

Interactive effects of wildfire, forest management, and isolation on amphibian and parasite abundance

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Abstract. Projected increases in wildfire and other climate-driven disturbances will affect populations and communities worldwide, including host–parasite relationships. Research in temperate forests has shown that wildfire can negatively affect amphibians, but this research has occurred primarily outside of managed landscapes where interactions with human disturbances could result in additive or synergistic effects. Furthermore, parasites represent a large component of biodiversity and can affect host fitness and population dynamics, yet they are rarely included in studies of how vertebrate hosts respond to disturbance. To determine how wildfire affects amphibians and their parasites, and whether effects differ between protected and managed landscapes, we compared abundance of two amphibians and two nematodes relative to wildfire extent and severity around wetlands in neighboring protected and managed forests (Montana, USA). Population sizes of adult, male long-toed salamanders (*Ambystoma macrodactylum*) decreased with increased burn severity, with stronger negative effects on isolated populations and in managed forests. In contrast, breeding population sizes of Columbia spotted frogs (*Rana luteiventris*) increased with burn extent in both protected and managed protected forests. Path analysis showed that the effects of wildfire on the two species of nematodes were consistent with differences in their life history and transmission strategies and the responses of their hosts. Burn severity indirectly reduced abundance of soil-transmitted *Cosmocercoides variabilis* through reductions in salamander abundance. Burn severity also directly reduced *C. variabilis* abundance, possibly through changes in soil conditions. For the aquatically transmitted nematode *Gyrinicola batrachiensis*, the positive effect of burn extent on density of Columbia spotted frog larvae indirectly increased parasite abundance. Our results show that effects of wildfire on amphibians depend upon burn extent and severity, isolation, and prior land use. Through subsequent effects on the parasites, our results also reveal how changes in disturbance regimes can affect communities across trophic levels.

Key words: *Ambystoma macrodactylum*; amphibian decline; burn severity; disturbance; fragmentation; global climate change; isolation; nematode; protected areas; *Rana luteiventris*; synergistic effects; transmission.

INTRODUCTION

Climate-driven changes to disturbance regimes are expected to have widespread effects on biological communities. In many areas, these changes will 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 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. Along with their effects on free-living organisms, such environmental changes and their interactions with land use histories could also have large effects on abundance, community structure, or effects of parasites (Gulland et al. 1993, Kutz et al. 2005). Parasites represent a large but often hidden component of biodiversity and are often at greater risk of decline after disturbances than their hosts (Dunn et al. 2009).

Wildfire is an integral component of many ecosystems, serving to maintain suitable habitat conditions for diverse communities (Hutto 1995, Hessburg and Agee 2003, Means 2006). Although wildfire may help structure amphibian habitats and communities in western North America, there are few studies from forests with long fire-return intervals, where wildfire is

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driven more by extended drought rather than by supply of fuels, and can cause long-lasting changes to terrestrial habitats (Morgan et al. 2008, Hossack and Pilliod 2011). Additionally, most forests in the region 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 amphibians and parasites that infect them are affected by the combination of stand-replacement wildfire and forest management is unknown. Native species evolved with wildfire, and most have persisted in managed landscapes, but the combined effects of wildfire and human disturbances on populations may be additive or synergistic (Laurance and Williamson 2001, Castro et al. 2010).

Changes in amphibian abundance are also likely to have important implications for their parasites. Parasites can strongly affect host fitness and population dynamics, can have large effects on ecosystem structure and function by modifying the outcome of species interactions, and can be good indicators of environmental change (Goater and Ward 1992, Lafferty et al. 2006, Kelehear et al. 2009). Disturbances can directly or indirectly affect parasite abundance or richness through several mechanisms. Parasites that use intermediate hosts such as snails often increase in response to aquatic eutrophication (Johnson et al. 2002, Poteet 2006), but little is known about how land use or disturbances that change amphibian abundance subsequently affect directly transmitted parasites (McKenzie 2007). Most parasitic helminths such as nematodes must complete part of their life cycle outside of a host, and thus can be limited by both variation in the environment and in host abundance (Dobson and Hudson 1992, Pietroock and Marcogliese 2003).

We used a natural experiment to measure the effects of wildfire and land use history on amphibians and their parasites. We compared population sizes of two amphibian species and mean abundance of two parasitic nematodes in neighboring managed and protected forests that were burned by the same wildfires. Long-toed salamanders (*Ambystoma macrodactylum*) spend the majority of their time underground, limiting surface activity primarily to cool, moist seasons (Werner et al. 2004). Despite their sedentary habits, there is substantial movement by long-toed salamanders between wetland breeding sites (Giordano et al. 2007), and habitat changes after forest harvest have been linked to reductions in their abundance (Naughton et al. 2000). Wildfire and forest harvesting reduce plant cover in the forest understory, and harvesting is also associated with roads and other disturbances. Therefore, we predicted that habitat changes after wildfire would result in reduced population sizes, especially in areas of high-severity fire, and that the effects of wildfire would be greater in managed forests than in protected forests. We also predicted that the effects of wildfire would be greater in steeper areas or where there were fewer

neighboring wetlands, because more wetlands in the surrounding area could facilitate movement and provide a source of colonists to rescue local populations (Brown and Kodric-Brown 1977).

Columbia spotted frogs (*Rana luteiventris*; hereafter, spotted frog) are more restricted to aquatic habitats than long-toed salamanders, but often move seasonally among different water bodies to breed, forage, and hibernate (Pilliod et al. 2002). We predicted populations in managed forests would be smaller than in protected forests because fragmentation by roads impedes movement and increases 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 (e.g., Werner and Glennemeier 1999).

