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The effect of severe wildfire on microhabitat structure varies over fine-scale distances away from amphibian breeding ponds in southwestern Alberta

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Abstract

Small-scale features of the environment create localized climatic conditions, influence the resources available to different organisms, and are key to diverse and resilient forests. Wildfire may alter critical microhabitat for sensitive taxa, yet studies directly quantifying these effects are limited. Here, we present a rare before-after-control-impact assessment of the impacts of severe wildfire on microhabitat structure around amphibian breeding ponds. Using 462 photoquadrats sampled eight years before and three years after the 2017 Kenow wildfire in Waterton Lakes National Park (Alberta, Canada), we quantified changes in 14 microhabitat features at three different distances (0, 3, and 10 m) away from burned and unburned amphibian breeding ponds. Non-parametric multivariate analysis of variance suggested distance from pond edge was a significant predictor of microhabitat composition before the wildfire, with the proportion of soil (bare ground) decreasing and the proportion of shrubs and forbs increasing away from pond edges. We detected a significant interaction between distance, burn status, and time, suggesting that the relationship between microhabitat and distance depended on the joint effects of burn status and time. This result was driven by changes 10 m away from pond edges in the burn zone, where sites experienced an increase in the proportion of forbs, soil, gravel, and rocks, and the loss of moss cover following the fire. Microhabitat change was more pronounced at high-elevation sites, although power to statistically isolate the effect of elevation was limited. Our results demonstrate fine-scale gradients in the impacts of wildfire on microhabitats around small wetlands, with areas immediately adjacent to pond edges being less impacted than sites further away. These findings advance our understanding of how wetland edges respond to wildfire and we discuss potential implications for amphibian movement, persistence, and recovery following severe wildfire.

Keywords Vegetation, Wetland, Refugia, Long-toed salamander, Western toad, Columbia spotted frog, Boreal chorus frog, Rocky Mountains

Resumen

Los rasgos o características del ambiente a pequeña escala (i.e., el microambiente), crean condiciones climáticas localizadas, influencian los recursos disponibles para los diferentes organismos, y son claves para la diversidad y resiliencia de los bosques. Los incendios de vegetación pueden alterar este microambiente para taxones sensibles, y aún

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así, los estudios que cuantifican directamente esos efectos son limitados. Presentamos en este trabajo una determinación rara sobre los impactos previos, posteriores y de control (sin impactos), de un incendio severo sobre la microestructura de un hábitat en derredor de lagunas pequeñas usadas por anfibios para su reproducción. Usamos para ello 462 parcelas fotográficas de muestreo desde ocho años antes y por tres años después del incendio de Kenow del 2017 en el Parque Nacional de los Lagos de Waterton (Alberta, Canadá), para cuantificar los cambios en 14 micro hábitats característicos a tres distancias diferentes (0, 3, y 10 m) alejadas de las lagunas de reproducción en sitios quemados y no quemados. Los análisis de variancia multivariados no paramétricos sugirieron que la distancia desde el borde de la laguna fue un predictor significativo de la composición del hábitat antes del incendio, con la proporción del suelo desnudo decreciendo cerca de las lagunas y aumentando la proporción de hierbas y arbustos a medida que se alejaba del borde de las mismas. Detectamos una interacción significativa entre distancia, el estatus de la quema, y el tiempo, sugiriendo que las relaciones entre microhábitat y distancia dependen de los efectos conjuntos del estatus de la quema y del tiempo. Este resultado fue determinado por cambios detectados a 10 m del borde de las lagunas en la zona quemada, donde los sitios experimentaban, luego del incendio, un aumento en la proporción de hierbas, suelo desnudo, fragmentos de rocas y otras piedras, y también la falta de cobertura de musgos. Los cambios en el micro-hábitat fueron más pronunciados en sitios altos, aunque la posibilidad de ser determinados como estadísticamente significativos fue limitada. Nuestro estudio demostró los impactos de los incendios en gradientes de microhábitats determinados a escala fina en ambientes alrededor de pequeñas lagunas (*charcos*), con áreas más cercanas a los bordes de estas lagunas menos impactados que sitios más alejados. Estos resultados avanzan en nuestro conocimiento sobre cómo los bordes de humedales (lagunas pequeñas o *charcos* en este caso), responden a incendios de vegetación, y discutimos las potenciales implicancias para el movimiento de anfibios, su persistencia y recuperación luego de incendios severos.

Introduction

The ecological importance of microhabitats (i.e., small-scale features of the environment that influence microclimatic conditions and support different flora and fauna) is widely recognized. For small-bodied species, microhabitats provide refuge and resources and buffer individuals against exposure to environmental extremes (De Frenne et al. 2021; Martin et al. 2022; Scheffers et al. 2014). Changes to microhabitats can have large effects on patterns of occupancy and abundance in some species (Ehlers Smith et al. 2017; Williams and Alexander 2023; Zou et al. 2017), making it important to understand where and how global change impacts the microhabitats used by sensitive wildlife taxa (De Frenne et al. 2021, 2025; Ellis 2018; Sallé et al. 2021).

Although wildfires are a natural part of the disturbance regime of many ecosystems, climate change coupled with a history of fire suppression has led to an increase in the frequency of high-severity wildfires (Coogan et al. 2019; Liu et al. 2010). Severe wildfires can alter the forest floor environment in a variety of ways (Wolf et al. 2021). In the immediate years following a severe burn, the loss of canopy and vegetative cover is expected to increase soil temperatures (Ebel 2012; Hossack et al. 2009). Severe wildfire can also alter soil properties (Agbeshie et al. 2022) and the movement of water (Guzmán-Rojo et al. 2024) and thus affect substrate moisture levels. Finally, post-fire changes in ground-level plant communities (Dickson-Hoyle et al. 2024; Lentile et al. 2007; Mack et al. 2008; Pinno and Errington 2016) and larger ecosystem transitions (Coop et al. 2020; Davis et al. 2019) may fundamentally alter the availability of specific microhabitats. These changes in turn may have consequences for the distribution, movement, and performance of small-bodied animals following major wildfire events (Driscoll et al. 2012; Lees et al. 2022; Plavsic 2014; Santos et al. 2014; Slovikosky et al. 2024).

With their requirement for cool, moist, and protected sites, amphibians tend to have strong microhabitat associations (Farallo and Miles 2016; McAlpine and Dilworth 1989; Thorpe et al. 2018) and are expected to be highly sensitive to microhabitat change or loss, including changes associated with wildfire (Bailey et al. 2025; Bury 2004; Gade et al. 2019; Muñoz et al. 2019; Papp and Papp 2000). Structural changes to the forest floor environment following wildfire may be particularly impactful for amphibians. For example, woody debris offers refuge for individuals in the terrestrial environment and consumption of such features by wildfire may put amphibians at greater risk of desiccation and/or predation (Pilliod et al. 2003). Likewise, patterns of aggregation on the landscape may change if cover objects become limiting (Cummer and Painter 2007; Patrick et al. 2008), influencing the frequency of intra- and interspecific interactions. Other structural changes following wildfire may impact other aspects of amphibian physiology and ecology. For instance, the loss of vegetative cover may increase the amount of solar radiation

and the temperatures that amphibians are exposed to, while the loss of duff and leaf litter may influence foraging and the movement of individuals (Pilliod et al. 2003; Brown et al. 2014). Assessing changes in microhabitat composition and structure following severe wildfire events is thus relevant to understanding the effects of these events on amphibian populations. Yet, despite considerable attention to the impacts of wildfire on amphibians (Dos Anjos et al. 2021; Hossack and Pilliod 2011; Pilliod et al. 2003), few studies have directly quantified changes to amphibian microhabitats following severe wildfire, and most of these have used space-for-time substitutions to draw inferences about wildfire effects (Cummer and Painter 2007; Hossack et al. 2009; Kaiser et al. 2022; Lindsay et al. 2023).

