetlands using a compound symmetry covariance structure (Littell et al., 2002). Before estimating the effects of interest, we sought to account for as much nuisance variation as possible. Specifically, infection can co-vary with season and elevation (Adams et al., 2010; Muths et al., 2008). Because we were not explicitly interested in this variation, we 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 parameters described the most variation in the response data. The model with year and the linear effect of elevation provided the best fit to the data and was used as the basis for all subsequent models.

We estimated the additive effects of capture environment, demographic group, and wildfire on infection status of boreal toads by fitting models with each covariate by itself as well as a model that included all three covariates. We hypothesized capture environment (aquatic or terrestrial) would affect infection because individuals captured in or near wetlands likely experienced greater, or at least more recent, exposure to Bd than individuals captured away from wetlands. Similarly, we expected the more aquatic tendencies of male boreal toads would increase their exposure to Bd relative to females (Bartelt et al., 2004). Finally, we hypothesized that the warmer temperatures in recently burned forests would reduce probability of infection relative to toads in unburned forest, so we tested if disease status was influenced by whether or not a toad was captured within a recently burned area.

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 the way individuals use habitats, such as frequency of use of aquatic versus terrestrial habitats according to age or sex, affected exposure and probability of infection. Similarly, the capture environment × fire interaction would be important if infection 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. Also, 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 (Hossack, 2011).

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 one group and re-ran the models. The estimated probability of infection for these two groups was always nearly identical, and combining them resulted in more parsimonious models and more precise estimates.

2.4. Statistical analysis: Columbia spotted frogs

We used similar methods for the analysis of Bd infection of Columbia spotted frogs, but we were interested solely in isolating the effect of wildfire on infection status of aquatic hosts. To estimate the effect of wildfire on infection, 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 only sampled five juveniles and preliminary analyses indicated no differences in infection between sexes. We did not consider the effect of capture environment in this analysis because only one 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.

3. Results

3.1. Boreal toads

We sampled 404 boreal toads across the 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 four models ($w_i = 0.13$–0.17), which all received similar levels of support because they included capture environment, the covariate with the largest effect size. Only 9% of toads captured terrestrially were infected, compared to >30% of toads captured within 10 m of a water body (Fig. 2a). Aquatic toads were more likely to be infected regardless of sex or developmental stage (Fig. 3a).

Although the effect of wildfire on infection status of toads received less support than capture environment, its inclusion improved the fit of models significantly, and the 95% confidence interval around its model-averaged coefficient excluded zero. Toads in recently burned areas were only half as likely to be infected as toads in unburned areas (Fig. 2b). This fire effect was consistent in both aquatic and terrestrial environments, although the imprecise estimates prohibit a strong conclusion about the interaction between capture environment and wildfire (Fig. 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 (Fig. 2c). The higher infection probability for males and juveniles was evident only for toads captured aquatically (Fig. 3a). Terrestrial toads of both demographic groups were equally likely to be infected (9%).

3.2. Columbia spotted frogs

Thirty-two percent of 98 Columbia spotted frogs tested positive for Bd in 2009. Probability of infection of Columbia spotted frogs increased slightly with body size ($b = 0.04$, $\mathrm{SE} = 0.02$), but it was similar for frogs from burned (0.33, $\mathrm{SE} = 0.07$) and unburned wetlands (0.28, $\mathrm{SE} = 0.06$).

4. Discussion

Our results show that infection of hosts by a potentially-lethal disease is strongly linked with landscape variation and habitat use. Only 9% of toads captured terrestrially were infected with Bd 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. Several studies have linked variation in Bd infection with species-level or habitat characteristics (e.g., Kriger and Hero, 2007; Longcore et al., 2007; Rowley, 2006; Savage et al., 2011). We found that habitat use by individuals within a species is linked with probability of infection. Although variation in infection could result from different rates of disease-induced mortality among habitats, we hypothesize that the large difference in probability of infection between animals from aquatic and terrestrial habitats reflects recent exposure to the aquatic fungus, as well as the enhanced ability of terrestrial animals to clear infections in an arid environment that is less conducive to pathogen growth (Murphy et al., 2011; Piotrowski et al., 2004). Bd infection causes a large reduction in annual survival of boreal toads, yet individuals commonly transition from infected to uninfected between years (Pilliod et al., 2010). Differences in habitat use among individuals may be a critical mechanism that helps promote variation in disease risk and resistance.

The effect of wildfire was secondary in importance to use of aquatic or terrestrial habitats, but all fire-effects models—including the best-supported model—predicted lower infection for toads in burned habitats than in unburned habitats. We suspect that 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. Mean temperature of physical models that simulated the operative body temperature of boreal toads was up to 5 °C higher in burned habitats after a 2003 wildfire in Glacier NP than in unburned habitats (Hossack et al., 2009).