We expected wildfire and forest management would also have direct or indirect effects on abundance of two nematode species with different life histories and contrasting levels of host specificity. *Cosmocercoides variabilis* hatches and develops into an infective stage in the soil before infecting a wide range of terrestrial amphibians and reptiles, including the long-toed salamander (Vanderburgh and Anderson 1987). *Gyrinicola batrachiensis* infects only anuran (frog and toad) larvae and cannot persist after its host metamorphoses (Adamson 1981, Rhoden and Bolek 2011). This nematode also infects multiple species, but the spotted frog was the only suitable host in almost all of our study sites. Both nematodes are transmitted directly and lack intermediate hosts, and thus nematode abundance should be correlated with host abundance (Arneberg et al. 1998). However, *C. variabilis* has a free-living stage in the terrestrial environment that we expected could be susceptible to both disturbance-related changes in soil microclimate and to differences in host abundance. In contrast, transmission of *G. batrachiensis* occurs by ingestion of resting eggs in water that are resistant to environmental variation (Adamson 1981). Thus, we expected *G. batrachiensis* would be associated with host density rather than habitat features. Furthermore, because it relied almost exclusively on a single host species in our study area, we expected abundance of *G. batrachiensis* would be more closely linked to its host compared with *C. variabilis*, which likely had multiple hosts at all wetlands. 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 community structure under future disturbance regimes.

METHODS

Study area

Our research focused on three stand-replacement fires that occurred in a single valley in northwestern Montana: the 1988 Red Bench fire (14 584 ha), the 2001 Moose fire (28 574 ha), and the 2003 Wedge

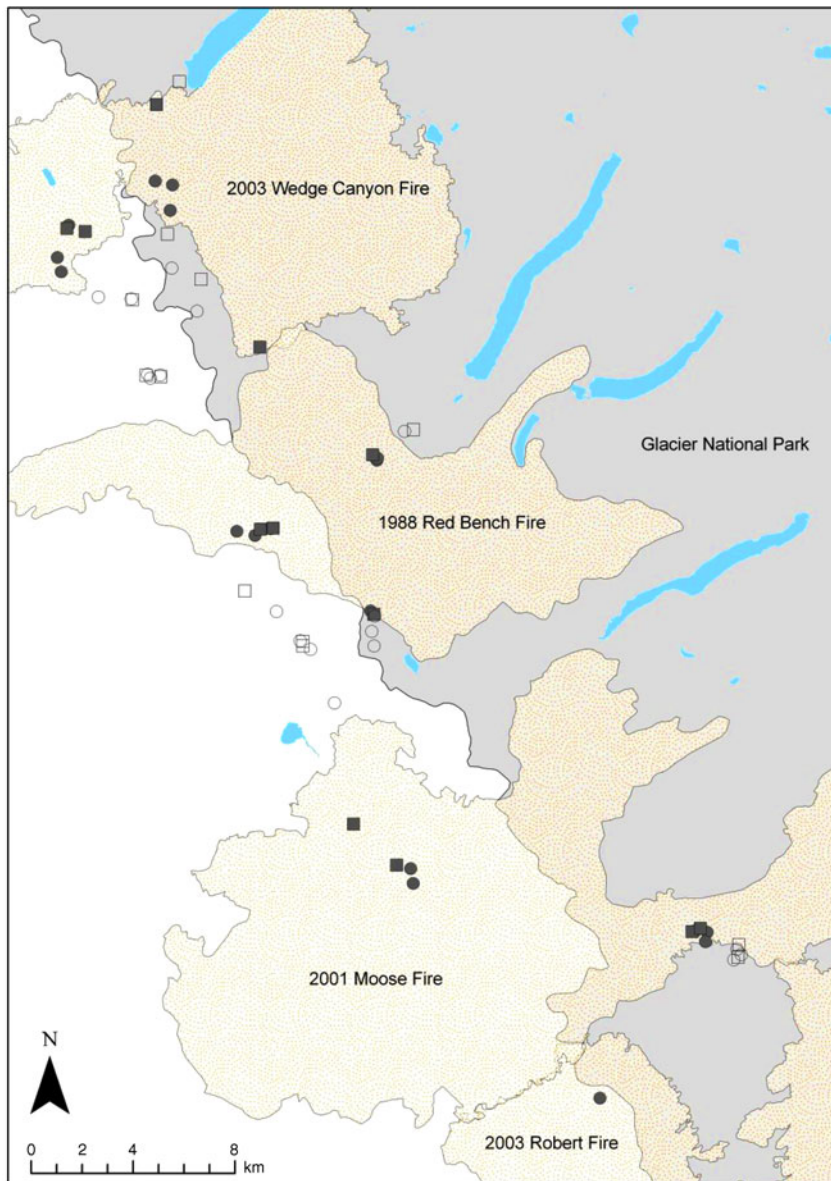


FIG. 1. The location of 60 wetlands sampled for long-toed salamanders (*Ambystoma macrodactylum*) and Columbia spotted frogs (*Rana luteiventris*) in the North Fork Flathead Valley, Montana, USA, and four stand-replacement wildfires that have burned since 1988. For wildfire areas, darker portions are within Glacier National Park; lighter portions are outside the park. 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. Some symbols have been adjusted to reduce overlap.

Canyon fire (21 615 ha; Fig. 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 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 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 three 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 in the area, fire suppression has not greatly altered the natural succession of most forest stands (Barrett 2002).