In this study, we use 462 photos of quadrats placed around amphibian breeding ponds before and after a severe wildfire event in western Canada to characterize and compare changes in amphibian microhabitat composition in burned and unburned areas. To the best of our knowledge this is the first before-after-control-impact (BACI) assessment of the impacts of a severe wildfire on amphibian microhabitats and provides a rare opportunity to disentangle the effects of wildfire from background temporal variability and/or pre-existing spatial differences. We focus on pond edges in this study because, although many amphibians make long-distance movements into the terrestrial environment outside of the breeding season (Rittenhouse and Semlitsch 2007), all breeding individuals interact with pond edges during the breeding season, and many individuals remain close to or return to breeding ponds during at least part of the non-breeding season (Blomquist and Hunter 2009; Pilliod et al. 2002). Furthermore, there is general interest in understanding the extent to which wetland edges demonstrate resistance or resilience to severe wildfire (Fairfax et al. 2024; Fairfax and Westbrook 2024; Fairfax and Whittle 2020), with smaller ponds, such as those used by many amphibians, being understudied in this regard. Our primary objectives were to characterize the relationship between microhabitat composition and distance from pond edges and to determine whether this relationship was altered by wildfire. We additionally explored the amount of change in microhabitat composition within sites and whether this varied with burn status and/or elevation. Apart from addressing timely questions as to the impacts of severe wildfire on microhabitats around forest pond margins, our study provides quantitative information about amphibian microhabitats in the Canadian Rocky Mountains—a region in which severe fires are expected to become more frequent.

Methods

Study region and wildfire

Waterton Lakes National Park (WLNP) or *Paahtómahksikimi* (Blackfoot) is a 505 km^2 federally protected area in southwestern Alberta, Canada (N 49° 03′ 0.288, W 113° 54′ 40.083″). Located along the Continental Divide in one of the narrowest parts of the Rocky Mountains, WLNP includes four ecoregions: foothills parkland, montane, subalpine, and alpine. These ecoregions differ with respect to the dominant vegetation, with fescue grasses (*Poaceae* spp.) and aspen (*Populus* spp.) being characteristic of the foothills parkland, coniferous forests (in particular, lodgepole pine, *Pinus contorta*) dominating montane and subalpine areas, and low-growing vegetation (lichens, mountain heather, *Phyllodoce* spp.; and sedges, *Carex* spp.) characterizing alpine areas (Strong and Leggat 1992). The park experiences moist, relatively mild winters and short, cool summers, with mean annual air temperatures of 2.4 °C and annual precipitation of ~1072 mm (Parks Canada 2025a). Precipitation varies in the park, with western parts of the park at the continental divide receiving more annual precipitation (1520 mm) than eastern parts of the park (76 mm; Parks Canada 2025a). Six amphibian species are found in WLNP including two salamanders (long-toed salamander: *Ambystoma macrodactylum*; western tiger salamander: *Ambystoma mavortium mavortium*), one toad (western toad: *Anaxyrus boreas*), and three frogs (Columbia spotted frog: *Rana luteiventris*; northern leopard frog: *Lithobates pipiens*; boreal chorus frog: *Pseudacris maculata*). In addition to these species, the park is home to over 1000 species of vascular plants, ~60 species of mammals, ~250 species of birds, 24 species of fish, and four species of reptiles (Parks Canada 2025b), making it one of the most biodiverse regions in Alberta.

Forested areas in WLNP historically had fire return intervals of 26 to 85 years (depending on ecoregion: Rogeau 2016) and experienced both mixed-severity and stand-replacing fires (Barrett 1996). Earlier fire history in the foothills parkland ecosystem also included intentional fires set by Indigenous peoples (Eisenberg et al. 2019). However, colonial fire suppression practices led to late successional stands and forest encroachment throughout much of the park (Stockdale et al. 2019; Trant et al. 2020), with the last major fire prior to this study (1998 Sofa Mountain fire, 1521 hectares) burning stands that were over 130 years old (O'Connor 2015). In late summer of 2017, the record-breaking Kenow Wildfire burned 19,303 hectares (~50% of vegetated areas) of WLNP. This was a fast-moving fire (most of the area impacted was burned over the course of a single night) that resulted in an unusually uniform and severe burn, with 75% of the burned area classified as extreme severity (Greenaway

et al. 2018). The wildfire was followed by several exceptionally dry years (Aspinall et al. 2025), likely increasing the importance of microhabitat refuges for amphibians in the burn footprint.

Data collection

We had visited 20 amphibian breeding ponds in WLNP in July 2009 (Fig. 1a), eight years prior to the Kenow wildfire, as part of other research activities focused on the long-toed salamander. Although breeding ponds were selected based on the distribution of this species, most of these sites are used by other members of the amphibian community in southwestern Alberta (Table S1; although both tiger salamanders and the recently reintroduced northern leopard frog occupy a limited number of sites in the park). Sites ranged in elevation from 1273 to 1973 m and were primarily located in the montane ($N=12$) and foothills parkland ($N=5$) ecoregions (Table S1). Breeding ponds ranged in size from 51 to 1405 m^2 but the majority were < 600 m^2 (Table S1).

At each site, we established four 10-m transects radiating away from the focal pond on different sides of the pond (Fig. 1b). Along each transect, 1 m^2 quadrat frames were placed at 0, 3, and 10 m away from the pond edge (Fig. 1b). A digital photo of each quadrat was taken from breast height, approximately parallel to the slope of the ground (to the extent possible). By chance, the Kenow wildfire burned nine of these survey sites, providing an opportunity to explore changes to microhabitat structure along multiple transects away from breeding ponds based on data collected from these photos and to compare with transects from unburned sites. In July 2020, three years post-fire, we revisited all 20 sites and collected post-fire quadrat photos. Although waypoints at each location along the original 2009 transects were not recorded, we had GPS coordinates taken from the 0 m quadrat of the first 2009 transect at each site, as well as photos capturing a view of the wetland taken from beside each of the 0 m quadrats from the 2009 surveys. Using these coordinates as well as landmarks in the site photos (ridge lines, rocky outcrops, etc.) to guide transect starting locations, we positioned the 2020 transects as closely as possible to the 2009 transects to minimize the effects of choice of transect location when comparing microhabitat composition across time at each site, although we note that transects were not sufficiently matched to enable paired analysis at the quadrat level.

Each site had a total of 24 photoquadrats (four transects, three distance classes, two time-points), with the exception of two sites for which one side of the wetland was inaccessible (only 18 quadrats sampled for these sites) and two sites, each with a single missing or blurry quadrat photo that could not be used (only 23 quadrats sampled for these sites). Photoquadrats were imported into Adobe Photoshop (version 21.2.3). Quadrat frames had physical markings at 10 cm intervals along each side that were used to digitally superimpose a 10×10 cm grid over each quadrat (Fig. 1b). Each of the 81 internal points formed by the intersecting grid lines was manually inspected by one of the authors (TS) and classified into