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 and year and elevation covariates. 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

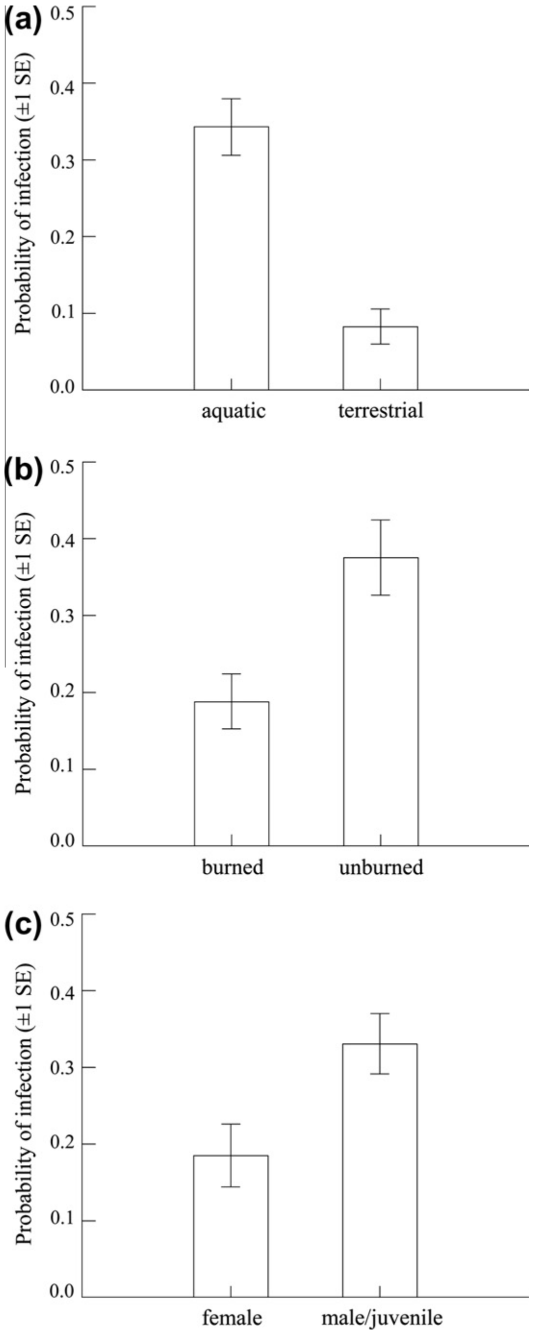

Fig. 2. Estimated probability that an individual boreal toad (*Anaxryus b. boreas*; $n = 404$) was infected by the aquatic fungus *Batrachochytrium dendrobatidis* according to (a) capture habitat, (b) burn status of habitat, and (c) demographic group.

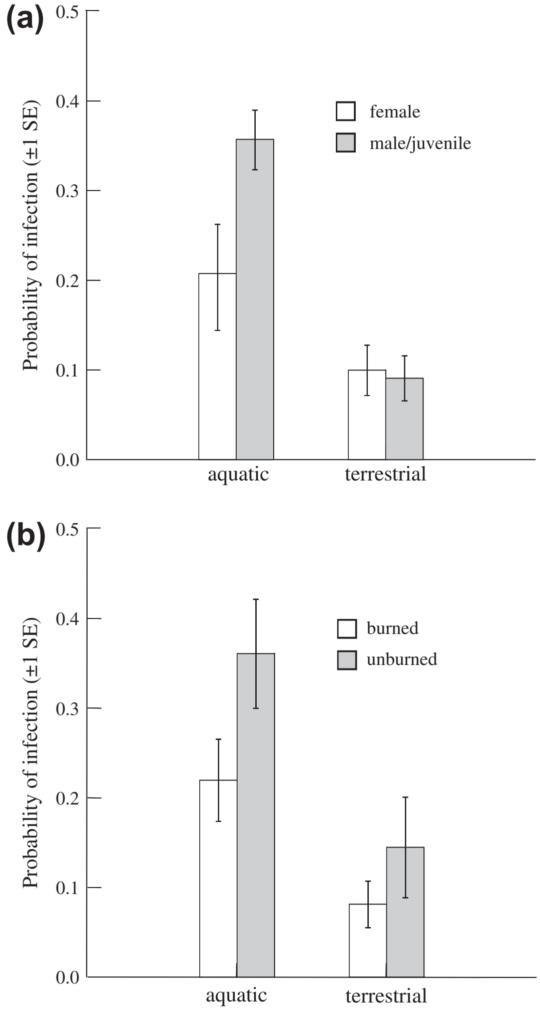

Fig. 3. Estimated probability that an individual boreal toad (*Anaxryus b. boreas*; $n = 404$) was infected by the aquatic fungus *Batrachochytrium dendrobatidis* according to (a) the interaction between capture habitat (aquatic or terrestrial) and demographic group and (b) the interaction between capture habitat and whether or not the toad was captured in recently burned forest.