The study area is densely populated by shallow wetlands. There are also a few lakes and large wetlands that we excluded from sampling (see *Sampling design*). The wetlands we sampled ranged in size from 0.01 ha to 1.4 ha and only three were >1 m in maximum depth. Most of these wetlands fill from snowmelt and rain in the spring and dry by mid-August. Two wetlands on Forest Service lands were human-created or modified, but contained suitable habitat for local amphibians. All wetlands had an open canopy and emergent vegetation (primarily *Carex* spp.) that recovers quickly after fire. As a result, wildfires caused greater differences in the terrestrial environment than in the aquatic environment (Hossack and Corn 2007).

Sampling design

To determine whether wildfire and fragmentation from forest management and roads affected abundance of amphibians and parasites, we 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 four classes of wetlands: burned/protected, unburned/protected, burned/managed, and unburned/managed. We limited the candidate population to small wetlands (≤ 1 ha) because we were not confident we could effectively trap larger sites. We also limited wetlands to those within 1 km of roads because we needed to access them several times when snow cover was still deep.

We trapped 36 wetlands for adult long-toed salamanders (three replicates of each class in each of the three fires). For example, for the 2003 Wedge Canyon fire, we selected three burned and three unburned wetlands in protected forest, and three burned and three unburned wetlands in managed forest (Fig. 1). We counted spotted frog egg masses in these 36 wetlands plus two additional wetlands in each combination of burn and management status ($n = 60$). The spotted frog occupies fewer wetlands than the long-toed salamander in our study area (Hossack and Corn 2007), 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 two fires overlapped, and one wetland >1 ha was included in our sample of wetlands where we searched for spotted frog egg masses.

Amphibian sampling and abundance

We captured adult salamanders by placing unbaited minnow traps along the margins of wetlands as they started to fill, when salamanders migrate from terrestrial hibernacula to breeding sites (Wilson and Pearman 2000). We scaled the number of traps to the area of open water, with ~ 1 trap every 10 m of open shoreline (range

= 2–13 traps). Trapping dates varied among wetlands according to topography and insolation, starting on 18 March 2010 at the southern end of our study area and ending on 25 April 2010 at the northern sites. Traps were left overnight and captured salamanders were sedated with tricaine methane sulfonate (MS-222) before being marked with a sample-specific toe clip. This trapping method primarily captured male salamanders (>90% of captures), so we excluded females from the population estimates. After the sampling event 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 until 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 (Stanley and Jon 2005). If closure was violated, we pooled adjacent sampling events as needed to satisfy the closure assumption (Kendall 1999), resulting in 2–5 capture occasions per wetland to estimate population size. For each wetland, we fit the data to models that assumed constant capture probability (M_0) and to models that allowed for temporal heterogeneity in captures (M_t). We used model weights based on Akaike Information Criteria (AIC_c) adjusted for small sample sizes to generate model-averaged estimates of population size of male salamanders (Burnham and Anderson 2002).

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 of the population estimate from MARK against peak number of captures at the other 27 wetlands ($y = 0.60 + 1.16x$; $r^2 = 0.79$). 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 abundance of spotted frogs by counting egg masses at wetlands. Spotted frogs lay one egg mass, providing an accurate estimate of the number of breeding females (Licht 1975). The egg masses float at the water's surface and are typically laid communally near shore, making them easy to detect. We conducted egg mass surveys by walking the entire shoreline and other shallow areas of each wetland on every visit and marked individual masses with a colored toothpick. To prevent counting errors, we also placed a flag pin at each location with eggs and labeled it with the date and count of egg masses. 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 two 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 (6–11 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 we examined them for nematodes.

Nematode sampling

We examined the digestive tract of 3–15 adult, male long-toed salamanders from 30 wetlands (375 total) under a dissecting microscope to measure abundance of *C. variabilis*. To measure abundance of *G. batrachiensis*, we excised the entire digestive tract of 2–15 spotted frog larvae from 22 wetlands (205 larvae total), removed the digestive contents, and counted the nematodes under a dissecting scope. We defined abundance for each wetland as the mean number of nematodes in each amphibian host, including uninfected individuals (Bush et al. 1997). There was no co-occurrence of these nematodes because *C. variabilis* only infects terrestrial hosts and *G. batrachiensis* only infects anuran larvae (Adamson 1981, Vanderburgh and Anderson 1987). 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. *C. variabilis* is a common parasite of terrestrial amphibians and reptiles (Vanderburgh and Anderson 1987, Anderson 2000), but it is possible some amphibians may also become infected by *C. dukae* after ingesting infected gastropods (Baker 1978). Both nematode species have similar life histories (Anderson 2000). However, isozymes and cross-transmission experiments showed that *Cosmocercoides* in anurans and gastropods were distinct, suggesting that *C. dukae* found in amphibians are accidental infections and are likely temporary (Vanderburgh and Anderson 1987). We refer to nematodes we found in salamanders as *C. variabilis*, but acknowledge that some could have been *C. dukae*. It is unknown whether *Cosmocercoides* cause pathology, but moderate infection of amphibians by other nematodes can result in significant reductions in performance or survival (Goater and Ward 1992, Kelehear et al. 2009). Voucher specimens identified as *Cosmocercoides* (*variabilis*?) were deposited by S. Locke (Environment Canada) in the U.S. National Parasite Collection (accession number USNPC 105088). To our knowledge, *C. variabilis* and *G. batrachiensis* represent new records for the long-toed salamander and Columbia spotted frog, respectively.