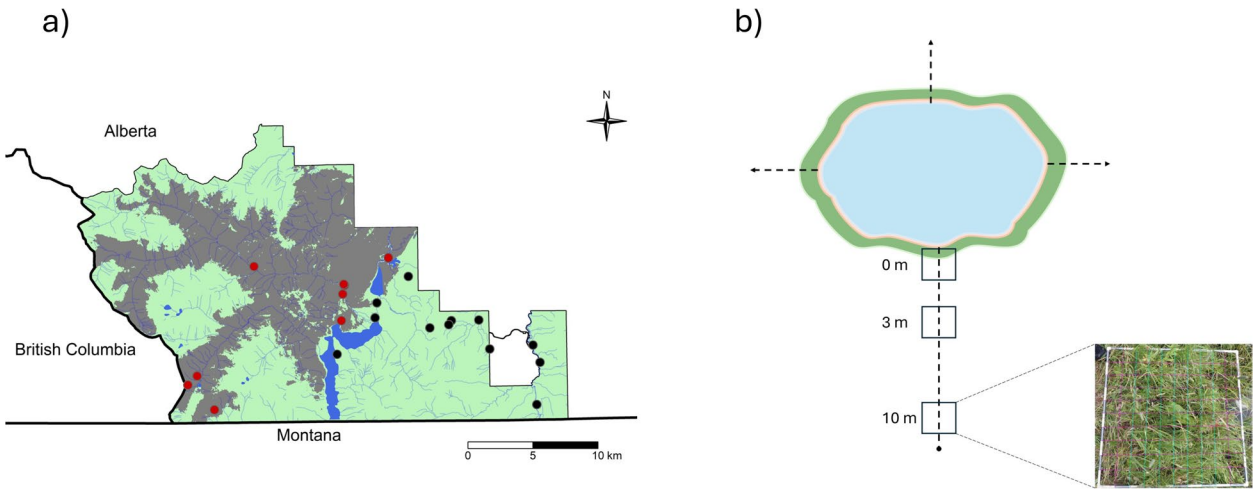

Fig. 1 **a** Distribution of the 20 amphibian breeding ponds included in microhabitat surveys in Waterton Lakes National Park with respect to the burn footprint of the 2017 Kenow wildfire (darker shading). Points represent ponds and are colored according to burn status of each site (red: 9 burned; white: 12 unburned). Rivers and larger lakes in the park are indicated in blue. **b** Schematic of the survey design at each site. Four transects were placed on different sides of each pond (single transect depicted here). Photos of 1 m^2 quadrats (example in inset) were taken along each transect at 0 m, 3 m, and 10 m away from the pond edge, allowing for digital overlay of a grid used to get counts of 14 different microhabitat features within each quadrat (see the "Methods" section and Table 1)

one of 14 microhabitat features (Table 1; see Booth et al. 2006; Degrassi 2018; Howes and Lougheed 2004 for similar methods). Where grid intersection points coincided with a stem, stems were followed to identify other vegetation characteristics that allowed for classification (e.g., flowers versus grass spikelets). Unclear classifications were scored as "NA." Focal microhabitat features fall into the broader categories of bare ground, dead organic or inorganic cover, moss, herbaceous vegetation, and woody-stemmed vegetation, all of which impact occupancy, abundance, and movement in temperate amphibians, including the species found in WLNP (Table 1). Quadrats where more than 20% of counts corresponded with submerged terrain or fell on roads (i.e., "nuisance" categories) were removed prior to analysis (three quadrats from two sites). A total of 462 quadrats were retained in our analysis (Table S1).

General analytical approach

The nature of our dataset (counts of features within quadrats) lends itself to multivariate analysis and our general approach was as follows. To prepare the data for analyses, we first converted counts of each microhabitat feature to proportions, ignoring remaining

Table 1 Features used to characterize microhabitat around wetlands in Waterton Lakes National Park, Alberta, Canada

Microhabitat Feature	Description	Rationale and focal species[±] examples[†]
Soil	Exposed mineral soil	Open substrates influence movement and habitat selection (NLFR: Blomquist and Hunter 2009; LTSA: Lee-Yaw et al. 2015)
Gravel	Small pebbles and rocks (< 10 cm in diameter)	Open substrates influence movement decisions (LTSA: Lee-Yaw et al. 2015) and may influence burrowing (LTSA: Sheppard 1977)
Rock	Rock > 10 cm in diameter, large enough to shelter adult amphibians (~ 7 cm)	Provides cover (LTSA: Jaeger 1980; WETO: Bull 2006)
Litter	Accumulated organic material from decaying leaves, grass, bark, or needles	Influences movement decisions and habitat selection (NLFR: Blomquist and Hunter 2009; LTSA: Jaeger 1980; Lee-Yaw et al. 2015); Associated with abundance (LTSA: Graham 1997)
Snag	Upright decaying wood or standing stump	Provides cover and overwintering sites (LTSA: Atkinson-Adams et al. 2018)
Coarse woody debris (CWD)	Decaying downed wood > 10 cm in diameter, large enough to shelter the adult amphibians (~7 cm)	Impacts on movement decisions (LTSA: Hoza and Bakker 2023) and habitat selection (NLFR: Blomquist and Hunter 2009; WETO: Browne and Paszkowski 2018)
Moss	Non-vascular flowerless plants in taxonomic division *Bryophyta* (e.g., *Ambylstegium varium*)	Influences movement and habitat selection (LTSA: Lee-Yaw et al. 2015; Associated with abundance (WETO: Browne et al. 2009)
Grass	Graminoids in family *Poaceae* (e.g., *Festuca scrabella*)	Influences movement and habitat selection (LTSA: Lee-Yaw et al. 2015); associated with abundance (BCRF: Ouellet et al. 2009)
Sedge	Grass-like families *Cyperaceae* and *Juncaceae* (e.g., *Carex utriculate*)	Associated with abundance (BCRF: Ouellet et al. 2009) and distribution (CSFR: Shive et al. 2010)
Forb	Non-woody, non-graminoid flowering plants (e.g., *Arnica cordifolia*)	Herbaceous cover influences distribution (BCFR: Constible et al. 2001)
Equisetum spp.	Plants in genus *Equisetum* (e.g., *Equisetum arvense*)	Herbaceous cover influences distribution (BCFR: Constible et al. 2001)
Shrub	Woody plants, usually multi-stemmed and less than 10 m when mature (e.g., *Cornus sericea*)	Influences distribution (BCFR: Constible et al. 2001) and habitat selection (WETO: Browne and Paszkowski 2018) and abundance (BCFR, WETO: Browne et al. 2009)
Tree: Deciduous	Deciduous tree species (e.g., *Populus tremuloides*)	Canopy cover influences habitat selection (NLFR: Blomquist and Hunter 2009) and abundance (BCFR, WETO: Browne et al. 2009)
Tree: Coniferous	Coniferous tree species (e.g., *Pseudotsuga menziesii*)	Canopy cover influences habitat selection (NLFR: Blomquist and Hunter 2009) and abundance (BCFR, WETO: Browne et al. 2009)

[±] *BCFR*, boreal chorus frog (*Pseudacris maculata*); *CSFR*, Columbia spotted frog (*Rana luteiventris*); *LTSA*, long-toed salamander (*Ambystoma macrodactylum*); *NLFR*, northern leopard frog (*Lithobates pipiens*); *WETO*, western toad (*Anaxyrus boreas*)

[†] Associations indicated may be positive or negative depending on species

"nuisance" counts when calculating the total number of counts in each quadrat. Because we are focused on compositional differences among samples with many zeros, we transformed the data using a Hellinger transformation (Legendre and Gallagher 2001). We visualized microhabitat composition in multivariate space using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities of the Hellinger-transformed data for all quadrats and fit environmental vectors onto the resulting ordination using the "metaMDS" and "envfit" functions respectively in the *vegan* package (version 2.7-1; Oksanen et al. 2025) in R (version 4.4.3; R Core Team (2025).

