

Macroscale effects of the Monument Fire on suitable habitat of the Trinity bristle snail in the Greater Trinity Basin, Klamath Bioregion, northern California

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FULL RESEARCH ARTICLE

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Abstract

I evaluated the impact and extent of the Monument Fire on the geographic range and suitable macrohabitat of the Trinity bristle snail (*Monadenia setosa*), a California endemic with limited distribution in northern California. Total area burned by the fire was ~87,984 ha or 46.0% of the species range (n = 191,156 ha). Total area of suitable macrohabitat for the species is ~107,913 ha of which 44.5% (n = 47,962 ha) was encompassed by the fire. Results show that the total area of forest cover-type vegetation and individual forest stand attributes impacted by the fire was not significantly different from areas within the species range not burned by the fire. There was no significant proportional differences in the six sequential categories of suitable macrohabitat burned by the fire (i.e., Low, Low-moderate, Moderate, Moderate-high, High, Critical suitability). The percentage of Moderate and Moderate-high suitable macrohabitat burned was only somewhat greater than predicted by the pre-fire species habitat suitability model (HSM). Many individual watersheds were encompassed by the fire and the resulting mosaic of burned watersheds was highly variable. Application of the Soil Burn Severity (SBS) map identified 8,293 ha (17.3%) of Unburned or very low burned soil, 24,191 ha (50.5%) of Low burned soil, 13,998 ha (29.2.1%) of Moderately burned soil, and 1,460 ha (3.0%) of Highly burned soil within the boundaries of the Monument Fire. When applied to categories of suitable macrohabitat, I calculated that 31,096 ha (100%) of Low to Low-moderate and 13,998 ha (96.1%) of Moderate to Moderate-high suitable macrohabitat were burned. High and Critical areas of macrohabitat suitability were much less impacted by high SBS (n = 1,461 ha [58.0%]) because these regions were small in size, highly fragmented, widely dispersed across the landscape, and separated by major topographic and riverine discontinuities.

Key words: fuels reduction, landscape, macrohabitat, management, *Monadenia setosa*, terrestrial gastropod, threatened species, watershed

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Introduction

Wildfires are a common natural occurrence in forest ecosystems of the Pacific Northwest (Burke et al. 1999). In northern California, decades of fire suppression, exclusion, and selective harvesting of timber has resulted in dense mixed-conifer and woodland forests, and overly congested riparian corridors. This condition is in large part a direct consequence of the lack of a comprehensive and coordinated program for long-term annual fuels reduction (Collins et al. 2019). Although natural fire regimes are often advocated, absence of progress in management of annual fuels reduction, at both state and federal levels, has greatly increased the susceptibility to fuels-driven mixed- and high-severity fire regimes (Wright and Agee 2004; Hessburg et al. 2005; Huff et al. 2005). Mixed- and high-severity fire regimes are potentially complex because of the combined influence of fuels variance, complex topography, stochastic climatic conditions, and fire suppression actions that produce intricate mosaic burn patterns (Halofsky et al. 2011). While climate has played a role in recent fire events and tree mortality, current forest conditions and lack of management are unquestionably contributing to both (Collins et al. 2019).

In recent decades the frequency and extent of fire has become one of the main ecological problems facing management and conservation planning of special status species, both in the context of prevention and restoration. The interaction between fire, fire management, and maintaining habitat for listed and rare species is of particular interest and importance within forests landscapes at high risk of fire (Agee 1993; Brown et al. 2004; Noss et al. 2006; Prather et al. 2008). As a consequence, the potential for high-severity forest fire has been identified as one of the primary risk factors for conservation of endemic species of terrestrial gastropods (Burke et al. 1999; Duncan et al. 2003; Duncan 2005). Numerous studies have documented that fire exerts a major impact on terrestrial snail communities by strongly reducing plant diversity and species richness (Nekola 2002; Kiss and Magnin 2006; Santos et al. 2009; Bros et al. 2011; Gaines et al. 2005, 2011). This is because wildfire-caused removal of vegetative cover and opening up the vegetation matrix fundamentally changes light and humidity levels, which are major threats to the survival of land snail populations. Still, there are a diversity of conclusions regarding the impact of wildfire on terrestrial gastropods (Whelan 1995; Caturla