Spatial 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 abundance of amphibians and nema-

todes. 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 obtained from the Monitoring Trends in Burn Severity project (MTBS; information *available online*),⁶ which uses pre- and postfire Landsat satellite imagery to delineate fire perimeters and quantify burn severity for each 30-m pixel (Eidenshink et al. 2007). We defined high severity as pixels with differenced Normalized Burn Ratio (dNBR) values ≥ 550 , which represents the midpoint of the moderate-high severity burn category defined for several wildfires in Glacier NP (Key and Benson 2006). The dNBR is based on changes in vegetation between prefire and postfire Landsat imagery. The length of roads within each 2-km buffer was calculated from a GIS layer for Flathead County (*available online*).⁷ Only one road was paved. The area of emergent wetlands and freshwater ponds was measured using the National Wetlands Inventory data set (*available online*).⁸ We estimated mean canopy cover for forested vegetation only (i.e., we excluded riparian areas, meadows, and water) within each buffer using LANDFIRE data (*available online*)⁹ (Rollins 2009). Mean topographic slope was calculated from a 30-m digital elevation model for the study area (*available online*; see footnote 7).

Statistical analyses

Amphibian abundance.—Before evaluating our research hypotheses, we 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. Steeper areas impose greater energetic costs for movement and likely increase effective isolation (e.g., Ricketts 2001). 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 standing water. To describe the covariation between slope and wetlands, we used principal components analysis to reduce them into a single variable that we used as a measure of population isolation. The first principal component accounted for 85% of the covariation between slope and wetland area and was included in all linear models. Positive values of the principal component represented areas of high slope and few wetlands (i.e., greater isolation). Using a single variable

⁶ <http://mtbs.gov/index.html>

⁷ <http://nris.mt.gov/gis/>

⁸ <http://www.fws.gov/wetlands/data/>

⁹ <http://www.landfire.gov>

TABLE 1. Mean (with SD in parentheses) wetland and landscape characteristics according to forest management (managed vs. protected) of 30 burned and 30 unburned wetlands.

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

Notes: All data except wetland size were measured from 2-km buffers around the sampled wetlands. "Surrounding wetlands" refers to the area of wetland habitat within the 2-km buffers around sampled wetlands.

to represent these highly correlated attributes reduced multicollinearity among predictors in the linear models and increased precision of the estimates. We included this isolation term in all models to account for differences in landscape characteristics among wetlands.

To describe variation in amphibian abundance, we evaluated 15 models that included additive and interactive effects of isolation, length of roads, forest management (managed vs. protected), percentage of area burned (burn extent), and percentage of area that burned severely. We hypothesized the effects of wildfire would be greater in steeper areas or where there were fewer neighboring wetlands because 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 that high densities of roads would be associated with small population sizes because roads 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, which can reduce population sizes (Naughton et al. 2000, Marsh and Beckman 2004).

We included the management term to account for differences in timber harvest between forests inside and outside of the park, but it also reflects differences in road density and fragmentation by private residences and ranches. Because management and roads were strongly 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 percentage of area burned ($r = -0.73$) and percentage of area burned severely ($r = -0.86$), and thus was excluded from 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 used linear regression to model salamander abundance (on the logarithmic scale; program R 2.12.2 [R Development Core Team 2011]). Counts of spotted frog egg masses were modeled using generalized linear models with a negative binomial distribution and log link, because the counts were overdispersed (mean = 5.23, $\sigma^2 = 108.45$). We included the 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. Plots were constructed using the effects package (Fox 2003). 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 was a useful predictor for either species. For these and subsequent analyses, we ranked models in each respective set using AIC_c and Akaike weights to evaluate support for our hypotheses. Akaike weights represent the probability that a particular model is the best for the given data set (Burnham and Anderson 2002).

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 Vario-gram, SAS 9.2; SAS 2009). 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 ($I = 0.10$, $P > 0.05$) or spotted frog data ($I = 0.12$, $P > 0.05$).

We originally fit these 15 models to data measured from both 500-m and 2-km wetland buffers. We present results only from the latter because results from the two spatial scales were nearly identical for both species. Data measured from 2-km wetland buffers also explained more variation in the data.

Nematode abundance.—We used confirmatory path analysis to fit models that described the relationship among environment, host abundance, and parasite abundance (program Mplus 6.12; Muthén and Muthén 2010). Path analysis allows the simultaneous modeling of two or more correlated regression relationships and is effective at describing complex relationships that are

TABLE 2. Models fitted to estimated population size of adult, male long-toed salamanders in 18 burned and 18 unburned wetlands using fire and landscape information measured from 2-km buffers.

Model	$-2\log(L)^\dagger$	AIC _c	w_i
Isolation + % burned + % burned $\times$ isolation	121.80	133.80	0.27
Isolation + % severe + roads	122.29	134.29	0.21
Isolation + % severe + management + % severe $\times$ management	119.64	134.54	0.19
Isolation + % severe + roads + % severe $\times$ roads	119.99	134.88	0.16
Isolation + % severe + % severe $\times$ 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 $\times$ 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 $\times$ roads	130.58	145.47	<0.01
Intercept only	147.41	151.77	<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

Notes: The isolation term describes the covariation between topographic slope and wetland area and was included in all models to account for differences in landscape characteristics surrounding sampled sites, except for the intercept-only model. Models are ranked according to AIC_c and model weights (w_i).

$^\dagger \log(L)$ represents log-likelihood.

common in host–parasite systems (e.g., Cobb et al. 2010). Our goal was to determine if the same disturbances that affected abundance of amphibians also affected abundance of directly transmitted nematodes. Therefore, we based the path analyses on the best predictors of abundance for each amphibian species, as identified by the linear models previously described. We fit three path analysis models for each combination of parasite and host that allowed us to measure support for both direct and indirect effects of disturbance on parasite abundance.