Our main questions involved testing the effects of categorical predictors on multivariate microhabitat composition (distance class, burn status, etc.). To do so, we used permutational multivariate analysis of variance (PERMANOVA). PERMANOVA specifically tests for differences in the centroids and/or dispersion of specified groups in multivariate space (Anderson 2017). In the present case, both differences in the central tendencies and differences in the variances among groups, or changes in these properties, are of interest. For example, in addition to changes in the position of quadrats in multivariate microhabitat space following a wildfire (and thus shifts in the centroids of burned groups), removal of vegetation during wildfire might homogenize microhabitat composition across quadrats in the burn zone, resulting in a reduction in multivariate dispersion—at least in the short-term. We used tests of homogeneity of dispersion to assess differences in dispersion among groups (note a non-significant test of dispersion suggests a significant PERMANOVA is better explained by differences in the centroids). Significant PERMANOVAs were also followed by post hoc tests (pairwise PERMANOVAs) to identify specific groups that differ. All PERMANOVAs, tests of homogeneity of variance, and post hoc tests were based on Bray–Curtis dissimilarities of the Hellinger-transformed data and run in PRIMER-e (Anderson et al. 2008). Finally, significant PERMANOVAs were also followed by an indicator analysis to identify the microhabitat features most strongly associated with groups (Dufrêne and Legendre 1997). Indicator analyses were run using the "multipatt" function in the *indicspecies* package (version 1.8.0; De Cáceres and Legendre 2009) with the association function set to "r.g". We set the number of permutations to 5000 in all permutation-based analyses.

Relationship between distance to pond edge and microhabitat composition

We first asked whether microhabitat composition varied among the three distance classes prior to the fire (i.e., baseline conditions). To address this question, we used PERMANOVA to test the effects of distance class on multivariate dissimilarity among quadrats in the 2009 dataset (i.e., pre-fire microhabitat dissimilarity ~ distance class). To account for non-independence associated with quadrats within sites, we included *site* as a random effect in this model, allowing quadrats to be shuffled across distance classes within site to test the significance of distance class while preserving the assignment of quadrat to site.

To assess whether the relationship between microhabitat and distance class in the burn zone changed following the fire, we used PERMANOVA to test the effects of the three-way interaction between distance class, time, and burn status on microhabitat composition (i.e., multivariate dissimilarity ~ distance class*time*burn status). As this analysis involved a complex repeated-measures design (data collected from two time periods for each site, with sites uniquely assigned to burn status), to simplify the analysis, we summed the counts of each microhabitat feature from quadrats from the same distance class and time period within sites, recalculated microhabitat proportions, and re-transformed the data prior to conducting this analysis (hereafter this dataset is referred to as the "aggregated dataset"). Site was included as a random effect in this analysis to account for non-independence associated with repeated measures of the same site over time. Post hoc tests were used to explore meaningful comparisons (e.g., significant differences between pre- and post-fire composition within burn status and/or differences between burned and unburned sites within each time period) and an indicator analysis was used to look for microhabitat features significantly associated with different distance × burn status × time groups. For the latter, a custom hierarchical permutation scheme was used to account for non-independence associated with site and repeated measures within site. Specifically, sites were shuffled as intact units, time period was shuffled within site, and distance class shuffled within time period within site. Significance was assessed by comparing observed association statistics from *multipatt* to a null distribution of values based on the permuted dataset. We also tested for differences in dispersion among groups, asking whether multivariate dispersion was lower for post-fire samples than for pre-fire samples at the same sites (i.e., expected if there has been homogenization over time), and especially lower for post-fire samples in burned areas relative to unburned areas (i.e., expected if the wildfire and not just time is the cause of any homogenization).

Differences in the amount of change among sites

We next explored the impacts of burn status on the amount of change in microhabitat composition over

time. We calculated the Bray–Curtis dissimilarity between the 2009 and 2020 surveys at each distance class based on the aggregated dataset and used the dissimilarity between time points at a given site as an estimate of the amount of change in microhabitat composition at that distance class at that site (Lloren and McCune 2024). Dissimilarities range from 0 (no discernible change) to 1, with larger values indicating a greater amount of change. We used Spearman Rank correlation to assess whether there were associations between the rank amount of change at one distance class and the rank amount of change at other distance classes within sites. For each distance class, we used a generalized linear model with a beta distribution in the *betareg* package in R to assess the effects of burn status on the amount of change within sites. Because the relative importance of different microhabitat features for amphibians may vary across elevation (Farallo et al. 2018), we also included elevation and the interaction between burn status and elevation in our models (i.e., within-site dissimilarity across time ~ burn status * elevation). Elevation was centered to better meet model assumptions. Small sample sizes and lack of variation across levels of other predictors that may moderate the effects of wildfire on microhabitats (ecoregion, pond size, and burn severity) prevented inclusion of these predictors in our models. Likelihood ratio tests were used to obtain *p*-values for each term in these models. To test the significance of the interaction between burn status and elevation, the model including the interaction was compared to a model with additive effects only. To obtain *p*-values for each predictor (burn status and elevation), the full model was compared to a reduced model without the predictor of interest and the interaction between predictors. Standard diagnostic methods (examination of residuals, influential observations, and model fit) were used to assess how well our models met the underlying assumptions of generalized linear models. Sensitivity tests were conducted to test the robustness of the results to violations of these assumptions—in this case, the influence of three high-leverage observations. NMDS plots based on the aggregated data and with the associated environmental vectors based on an envfit analysis for each distance class were generated to facilitate interpretation of results.

Results

Relationship between distance to pond edge and microhabitat composition

We first characterized baseline microhabitat structure and explored fine-scale gradients in microhabitat composition away from pond edges before the wildfire. PERMANOVA based on the 2009 data revealed significant differences in microhabitat composition at different distances away from pond edges ($F_{2,\ 57} = 2.9441$, $p = 0.006$; Table S2). A test of differences in multivariate dispersion suggested the significant PERMANOVA result was largely driven by differences in the mean (centroid) of groups rather than differences in dispersion (Table S3). Post hoc tests point to differences in pre-fire microhabitat composition between the 0 and 10 m distance class (Table S4). Results from an indicator analysis suggest that quadrats adjacent to pond edges tended to have a greater proportion of sedge relative to quadrats 3 and 10 m away from the shoreline prior to the fire, whereas quadrats 10 m away from the shoreline had more deciduous trees (Table S5), though the latter made up a relatively small proportion of counts across the entire dataset (Fig. S1). There was more bare soil immediately at and 3 m away from the shoreline than 10 m away from the shoreline prior to the fire, and shrubs and forbs were more prominent at 3 and 10 m away from the shoreline than at the shoreline (Table S5; Fig. S1).

We next asked whether the relationship between microhabitat composition and distance changed following the wildfire and whether these changes depended on whether sites were burned. Consistent with an effect of the fire on the relationship between microhabitat composition and distance from pond edge, we found a significant three-way interaction in the PERMANOVA testing the joint effects of distance class, time, and burn status on microhabitat composition (Fig. 2, Table 2). Post hoc tests revealed that this result was largely driven by changes in microhabitat

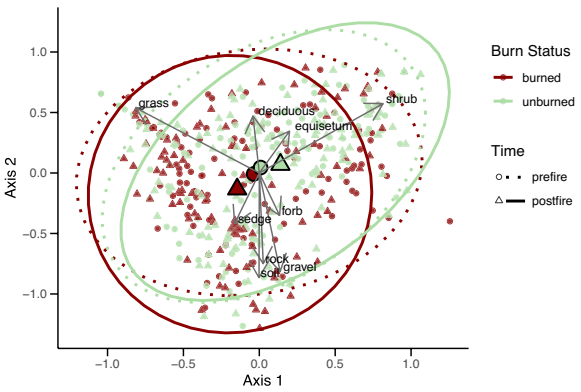

Fig. 2 Non-metric multidimensional scaling (NMDS) ordination of microhabitat composition (NMDS based on Bray–Curtis dissimilarities; k = 3, stress = 0.125) among 1 m2 quadrats collected around amphibian breeding ponds in Waterton Lakes National Park before (circles) and after (triangles) the Kenow wildfire in burned (red) and unburned (green) parts of the park. For illustrative purposes, 95% confidence ellipses around burn status × time groups are shown, with group centroids indicated by the larger-sized symbols. Environmental vectors significantly associated with the first two axes are shown