et al. 2000; Pausas and Verdu 2005; Moretti et al. 2009). For example, Bros et al. (2011) found that postfire management produced variation in habitat structure according to different levels of wood removal and the moist microhabitats provided by accumulated wood debris on the ground. In contrast, taxa occupying deep ground fissures may survive wildfire if associated with surface and buried rock accumulations, even though high intensity fires may eliminate most individuals in local populations, their microhabitat requirements, and primary food sources. As such, understanding mechanistic causes of this heterogeneous response is a conservation concern for the management of regional wildlife areas heavily affected by fire (Kiss and Magnin, 2002, 2003; Kiss et al. 2004; Santos et al. 2009; Driscoll et al. 2010).

Currently, there are ~113 species of terrestrial snails on the California Department of Fish and Wildlife Special Animal list (CDFW 2022; CNDDDB 2022). The Trinity bristle snail (*Monadenia setosa*) is the only land snail in California with a threatened listing. (CDFW 1972). This species is endemic to watersheds of the Greater Trinity Basin, Klamath Bioregion, northern California (Talmadge 1952; [Fig. 1](#)). It inhabits older growth stands of mixed conifer and woodland forests, and riparian corridors of high decadence and dense understories. These conditions characteristically include standing deadwood and down logs important in substrate stability and juvenile survival (Roth 1978). Accumulations of live individuals are found most frequently in deep accumulations of surface or buried boulders with well-developed subterranean structure, and internal spacing within a stable saxicolous matrix, or in association with large underground root systems (Sullivan 2022b).