In the first model for *C. variabilis*, abundance of salamanders was predicted using wetland isolation and burn severity. Mean abundance of *C. variabilis* was then predicted according to burn severity and abundance of long-toed salamanders. The second model was the same except that the effect of burn severity was mediated only through salamander abundance, and was not allowed to directly affect parasite abundance. The third model did not contain fire effects for either salamander abundance or parasite abundance. We used the normal distribution to model density of log-transformed population size of salamanders, and the Poisson distribution to model counts of *C. variabilis*. We did not scale abundance of salamanders according to wetland size because they acquire *C. variabilis* only in the terrestrial environment, and it is unlikely that the density of salamanders in a wetland is directly proportional to their density in the forest.

We used similar model structures to describe variation in mean abundance of *G. batrachensis* in spotted frog larvae, except that we used burn extent (the best predictor of spotted frog abundance) rather than burn severity and used host density rather than population size. Log-transformed density of spotted frog egg masses

(number of egg masses per hectare of wetland) was used as a surrogate for density of spotted frog larvae. We used the normal distribution to model density of spotted frog larvae and the negative binomial distribution to model counts of *G. batrachensis* abundance. As with the analysis of amphibian abundance, we included wetland isolation in all models to control for extraneous variation. For both nematode species, we used the number of hosts examined at each wetland as a weighting variable to account for differences in sample size. We compared models using differences in AIC (Burnham and Anderson 2002).

RESULTS

Amphibian abundance

We captured long-toed salamanders in 35 of 36 wetlands. Estimated population sizes for long-toed salamanders from program MARK ranged from 8 to 4220 (599 ± 126 salamanders, mean $\pm$ SE). The model with the interaction between isolation and burn extent received the most support (based on Akaike weights) and predicted a negative effect of wildfire on population size in areas with greater burn extent and in steep areas with few wetlands (Table 2, Fig. 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 $\times$ burn severity interaction received less support but predicted a similar response to that of the isolation $\times$ burn extent model, with increasingly negative effects of high-severity burn for isolated populations (Table 2).

There was also substantial support for models that described additive or interactive effects of burn severity

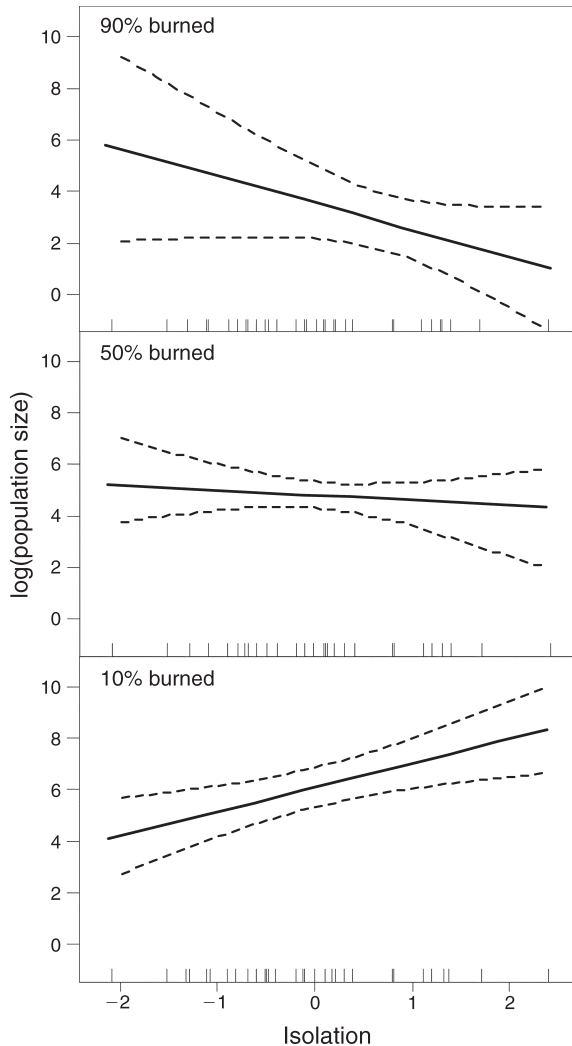


FIG. 2. The predicted mean effect (dashed lines indicate 95% CI) of isolation on population size of male long-toed salamanders given 10%, 50%, and 90% burn extent in 2-km buffers around breeding wetlands. Isolation describes the covariation between topographic slope and wetland area, with high values representing steep areas with few wetlands. Hatch marks on the horizontal axis represent the distribution of the predictor variable.

and forest management or length of roads on population size of salamanders (Table 2). Collectively, there was more support for models based on burn severity (sum of Akaike weights $[\Sigma w_i]$ for all models with burn severity = 0.70) than for models based on 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. The negative effects of roads were greater in areas that burned with high severity (Fig. 3), and overall, the effect of high-severity burn was stronger in managed forests than in protected forests (Fig. 4).

To evaluate the influence of the nine populations for which we had to estimate population size using linear

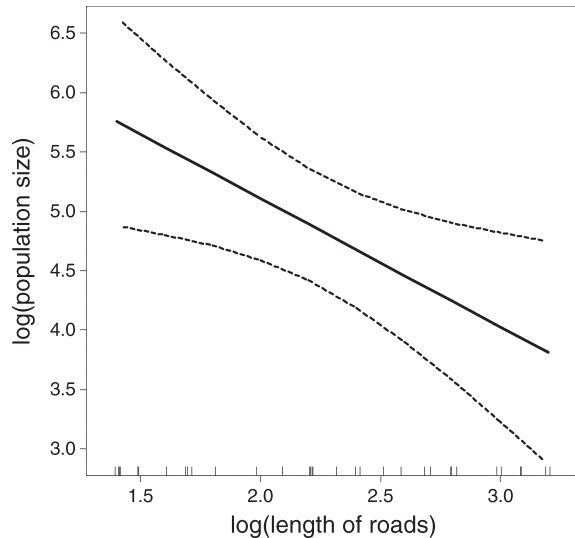


FIG. 3. The predicted mean effect (dashed lines indicate 95% CI) of length of roads (measured in kilometers) within 2 km of breeding wetlands on population size of male long-toed salamanders, after accounting for the effect of high-severity burns. Hatch marks on the horizontal axis represent the distribution of the predictor variable.