Table 2 Results from a PERMANOVA testing the effects of distance class (0, 3, or 10 m), time (pre- or post-fire), and burn status (burned or unburned) on differences in relative microhabitat composition at 20 amphibian breeding sites in Waterton Lakes National Park*

Response	Predictor	df	SS	R^2	*F*	*p*-value**
Dissimilarity in relative microhabitat composition	Distance class	2	13,980	6990.1	11.518	0.00020
	Burn status	1	3410.1	3410.1	0.94211	0.44630
	Time	**1**	**2230.2**	**2230.2**	**2.6361**	**0.04400**
	Site (burn status)	**18**	**65,154**	**3619.7**	**10.356**	**0.00020**
	Distance class × Burn status	2	656.96	328.48	0.54125	0.83060
	Distance class × Time	2	326.58	163.29	0.46717	0.81720
	Burn status × Time	1	2141.2	2141.2	2.5309	0.05640
	Distance class × Site (Burn status)	**36**	**21,848**	**606.89**	**1.7363**	**0.00040**
	Time × Site (Burn status)	**18**	**15,229**	**846.04**	**2.4205**	**0.00020**
	Distance class × Burn status × Time	**2**	**1899.7**	**949.85**	**2.7175**	**0.01320**
	Residual	36	12,583	349.53		
	Total	119	1.39000			

* Significant predictors are bolded

**Based on 5000 permutations

composition at the 10 m distance class in the burn zone (Table S6). Visualization of mean change for each distance class in burned and unburned areas along the different axes resulting from the NMDS ordination of all quadrats suggest the greatest shift for the 10 m distance class was along axis 3 (Fig. 3). In particular, quadrats 10 m away from the pond edge in the burn zone showed decreases along axis 3 (Fig. 3), corresponding to shifts towards more forbs (Table S7; Fig. S1; slight decreases in mean values along axis 2 for the 10 m distance class were also observed, but this and all other pre- and post-fire comparisons had overlapping confidence intervals around the mean: see Fig. 3). A corresponding indicator analysis further suggests that mosses/lichen were significantly associated with all distance classes in the burn zone before the fire, but only with the 0 and 3 m distance classes in the burn zone after the fire (association coefficient = 0.373, $p = 0.013$; Table S8; see also Fig. S1). There was substantial variation in microhabitat composition across quadrats (Figs. 2 and 3) and differences in multivariate dispersions among distancex burn status x time period groups were not significant (PERMDISP: $F_{11,108} = 1.2871$, $p = 0.3975$, nperm = 5000; Fig. S2).

Magnitude of microhabitat change within sites

The magnitude of change in microhabitat composition (i.e., dissimilarity between time points in multivariate space) at adjacent distance classes was correlated (Spearman's rho 0 to 3 m: 0.574, $p = 0.009$; Spearman's rho 3 to 10 m: 1, $p = 6 \times 10^{-6}$) but the magnitude of change at 0 and 10 m was not correlated (Spearman's rho: 0, $p = 0.841$). Dissimilarity within sites across time immediately at shoreline (0 m) ranged from 0.117 to 0.585 (median = 0.295). Site shorelines did not tend to change in a consistent direction (Fig. 4a) and none of our predictors of interest were significantly associated with the amount of change within sites at this distance class (Table 3; Fig. 5a). For the 3 m distance class, dissimilarity between temporal samples from the same site ranged from 0.175 to 0.637 (median = 0.265). As per the 0 m distance class, sites did not change in a consistent fashion at 3 m away from pond edges (Fig. 4b) and none of our predictors were significantly associated with the amount of change at 3 m (Table 3; Fig. 5b). For

(See figure on next page.)

Fig. 3 Relationship between microhabitat composition and distance away from pond edge (measured at 0, 3, and 10 m) before (green) and after (grey) the 2017 Kenow wildfire at nine burned (left panels) and eleven unburned (right panels) amphibian breeding sites. Each plot shows a different axis from a non-metric multidimensional scaling analysis summarizing the variation in the dataset (k = 3; stress = 0.125), with arrows along the y axes indicating environment vectors significantly and strongly associated with that axis (Table S7). Points represent values for individual 1 m2 quadrats. Error bars are 95% confidence intervals based on a custom bootstrapping scheme that involved sampling sites with replacement, then, for each site, calculating mean values for each distance class and time period, and finally averaging values across sampled sites within each of the distance-time-burn status groups

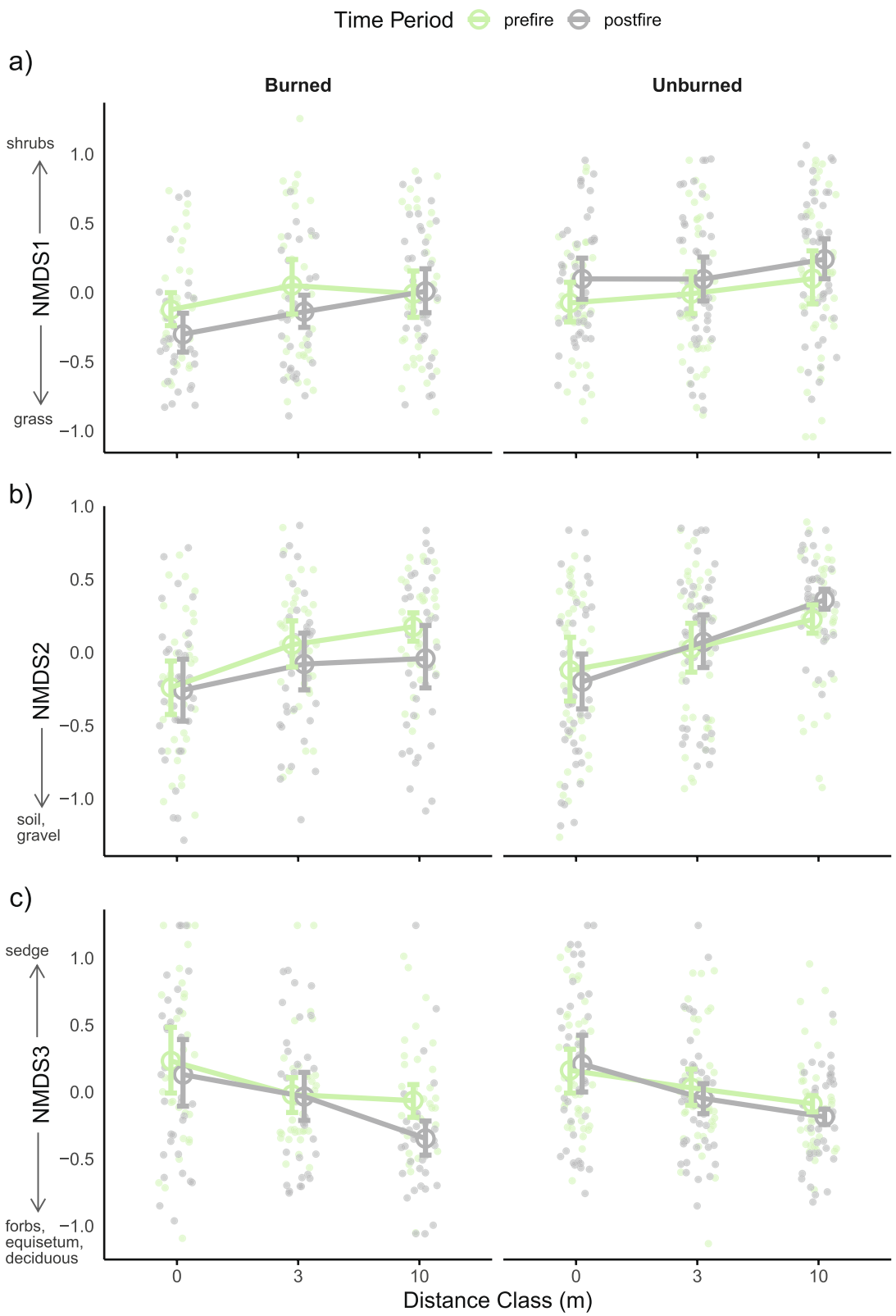

Fig. 3 (See legend on previous page.)