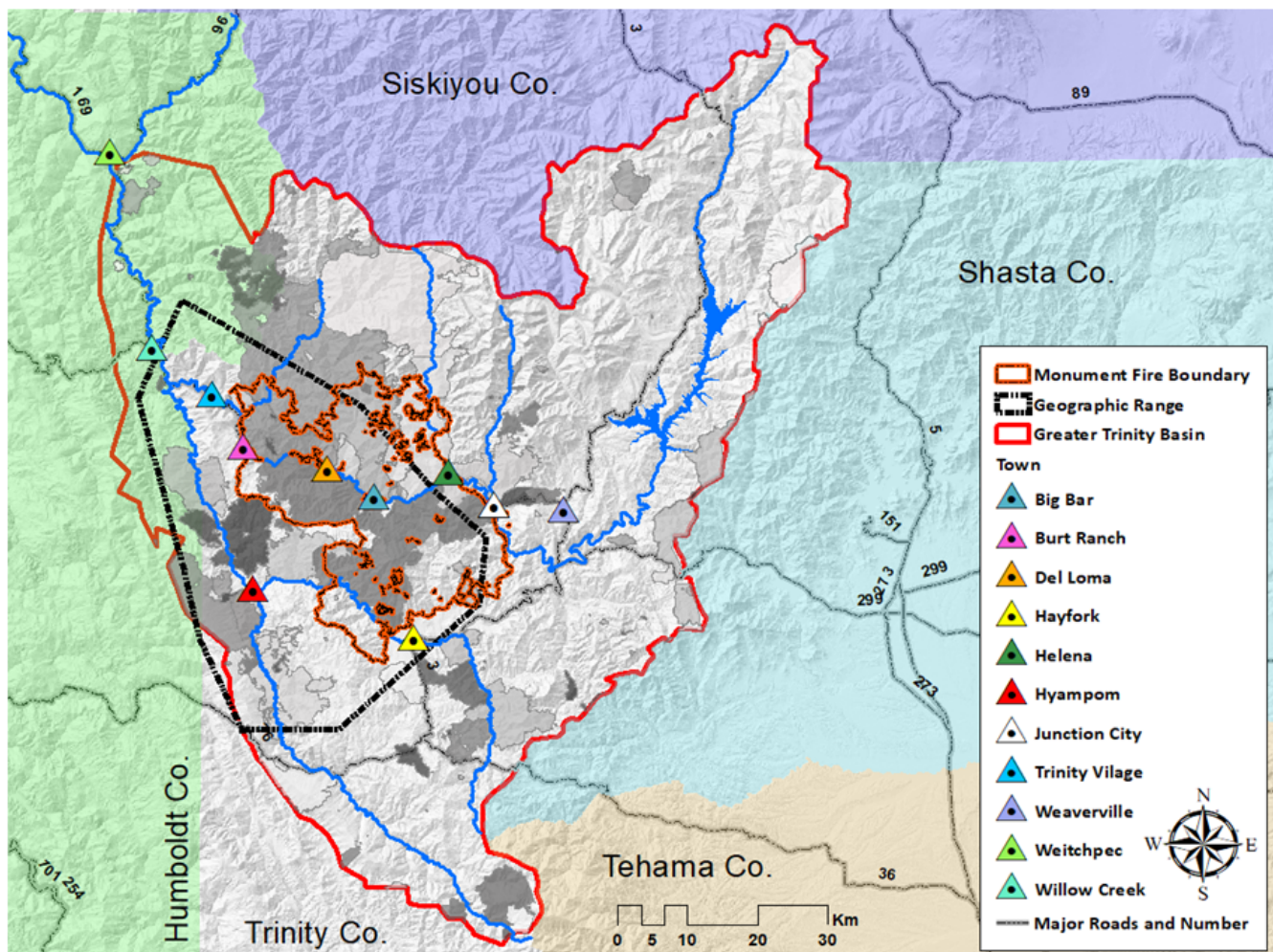


Figure 1. Study area showing historic fire scars colored shades of gray (years 2000–2018), boundary of the Greater Trinity Basin (745,817 ha), known geographic range of *M. setosa* (191,156 ha), and boundary of the Monument Fire in northern California.

The recent Monument Fire was the largest wildfire to impact the Greater Trinity Basin in the last 20 years ([Fig. 1](#)). It was caused by a lightning strike in the vicinity of the town of Del Loma near Monument Peak, Trinity County on 16 August 2021. As of 18 September 2021, the area encompassed by the Monument Fire was estimated to be 87,984 ha or ~ 46.0% of the geographic range *M. setosa*. At a macroscale, this fire provided a unique opportunity to assess the potential impacts of wildfire on categories of suitable macrohabitat for the Trinity bristle snail (Sullivan 2022a). Lack of knowledge about the degree of coverage by the Monument Fire at the ground level precludes a discussion of the extent of microhabitat loss to the species without ground-truthing, given both the heterogeneity of the fire behavior and the mosaic distribution of polygons of suitable macrohabitat. However, the extent of microhabitat loss due to severe soil burn can be approximated at the macrohabitat level by superimposing a recent Soil Burn Severity map (SBS) onto the original habitat suitability model (HSM) for the species.

Irrespective of protective status, no study has ever evaluated the impact of a high-severity forest fire on an individual species or a community of terrestrial mollusks at a landscape-level in California. Land snails constitute an excellent model to study the impact of fire and the subsequent patterns of re-colonization, because they are highly sensitive to fire and have low dispersal abilities (Baur 1986; Baur and Baur 1990; Hansson 1991). Moreover, implementation of post-fire restoration and pre-treatment of local populations with low intensity fire management are actions easily surveyed and monitored. As such, my objectives were two-fold. First, I assess the impact of the Monument Fire on the geographic distribution of hypothesized suitable macrohabitat of the species using GIS-based fire and soil burn severity shapefiles applied to subsets of a recent habitat suitability model (HSM; Sullivan 2022a). Second, I examine the differential extent and severity of burning to categories of preferred suitable macrohabitat at both landscape and watershed levels. This information should prove useful to resource managers in understanding and evaluating the potential impact and response of this species to wildfire given its unique biology and ecology (Sullivan 2021, 2022a, 2022b). My study also provides a knowledge base for post-fire restoration, conservation, and biological diversity assessments of molluscoid forest-dwelling faunas in this fire prone region of northern California (Driscoll et al. 2010; Dunk et al. 2004).