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 data set was reduced support for the isolation $\times$ burn extent model (w

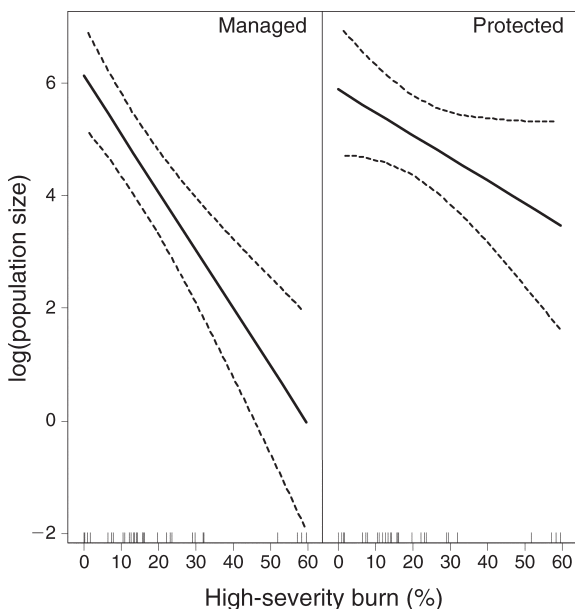


FIG. 4. The predicted mean effect (dashed lines indicate 95% CI) of the percentage of 2-km wetland buffer that burned with high severity on population size of male long-toed salamanders in managed vs. protected forest. Hatch marks on the horizontal axis represent the distribution of the predictor variable.

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.

Model	$-2\log(L)^\dagger$	AIC _c	w_i
Isolation + % burned	243.32	252.05	0.37
Isolation + % burned + % burned $\times$ 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 $\times$ management	241.67	255.25	0.08
Isolation + % burned + roads + % burned $\times$ 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 $\times$ roads	244.28	257.87	0.02
Isolation + % severe + management + % severe $\times$ 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 $\times$ isolation	248.18	259.29	0.01
Isolation + management	250.99	259.71	<0.01
Intercept only	263.28	267.49	<0.01

Notes: The isolation term describes the covariation between topographic slope and wetland area and was included in all models to account for differences in landscape characteristics surrounding sampled sites, except for the intercept-only model. Models are ranked according to AIC_c and model weights (w_i).

$^\dagger \log(L)$ represents log-likelihood.

= 0.02 instead of $w = 0.27$ for the full data set). This change resulted because some of the wetlands where we could not estimate population size using closed population estimators 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. 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). In contrast to salamanders, counts of spotted frog egg masses were positively correlated with burn extent near wetlands, although there is considerable uncertainty for wetlands where >70% of the surrounding area burned (Fig. 5). The isolation $\times$ burn extent term in the second-ranked model indicated that wildfire had a negative effect on isolated populations; however, the standard error around the estimate included 0. Across all models, those with burn extent received 86% of summed Akaike weights, compared with only 10% for models with the burn severity term.

Nematode abundance

We found *C. variabilis* in 39% of salamanders; infection intensity ranged from 1 to 7 worms (mean abundance = 1.84, $\sigma^2 = 1.45$). All nematodes were juveniles or gravid females and were found in the intestine or (rarely) the body cavity. Of the three path models we fitted, the one that allowed direct effects of fire severity on abundance of salamanders and *C. variabilis* provided the best description of the data ($\Delta\text{AIC} \geq -3.49$ vs. other models), consistent with our

hypothesis that wildfire could affect this nematode indirectly through changes in host abundance, as well as directly. The model-averaged regression coefficients indicated that population size of long-toed salamanders was strongly, positively correlated with mean abundance of *C. variabilis*, and that burn severity negatively affected both population size of salamanders and abundance of *C. variabilis* (Fig. 6a).

We found *G. batrachensis* in 66% of spotted frog larvae; intensity ranged from 1 to 107 worms (mean abundance = 11.27, $\sigma^2 = 188.35$, $k = 0.86$). The best-supported model for *G. batrachensis* indicated an indirect

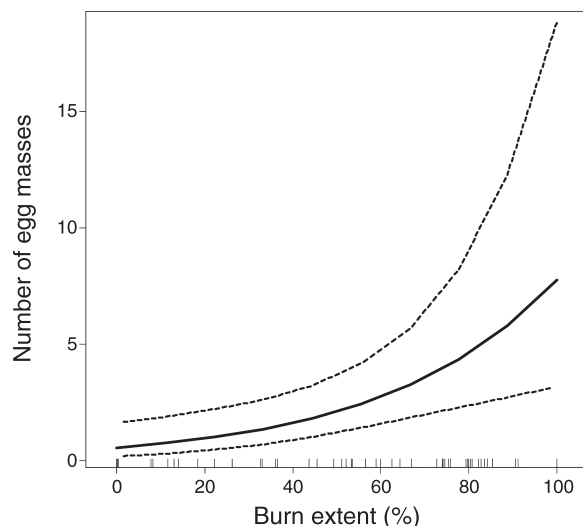


FIG. 5. The mean predicted count (dashed lines indicate 95% CI) of Columbia spotted frog egg masses according to burn extent in the 2-km area around wetlands. Hatch marks on the horizontal axis represent the distribution of the predictor variable.