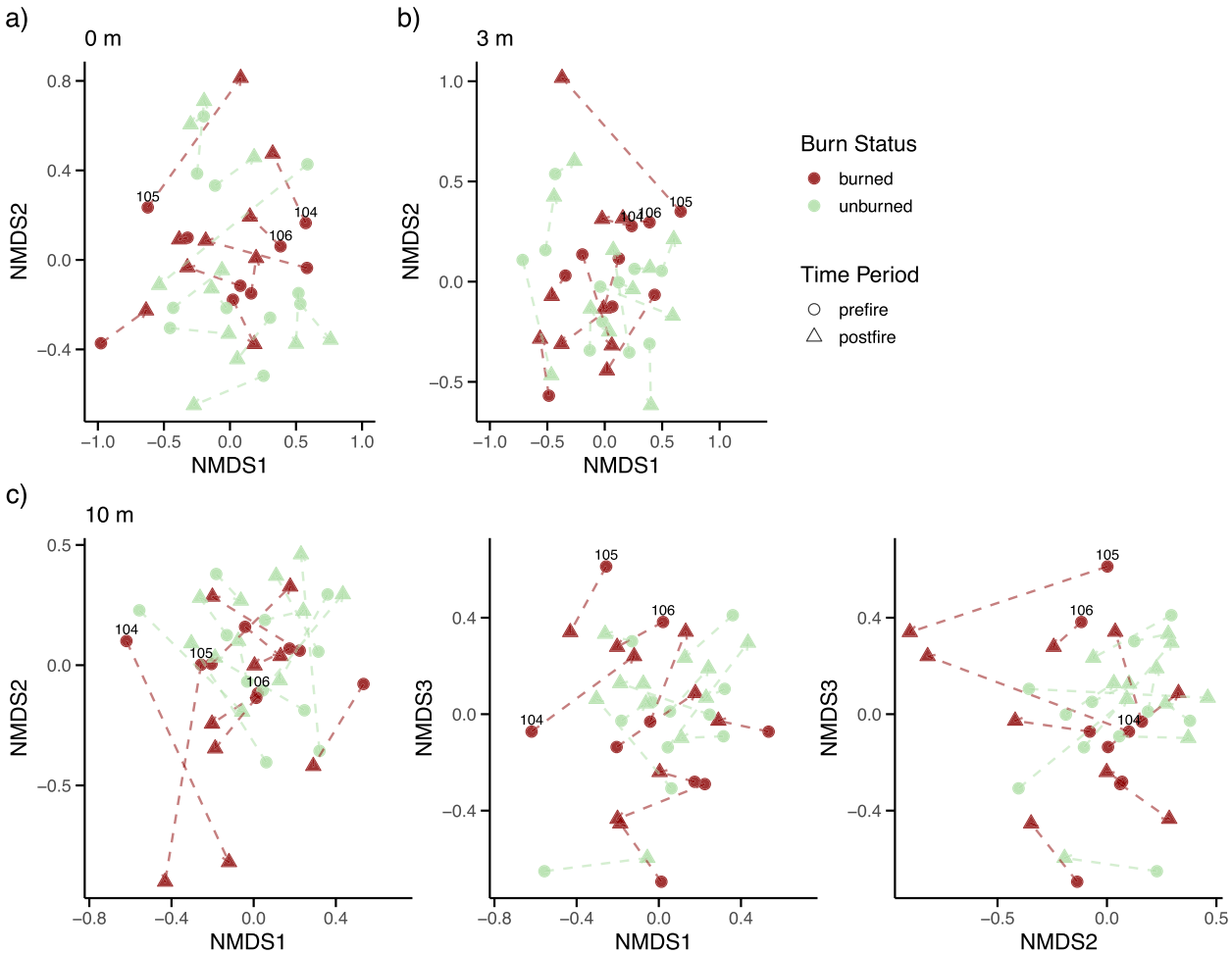

Fig. 4 Non-metric multidimensional scaling (NMDS) plots showing shifts in microhabitat composition at **a** 0 m, **b** 3 m, and **c** 10 m away around burned (red) and unburned (green) amphibian breeding ponds following a major wildfire in Waterton Lakes National Park. Dashed lines connect each site before (circles) and after (triangles) the wildfire. NMDS plots are based on Bray–Curtis dissimilarities and were fit with $k = 2$ for the 0 m and 3 m distance classes and with $k = 3$ for the 10 m distance class. The three highest-elevation sites in the burn zone are labeled

the 10 m distance class, dissimilarity between temporal samples from the same site ranged from 0.120 to 0.624 (median = 0.314). Sites in the burn zone showed decreases along axis 2 of a NMDS plot based on this distance class (Fig. 4c), corresponding to increases in rocks, soil, and forbs (Table S9; see also Fig. S1). Our full model explained a substantial amount of the variation in change within sites for this distance class (Pseudo $R^2 = 0.388$; Table 3). In this model, the interaction between burn status and elevation was marginally significant and the main effect of elevation was significant (Table 3). In general, the amount of change in microhabitat composition increased with elevation, and this appeared to be driven by three high-elevation sites (sites 104, 105, and 106) in the burn zone (Fig. 5c). These sites had high leverage in all models and results for the 3 and 10 m distance class were sensitive to the sequential removal of these sites (Table S10). Of these sites, site 105 is particularly noteworthy as it demonstrated either the highest or second highest amount of change at all distance classes (Fig. 4).

Discussion

Understanding how microhabitats are altered by changing disturbance regimes is critical to our ability to predict and mitigate the effects of climate change on small-bodied taxa. In this study, we took advantage of a rare opportunity to use a natural, before-after-control-impact design to examine the effects of a severe wildfire event on microhabitats associated with amphibian breeding sites. We found a limited effect of the Kenow wildfire on the composition of microhabitats immediately around ponds in Waterton Lakes National Park, suggesting that the local processes influencing microhabitat composition

Table 3 Results from linear models (beta regression) testing change in proportional microhabitat composition (pairwise Bray–Curtis dissimilarity) around amphibian breeding ponds in Waterton Lakes National Park with respect to burn status and elevation*

Response	Predictor	Coefficient*	SE	*Z*	*p*-value**
Change in microhabitat composition 0 m away from pond edges	Intercept	− 0.871	0.182	− 4.78	
Pseudo R-squared: 0.121	Burn status	− 0.0258	0.248	− 0.10	0.373
	Elevation	0.000948	0.000701	1.35	0.293
	Burn status × Elevation	− 0.00224	0.00161	− 1.38	0.167
Change in microhabitat composition 3 m away from pond edges	Intercept	− 0.620	0.147	− 4.225	
Pseudo R-squared: 0.196	Burn status	− 0.341	0.207	− 1.65	0.179
	Elevation	0.000605	0.000577	1.048	0.430
	Burn status × Elevation	− 0.00159	0.00138	− 1.15	0.247
Change in microhabitat composition 10 m away from pond edges	Intercept	− 0.802	0.166	− 4.83	
Pseudo R-squared: 0.388	Burn status	− 0.0509	0.224	− 0.23	0.147
	Elevation	0.00230	0.000633	3.63	**0.00558**
	Burn status × Elevation	− 0.00292	0.00145	− 2.011	0.0506