Methods

Study Area

My study area was located in part of the Klamath Bioregion centered on the Greater Trinity Basin watershed, which includes geographic regions throughout the northwestern segment of the Trinity River and its tributaries in Trinity and Humboldt counties. The geographic range of *M. setosa* is ~191,156 ha ([Fig. 1](#)). This area is 25.6 % (745,817 ha) of the area encompassed by the Greater Trinity Basin, 20.3% (830,725 ha) of the area encompassed by Trinity County, but only 20.6% (927,728 ha) of the jurisdictional boundary of Humboldt County. This segment of the Klamath Bioregion extends to south-central Trinity County. This area is dominated by Klamath montane forest of Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), tanoak (*Lithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*) cover-types; and interdigitates with montane coastal forest of the North Coast Bioregion (Welsh 1994). Watersheds within this bioregion are almost entirely within mountains, with the only level

land in a few narrow valleys (i.e., Weaverville Basin, Hyampom, and Hayfork valleys). These areas are dominated by mixed conifer and hardwood forest, riparian corridors of white alder (*Alnus rhombifolia*), big leaf maple (*Acer macrophyllum*), and various species of willow (*Salix* spp.). Upland environs are characterized by a deciduous hardwood understory of Pacific madrone, giant chinquapin (*Castanopsis chrysophylla*), tanoak, and canyon live oak (*Quercus chrysolepis*) cover-types.

Climate of this region is Mediterranean, with cool, wet winters and hot, dry summers. Annual precipitation over the Trinity River watershed averages ~1,400 mm. Precipitation ranges from 940 mm in lowlands (Weaverville and Hayfork) to as high as 2,200 mm (Barrett 1966). High rainfall combined with rugged geography results in extremely fast runoff and a high risk of flooding during winter storms. Soils are dominated by brown forest, gray-brown podzolic (i.e., acidic), and some immature soils, and Sierra-Nevada rock types (Mesozoic eugeosynclinal formations) intruded by Mesozoic granite (Welsh 1994). Large volumes of rocks and sediment carried by floods are spread along the rivers forming wide alluvial channels.

Data Collection

Field surveys focused on historical qualitative accounts of suitable habitat for the species based on documented occurrences (Talmadge 1952; Walton 1963; Roth 1978; Roth and Eng 1980; Sullivan 2022a). I sampled for active bristle snails during warm, wet, foggy, or rainy conditions during March to May and September to October 2008 and 2009. Typical microhabitat for this species included the surface of the soil, under objects large enough to accommodate a large (3.0–3.8 cm) adult shell (e.g., under boulders, slabs of thick sluffed-off bark from snags, dead wood, talus), on tree trunks and dead standing branches at the base of Pacific madrone and tan-oak root wads, and in other crevices with a well-developed organic soil base (Martin and Sommer 2004). I hand-picked snails in focal areas using the opportunistic visual search method, which was rapid (~30 min/per site) and entailed neither degradation nor soil removal (Gotmark et al. 2008; Raheem et al. 2008; Sullivan 2022b). Because land snails are dependent on microhabitat, different search images were required to prevent bias depending upon what substrate was encountered (i.e., boulder vs. tree vs. depression vs. flat ground; Fontaine et al. 2007; Cucherat and Demuynck 2008).

I derived model variables from descriptions of “suitable” habitat based on historical accounts for *Monodenia* spp. snails (Roth 1982; Roth and Pressley 1986; Duncan et al. 2003; Furnish et al. 1997). I used GIS-based landsat Visual Ecological Groupings (CALVEG; USFS 1981) and California Wildlife Habitat Relationships (CWHR; Airola 1988; Mayer and Laudenslayer 1988; Garrison et al. 2002) to assess geographic variation in forest type and stand structure (Parker and Matyas 1979; Goodchild et al. 1991; Sawyer and Keeler-Wolfe 1995).

A minimum mapping size of 2.5-ha pixels was used to contrast vegetation based on cover-type, vegetation type, tree cover from above, and over-story tree diameter. Non-forest abiotic environmental attributes were obtained from geo-rectified raster data sets for Northern California. Climate attributes were derived from the PRISM Climate Group (<https://prism.oregonstate.edu/>), and topographic variables (i.e., elevation and distance to nearest stream) were generated from 10-m digital elevation models ([Table S1](#)).