Further, burned habitats provided a greater range of microenvironments in which toads could thermoregulate. The largest temperature differences between burned and unburned habitats were in burrows and under large debris, where toads tend to reside when terrestrial (Bartelt et al., 2004; Guscio et al., 2008; Hossack et al., 2009). These temperature differences would shrink over time, but increased soil temperatures in cold forests can last for several years after fire (Bissett and Parkinson, 1980; Kasischke and Johnstone, 2005; Zhuang et al., 2002).

There is increasing evidence that small, achievable increases in body temperature may confer important survival advantages to hosts infected by Bd (Bustamante et al., 2010; Murphy et al., 2011). During a chytridiomycosis epidemic in Panama, frogs that induced fever were less likely to become infected than frogs that did not induce fever (Richards-Zawacki, 2010), and survival of Bd-infected frogs in Australia was linked with changes in seasonal temperatures (Murray et al., 2009). Also, prevalence and intensity of Bd infection on amphibians in New World and Australian tropics were negatively related to deforestation, possibly as a result of less hospitable conditions for the fungus in open habitats (Becker and Zamudio, 2011; Van Sluys and Hero, 2009). It is uncertain whether Bd infection in free-ranging animals is directly limited by environmental conditions (including host microclimate), increased immune response of hosts, or a combination of these factors. However, boreal toads and other species can clear Bd infection even at optimal growth temperatures for the pathogen (Bustamante et al., 2010; Márquez et al., 2010; Murphy et al., 2011), indicating that the combination of environmental conditions and host behavior may be critical to buffering some individuals from disease.

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 (Anderson and May, 1978; Lafferty and Holt, 2003). Our study system has low amphibian richness, composed primarily of two pond-breeding anurans that host Bd and one pond-breeding salamander that is rarely infected. Boreal toads tend to remain stable or increase in distribution after wildfire, whereas abundance of Columbia spotted frogs may increase or decrease, depending upon burn severity and time since fire (Hossack et al., in press-a, in press-b). Therefore, it seems unlikely that the reduced probability of infection for toads in burned forests resulted from changes in the transmission process, host density, or disease-related mortality linked with habitat use, although we cannot exclude these hypotheses. For example, infection was less common on Stony-creek frogs (*Litoria wilcoxii*) in fragmented habitats in Australia even though host density was higher than in intact forests (Van Sluys and Hero, 2009). For a different species in the same genus (*Litoria lorica*), environmental variation may have facilitated coexistence with Bd despite high infection prevalence (Puschendorf et al., 2011).

The comparable infection prevalence on Columbia spotted frogs from burned and unburned wetlands in our study area further suggests the lower infection probability for boreal toads in burned areas was not a result of changes in wetland characteristics or host community.

Counter to our expectation, we found only moderate evidence that infection differed among demographic groups of boreal toads. 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. We suspect the more frequent infection of males and juveniles resulted from greater exposure to the pathogen than females, rather than differences in susceptibility to infection or immunocompetence. Most male toads likely try to breed every year and often spend >1 month at a breeding site, whereas females likely do not breed every year in our study area (Pilliod et al., 2010). Males and juveniles are also more aquatic than females outside of the breeding season, further increasing risk of Bd infection (Bartelt et al., 2004). Our results suggest aquatic females may have a slightly higher prevalence of infection than terrestrial females. More importantly, however, terrestrial toads had the same low prevalence of infection (9%) regardless of demographic group, evidence that leaving the source of pathogen exposure and hospitable environments for pathogen growth provides all individuals with similar opportunities to avoid or clear infection.

Our results illustrate the importance of landscape structure for host–pathogen interactions and show that natural disturbances like wildfire can have a large effect on the probability that an individual is infected with Bd. The habitat- and sex-specific results we found also highlight the importance of sampling the full range of habitats used by a species to better understand disease risk, as well as potential fitness and population-level implications. Overall, these results indicate that the ability to avoid or clear infection is linked with habitat use and the natural fire regime, and strongly suggest that both natural and anthropogenic variation in landscape structure can have important implications for host fitness and disease dynamics. More broadly, our results show that preserving natural disturbance regimes and diverse habitats can modify infection prevalence across large landscapes, which may help maintain local refuges from disease and habitat selection behaviors that could facilitate evolution of disease resistance.

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