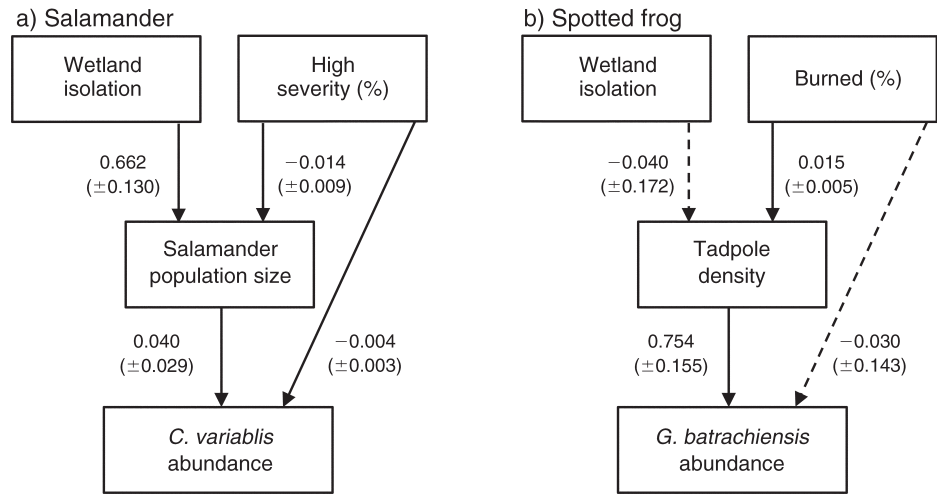


FIG. 6. Path analyses relating habitat characteristics, host abundance, and parasite abundance. The numbers next to the arrows are model-averaged regression coefficients (with 95% confidence limits in parentheses). Burn severity limited population size (log-transformed) of adult long-toed salamanders and had indirect and direct negative effects on mean abundance of the nematode *Cosmocercoides variabilis*. The positive effect of burn extent on mean abundance of the nematode *Gyrinicola batrachensis* in Columbia spotted frog larvae was mediated through its effect on host density (log-transformed). Dashed-line arrows indicate effects with confidence intervals that include zero.

effect of burn extent that was mediated through its positive effect on host density (Figs. 6b, 7). The second-ranked model ($\Delta\text{AIC} = 0.41$) estimated a weak, direct negative effect of burn extent on *G. batrachensis* abundance, but the estimate was imprecise and the confidence interval included 0. For both nematode species, path models that did not include a wildfire effect at either level were poorly supported ($\Delta\text{AIC} \geq 252.55$). We summarize our predictions and observed results for both amphibians and both parasites in Table 4.

DISCUSSION

Our data collected 7–22 years after wildfires show that projected changes to disturbance regimes are likely to

affect amphibians and abundance of their parasites. Effects of wildfire on population size of long-toed salamanders depended most strongly on burn severity and isolation. Wetlands in areas that burned with high severity and isolated wetlands surrounded by burned forests hosted smaller populations compared with wetlands in unburned forest or where populations were not isolated. We suspect the increased vulnerability of isolated populations in steep, burned areas reflects the effect of wildfire on habitat and subsequent increased costs of dispersal. Loss of tree canopy results in reduced movement and increased desiccation and mortality of other ambystomatid salamanders (Rothermel and Luhring 2005). Also, many amphibians are less likely to

TABLE 4. Summary of the predicted and observed effects of wildfire and forest management on population size of adult, male long-toed salamanders (*Ambystoma macrodactylum*), egg mass counts of Columbia spotted frogs (*Rana luteiventris*), and mean infection of two widespread nematodes that target each of these amphibians.

Species	Prediction	Observation
<i>Ambystoma macrodactylum</i> (long-toed salamander)	1) Population size is negatively associated with wildfire. 2) Population size is negatively associated with forest management.	1) Population size was negatively associated with the severity and extent of wildfire. 2) Population size was negatively associated with forest management only in areas that burned.
<i>Rana luteiventris</i> (Columbia spotted frog)	1) Egg mass abundance is neutrally or positively associated with wildfire. 2) Egg mass abundance is negatively associated with road density.	1) Egg mass abundance was positively associated with burn extent. 2) No relationship between egg mass abundance and road density.
<i>Cosmocercoides variabilis</i> (salamander nematode)	1) Mean infection is indirectly, negatively associated with wildfire through effects on salamander abundance. 2) Mean infection is directly, negatively associated with wildfire.	1) Mean infection was indirectly, negatively associated with wildfire via its effect on salamander abundance. 2) Mean infection was directly, negatively associated with wildfire.
<i>Gyrinicola batrachensis</i> (frog nematode)	1) Mean infection is indirectly, positively associated with wildfire though its effects on density of larvae. 2) Mean infection is not directly associated with wildfire.	1) Mean infection was indirectly, positively associated with wildfire via its effect on density of frog larvae. 2) Mean infection was not directly, negatively associated with wildfire.

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 National Park 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 (Duellman and Trueb 1986, Hossack et al. 2009). Similarly, 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). Reduced cover and greater temperatures in burned forests could limit surface and foraging activity or increase desiccation and mortality during dispersal for salamanders and other moisture-sensitive species, ultimately reducing population size or distribution over time (Hossack et al., *in press*).

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 streams 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. 2010). Isolation was negatively associated with population size of long-toed salamanders 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 is counterintuitive but has been documented previously for salamanders, possibly resulting from focused breeding efforts at the fewer available breeding sites (Veysey et al. 2011). Stronger negative effects of wildfire on isolated populations suggests these populations will be the most vulnerable to future increases in frequency or severity of wildfire, and underscores the importance of maintaining suitable habitat between breeding sites to facilitate colonization and recovery after disturbances.