Partitioning the GIS-based Habitat Suitability Model

I used subsets of the original macrohabitat suitability model (hereafter referenced as “HSM”; Fig. 2) developed for *M. setosa* (Sullivan 2022a) to evaluate the impact of the Monument Fire on the geographic range of the species and affected watersheds. This HSM included collection of macrohabitat attributes at 333 sample sites, which were attached to 80,000 random points that encompassed the total range of the species. For comparative purposes, I partitioned the original HSM into areas encompassed by the Monument Fire (referenced as “Monument Fire HSM”; $n = 47,962$ ha) and areas not impacted by the fire (referenced as “Non-fire HSM”; $n = 59,951$ ha). This process allowed a comparison between fire- and non-fire impacted models for all environmental variables, categories of macrohabitat suitability, and SBS. The original HSM was developed using pre-fire CALVEG forest vegetation cover-type layers in combination with digital orthoquads of other environmental base-layers (ArcMap; ESRI 2022).

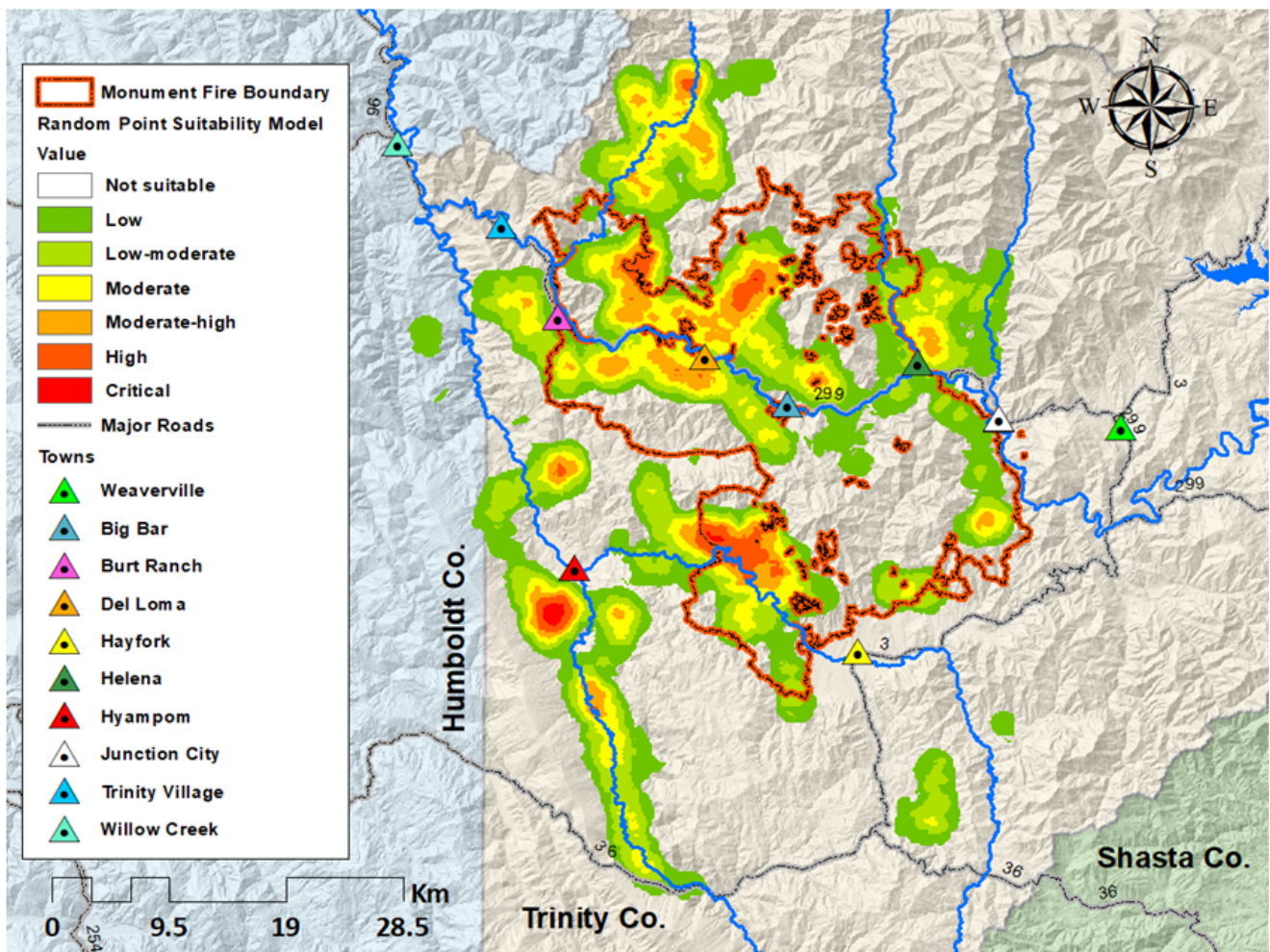


Figure 2. Map of the Monument fire (87,984 ha) superimposed upon the original landscape-level macrohabitat suitability model for *M. setosa* (HSM; 107,913 ha; Sullivan, 2021). The suitability model for the Monument Fire (Monument Fire HSM) encompasses the burn area within the boundaries of the original HSM. The non-fire suitability model (Non-fire HSM) includes all of the original HSM outside the boundary of the Monument Fire.

These variables were used as selection criteria in a GIS-based landscape-level HSM for the species to query vector-based polygons (shapefiles; Query Builder tool) throughout the range of the species. I used

point density surfaces, parameterized by theoretical point-density functions representing hypothetical limits, which defined a range of relative macrohabitat suitability. I then compared point density surfaces among HSM groups and burned watersheds. Six categories of macrohabitat suitability were identified: Low, Low-moderate, Moderate, Moderate-high, High, and Critical.

Soil Burn Severity

Raw SBS data (raster scale = 30 m) were converted to a polygon (vector) shapefile to assess the mosaic pattern of SBS in the Monument Fire-HSM (Raster-to-Polygon tool, ArcMap). These data were provided by the Burned Area Emergency Response Program (BAER 2022) and the United States Forest Service, Weaverville District (K. Bloomer, pers. comm.), and involved use of remote sensing imagery with field validated soils data to develop the final “best” fit SBS map. I approximated the degree of coverage at ground level by overlaying the SBS map onto the shapefile of suitable macrohabitat encompassed by the Monument fire. Categories of SBS in the layer included four levels: 1) Unburned-very low, 2) Low, 3) Moderate, and 4) High. Low SBS indicates only partial consumption of fine fuels while litter coverage remains relatively intact on the soil surface.