* Coefficients for burn status represent comparison to the reference category "unburned"

* Significant predictors are bolded

** *p*-values reflect marginal effects of predictor and were obtained from likelihood ratio tests comparing model with and without the predictor; to test main effects, both the main effect and the interaction term were removed in the reduced model

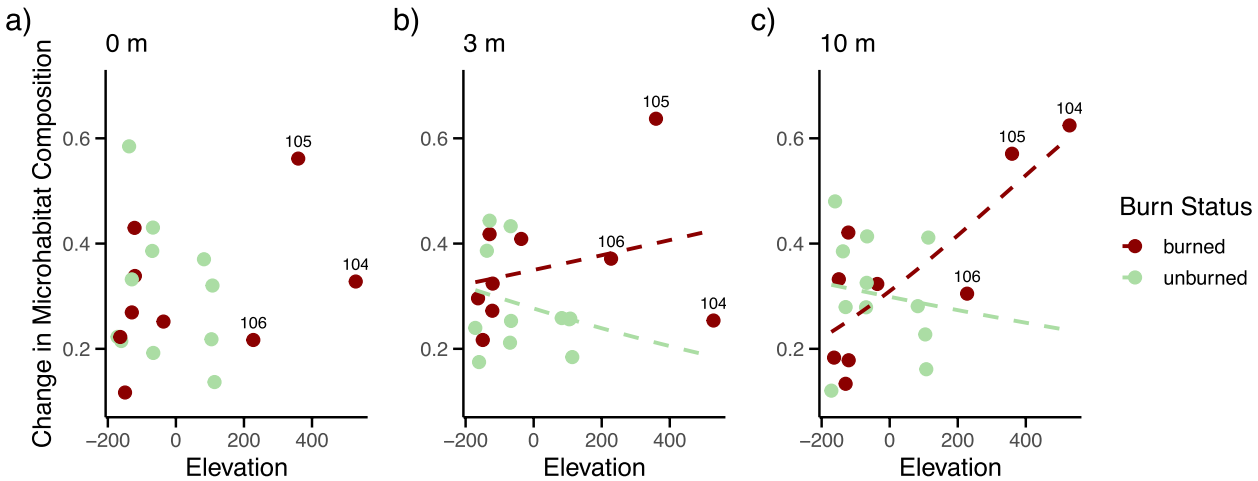

Fig. 5 Change in multivariate microhabitat composition around amphibian breeding ponds at **a** 0 m, **b** 3 m, and **c** 10 m away from the pond's edge in relation to burn status and elevation (m, centered). Dashed lines in **b** and **c** show the interaction between burn status and elevation, the significance of which was sensitive to three high-elevation sites in the burn zone (labeled in each panel; see Tables S3 and S9)

immediately adjacent to pond edges were either relatively unimpacted by, or quickly recovered from, the wildfire. At the same time, we detected a wildfire effect by 10 m away from pond edges. These results suggest that small ponds may have a buffering effect on microhabitats, but that this effect may be restricted to very small spatial scales. Sites at high-elevation also showed signs of being more impacted than sites at lower elevations. We discuss the potential implications of these results for amphibians in the park.

Variation in microhabitat features in relation to distance from pond edges and wildfire

We observed fine-scale gradients in microhabitat structure moving away from pond edges in the park before the Kenow wildfire, with near-shore quadrats (0 and 3 m) being characterized by more bare ground than quadrats further away (10 m) from pond edges. In general, vegetation transitioned from more sedges around pond edges to increasing shrubs and forbs at 3 m, to more deciduous trees by 10 m away from pond edges. Like other studies that have examined microhabitat attributes in relation

to wildfire at resolutions on the order of meters (Kaiser et al. 2022; Lentile et al. 2007), we observed substantial variation in composition among quadrats across space (and time). Such variation in microhabitat composition is generally thought to reflect the influence of microsite characteristics, including soil composition, drainage, individual plant characteristics, and in the case of burned sites, fine-scale variation in fire intensity (Lentile et al. 2007; Lindsay et al. 2023; Loudermilk et al. 2022).

The significant three-way interaction between burn status, time, and distance from pond edge observed in the present study is further suggestive of local controls on microhabitat composition. Specifically, the lack of a discernible effect of the wildfire on microhabitat composition immediately at (0 m distance class) or 3 m away from ponds when contrasted with the significant effect further into the terrestrial environment is consistent with a buffering effect of ponds on microhabitat composition. That wetlands may play an important role in buffering terrestrial habitats during wildfire is increasingly recognized, with beaver (*Castor canadensis*) wetlands in particular lowering burn severity and providing areas of plant persistence during wildfire (Fairfax et al. 2024; Fairfax and Westbrook 2024; Fairfax and Whittle 2020; Markle et al. 2022). Although the ponds studied here are small, several of these ponds are permanent (Table S1) and may have retained vegetative cover along their edges during the wildfire. Other ponds are small, ephemeral wetlands that were likely dry by the time of the wildfire (pond levels at the time of the wildfire are unknown and cannot be estimated from available satellite images). However, spring refilling of these ponds may have facilitated quick recovery of pond-edge vegetation post-fire. For example, another study looking at the impacts of the Kenow wildfire on vegetation documented faster recovery of herbaceous vegetation at a moist (non-wetland) site characterized by seasonal rills and temporary, groundwater-fed streams compared to a nearby dry site within the burn footprint (Aspinall et al. 2025). Whether by enabling pockets of persistence during, or rapid recovery of vegetation following wildfire, these observations collectively highlight the potential importance of even small wetlands in moderating the effects of severe wildfire on microhabitats.

By 10 m away from pond edges, quadrats in the burn zone tended to have more forbs and less moss after the fire than prior to the fire. Moreover, consistent with significant consumption of the organic layer by the fire and delayed regeneration of some plant species (Musk et al. 2024), the composition of burned sites at this distance class generally shifted toward a greater proportion of bare ground (represented as soil, rocks, and gravel). Although the limited number of high-elevation sites in unburned areas precluded a clear statistical understanding of the joint effects of elevation and wildfire on microhabitat composition, changes in the burn zone were most pronounced at high-elevation sites, with the most change observed at the two highest-elevation sites (1804 and 1973 m) in our survey. The compositional shifts observed here share similarities to changes in response to severe wildfire in other parts of western North America. For example, the loss (and slow recovery) of lichen and mosses from the forest floor was noted in response to wildfire in the jack pine (*Pinus banksiana*) forests of northern Alberta (Pinno and Errington 2016) and in the black spruce (*Picea mariana*) forests of interior Alaska (Mack et al. 2008). Likewise, an increase in forb cover was noted for fires of varying severity in western and northern Montana, with high severity sites also having significantly more exposed soil (Lentile et al. 2007). Many factors influence the recovery of vegetation following wildfire and thus the effects of severe wildfire on microhabitats are expected to vary across regions and fire events (Kuntzemann et al. 2025; Lentile et al. 2007; Wolf et al. 2021). However, identifying shared responses to severe wildfire across regions is useful for identifying any general impacts of shifting fire regimes.

Implications for amphibian populations and park management activities

With their need for moist conditions, access to invertebrate prey, and protective cover, amphibians are highly sensitive to microhabitat conditions. The substantial variation in microhabitat composition among quadrats observed here aligns with previous suggestions that even within large, severe burn footprints, some suitable microsites are likely available for small-bodied species such as amphibians (Kaiser et al. 2022). These microsites may play an important role in the post-fire landscape, allowing individuals to persist in the burn footprint and/or facilitating the nucleated recovery of populations post-fire (Bailey et al. 2025; Banks et al. 2015, 2017).