Greater 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 synergistic (Laurance and Williamson 2001, Castro et al. 2010). Our results show that 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,

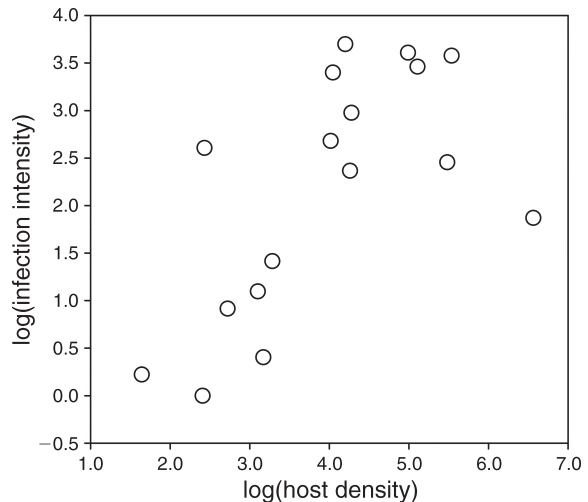


FIG. 7. The relationship between the density of Columbia spotted frog larvae and infection intensity by the nematode *Gyrodactylus batrachii*.

high road densities and associated habitat changes on managed forests exacerbated effects of wildfire on salamander populations.

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 mobile anurans are likely to encounter roads, increasing the risk of mortality or reducing dispersal (Funk et al. 2005, Eigenbrod et al. 2008). Instead, we found a 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. 2010). Some ranid frogs have suffered population losses or persistent declines after large wildfires, particularly in the U.S. 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. Burn severity was not an important predictor for variation in population size in the wetlands we sampled, but over time, persistent changes in forest habitat that could cause reductions in recruitment or dispersal away from the most severely burned areas could reduce population growth or wetland occupancy (Hossack et al., *in press*).

Parasites are expected to be sensitive indicators of ecosystem change, although the direction of change is dependent upon host abundance, community structure, and sensitivity of parasites to environmental variation (Marcogliese 2005, Vidal-Martínez et al. 2009). Few studies have used population estimates of amphibians to demonstrate the expected link between host and parasite

abundance, but our results show that the same environmental factors simultaneously affected amphibian and nematode abundance. Path analysis revealed that the reduction in population size of long-toed salamanders after wildfire subsequently reduced mean abundance of *C. variabilis*, suggesting that high-severity fire indirectly reduced parasite transmission (Arneberg et al. 1998). The strong relationship between host and parasite abundance was evident, even though *C. variabilis* can infect terrestrial stages of other local amphibians and reptiles, most of which likely do not decline after wildfire.

We also found evidence of direct effects of burn severity on abundance of *C. variabilis*. These effects could have resulted from several mechanisms, including reduced survival of eggs and the free-living larval stages of *C. variabilis* (Anderson 2000). The free-living transmission stages of many parasites are sensitive to environmental change (Dobson and Hudson 1992, MacKenzie 1999). Many of the same changes that occur after fire or other forest disturbances that reduce habitat suitability for salamanders, such as reduced litter cover and increased soil heating, can also reduce abundance of nematodes and other soil invertebrates (Panesar et al. 2001, Sohlenius 2002, Certini 2005). Similarly, clear-cutting of boreal forest around lakes was associated with reduced parasite richness and mean infection in minnows, including the potential extirpation of a nematode (Marcogliese et al. 2001).

Through its positive effect on density of spotted frog larvae, wildfire indirectly increased abundance of the gut nematode *G. batrachiensis*. The link between density of spotted frog larvae and *G. batrachiensis* was much stronger than the link between population size of adult salamanders and *C. variabilis*. This stronger relationship likely reflects in part our ability to estimate host density for spotted frogs, as well as the near dependence of *G. batrachiensis* on the spotted frog in our study area (the only other potential host was found in <3% of wetlands). This dependence on spotted frogs in our area also likely makes *G. batrachiensis* more sensitive to decline compared to parasites that infect several host species (Dobson 2004). In contrast to *C. variabilis*, we did not find clear evidence that wildfire directly affected the abundance of *G. batrachiensis*. We suspect the reliance of *G. batrachiensis* on wetlands, where habitat recovers more quickly after wildfire than in forests, and life history characteristics such as desiccation-resistant eggs and lack of a free-living stage, helped buffer it from environmental change (Adamson 1981).

Expected increases in drought and conditions that foster wildfire, along with increases in insect-related tree mortality and the use of forest harvest to mitigate wildfire hazards, make it critical to understand how interactions among these disturbances will affect native species at all trophic levels (IPCC 2007, Reinhardt et al. 2008, Bentz et al. 2010). Importantly, our results indicate that changes in frequency or severity of wildfire

may have different implications for managed and protected forests. The additive and synergistic effects of wildfire and forest management could increase the threat of wildfire to salamanders and other species that are sensitive to post-fire changes in habitat or microclimate. Despite differences in life history characteristics, transmission strategies, and the habitat where infection occurs, abundance of both nematodes we sampled was strongly related to abundance of their hosts, underscoring the important role of disturbances like wildfire in structuring ecological communities. The strong associations between host and parasite abundance also illustrate the hidden loss of parasite biodiversity that has likely resulted from the global decline of amphibians and other hosts, particularly in areas where host diversity is low or where host–parasite relationships are specific (Dunn et al. 2009). Collectively, our results emphasize 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 driving changes in abundance, especially how those mechanisms differ between managed and protected forests, and how the mechanisms may be affected by changes to climate-driven disturbance regimes.

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