At the same time, we observed fine-scale gradients in the effects of the wildfire on amphibian microhabitat composition associated with distance to breeding pond edges. Individual amphibian movements are often on the order of a few meters per day (Hoza and Bakker 2023) and changes in microhabitat composition in the vicinity of ponds may influence the movement decisions individuals make as they move to and from breeding ponds and the overall dispersion of individuals in the terrestrial environment (Raymond and Hardy 1991; Rittenhouse and Semlitsch 2006). For example, red-legged salamanders declined in exposed upland sites but not riparian sites following a wildfire in the hardwood forests of North Carolina, with the juvenile class in particular being lost

from upland sites following the fire (Gade et al. 2019). Changes to the terrestrial environment farther away from pond edges several years into recovery of the landscape may encourage a larger number of individuals to remain near pond edges outside the breeding season, which may in turn influence the frequency of both intraspecific (Kerby and Kats 1998) and interspecific interactions (Hossack et al. 2013).

The changes in microhabitat composition observed further away from pond edges may have positive or negative effects on amphibians in the park. For example, western toads move large distances away from breeding ponds and their movement and colonization rates appear to increase following wildfire (Hossack and Pilliod 2011), potentially because warmer soil and burrow conditions attract toads (Hossack et al. 2009). Northern leopard frogs avoid wooded areas in many parts of their range (Blomquist and Hunter 2009; Werner and Glennemeier 1999), including in Alberta (Green and Taylor 2009). WLNP has made several attempts to reintroduce leopard frogs since their extirpation from the park (and much of province) in the 1980s, and the post-fire loss of canopy cover, combined with greater forb and equisetum cover away from wetland margins, may facilitate the establishment and spread of this species. Likewise, Columbia spotted frogs prefer open canopy sites for breeding and a positive relationship between egg mass counts and burn extent has been observed for this species following wildfires just south of WLNP (Hossack et al. 2013; although time-lagged declines in occupancy of this species following wildfire have also been observed: Hossack et al. 2013). In contrast, the loss of forest duff and moss may negatively impact long-toed salamanders, which are associated with thick litter in other parts of Alberta (Graham 1997) and showed a preference for moss substrates in choice trials (Lee-Yaw et al. 2015). The observed changes to microhabitats at high elevation sites may especially be cause for concern for this species. The stocking of non-native fish in Alberta has led to the extirpation of long-toed salamanders from much of the species' high-elevation range in southwestern Alberta, including in WLNP (Pearson and Goater 2008). Remaining high-elevation populations are isolated and expected to exist at small effective population sizes (Funk et al. 1999; Giordano et al. 2007). Pronounced changes to microhabitats at high-elevation sites following the Kenow wildfire may compound the risk of declines in these environments, with long-term decreases in occupancy and abundance in this species in response to wildfires in western Montana (Hossack et al. 2013) underscoring the need for careful post-fire assessment and monitoring of this species in WLNP going forward.

Limitations and future directions

As with any retrospective analysis of habitat change, our study has inherent limitations that should be considered when interpreting the observed patterns. First, the surveys were not explicitly designed to test a wildfire effect and the limited number of sites originally surveyed (and more generally, the limited number of amphibian breeding ponds that burned in the park) precluded evaluation of additional factors at the site- or landscape-level that contribute to variation in microhabitat and that could modulate the effects of wildfire. For example, both wetland size and configuration may influence the resistance of wetland edges to wildfire (Markle et al. 2022; Newaz et al. 2020). Likewise, slope and aspect influence the development of fire refugia, including in mountainous areas of western North America (Krawchuk et al. 2016). However, much of the work exploring these modifiers to wildfire effects has been conducted at larger spatial scales (e.g., 30 m resolution in remote-sensing based analyses). Whether and how these factors influence variation in wildfire effects at the types of very fine scales examined here warrants investigation across a larger set of sites encompassing a broader range of wetland characteristics.

An additional constraint that arises from the data at hand is that we cannot fully disentangle the effects of distance from pond edge and elevation on the patterns observed presently. The two highest-elevation sites in the burn zone were more strongly impacted by the wildfire than sites at lower elevations and some of our results were sensitive to the removal of these sites. However, examination of key individual microhabitat features (proportion of soil and forbs) contributing to the multivariate response reveals that substantial differences in pre- to post-fire counts at 10 m from pond edges in the burn zone remain after excluding these sites. Thus, the observed difference in wildfire effects with distance from pond edge is not solely driven by change at high-elevation sites. However, the pace of post-fire recovery at high-elevation sites is expected to be slower (Musk et al. 2024); thus, over time, we might expect these sites to retain signatures of impact for longer. Additional work evaluating the relative roles of elevation and proximity to wetlands in shaping the effects of wildfire on microhabitats and the timescale of such effects would provide valuable insight on these landscape controls on the formation of fire refugia and spatial variation in post-fire recovery.

Finally, we do not have concordant data on microclimatic conditions for the sites included in the current study. Although microhabitat structure influences microclimates in post-fire landscapes (Crockett and Hurteau 2022; Wolf et al. 2021), the extent to which structural features of the microhabitat serve as a proxy for suitable

microclimatic conditions may be limited (Evans et al. 2020). Furthermore, the potential implications of our findings for amphibians as discussed above require testing. Data on individual movement, habitat selection, and abundance are ultimately needed to understand the consequences of observed microhabitat changes on amphibians in the park.

Conclusion

Despite a growing body of literature documenting the effects of wildfire on amphibian populations (Dos Anjos et al. 2021; Hossack and Pilliod 2011; Pilliod et al. 2003), our understanding of changes to amphibian microhabitats following wildfire remains limited. To the best of our knowledge, our study is the first to use a before-after-control-impact design to examine the impacts of severe wildfire on small-scale environmental features that constitute key microhabitats for amphibians and other groups. Our study establishes a foundation for continued investigation of post-fire microhabitat changes within the park and the responses of amphibians and other small-bodied species that depend on these habitats for shelter, foraging, and movement. More generally, our findings highlight the potential for there to be fine-scale gradients associated with pond edges that interact with wildfire to shape the structural environment of the forest floor.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00562-9.

Supplementary Material 1: Table S1. Site information. Table S2. Differences in microhabitat composition among distance classes prior to the wildfire. Table S3. Pre-fire differences in dispersion among distance class groups. Table S4. Pairwise, pre-fire differences in microhabitat composition among different distance class groups. Table S5. Microhabitat features associated with different distance classes before the wildfire. Table S6. Average similarity between pre-fire and post-fire samples. Table S7. Association of individual microhabitat features with NMDS axes. Table S8. Microhabitat features associated with different distance x burn status x time groups. Table S9. Association of individual microhabitat features with NMDS axes from each distance class. Table S10. Sensitivity tests. Figure S1. Proportion of each microhabitat feature in each distance x burn status x time group. Figure S2. Comparison of multivariate dispersion across distance x burn status x time groups.

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Authors' contributions

JAL conceived of the study, acquired the funding, and took the prefire photographs as part of earlier surveys. TS took the postfire photographs, developed the approach to scoring microhabitat features, and collected the data. All authors developed the analytical framework, with the final analyses being completed by JAL. JAL led the writing of the manuscript with contributions from all authors.

CRediT authorship contribution statement

Julie A. Lee-Yaw: conceptualization, formal analysis, funding acquisition, investigation, methodology, visualization, writing—original draft; Tristan Skretting: data curation, formal analysis, investigation, methodology, writing-original draft; Ashley Smith: validation, formal analysis, investigation, writing—original draft; Jenny L. McCune: methodology, formal analysis, writing—review and editing.

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Data availability

The dataset and R code supporting analysis and conclusions from this study are available on figshare (Figshare: https://doi.org/10.6084/m9.figshare.32957027).

Declarations

Competing interests

The authors declare no competing interests.

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