Moderate SBS indicates consumption and conversion to ash of nearly all soil cover and vegetative litter and fine fuels. High SBS indicates high intensity fire behavior coincident with longer burn time at the surface of the soil. Due to high heat, nearly all soil covered by vegetative litter and fuels is consumed leaving bare soil prone to the impacts of precipitation and resulting water runoff. Importantly, the SBS model only characterizes the effects of wildfire on the soil surface and below-ground. It does not assess the effects of mortality to vegetation or canopy alteration (Abele 2010). Changes in soil cover, water repellency, and soil physical and biological changes determine the level of severity in burnt soil. These environmental elements are critical to survival and viability of populations of terrestrial gastropods and other soil-dwelling invertebrates important in maintaining soil quality (Martin and Sommer 2004).

Statistical Analyses

I performed all analyses using R Statistical Software (R Core Team 2022) and set statistical significance at $\alpha < 0.05$. I evaluated univariate normality of all GIS-based environmental variables by use of the adjusted Anderson-Darling (AD.adj) statistic (Razali and Wah 2011). All tests for normality failed for both the fire HSM (AD = $< 1,801.0$ and > 55.0 , $P < 0.001$, $n = 4,668$) and the non-fire HSM (AD = $< 2,698.0$ and > 86.0 , $P < 0.001$, $n = 6,971$). Thus, I used nonparametric statistical tests to evaluate significance between each HSM for all environmental parameters. I used the Kruskal-Wallis non-parametric analysis of variance (ANOVA) rank sum test (χ^2) to evaluate the null hypothesis of no significant difference between subsets of the original HSM for each environmental parameter. I used Spearman's rank correlation (r_s ; 2-tailed test) to calculate the strength and direction of the relationship between any two variables whether linear or not (Corder and Foreman 2014). I used paired samples Wilcoxon signed rank (V) test (Rosner et al. 2006) to compare the proportion of combined perimeter (m) and ha metrics among categories of suitable macrohabitat between both partitions of the original HSM.

Because environmental data were not normally distributed, I used Generalized Linear Modeling (GLM; family = Gamma [link = “log”]; Nelder and Wedderburn 1972) to evaluate the relationship between each environmental variable and the six categories of macrohabitat suitability for both partitions of the original

HSM. I used a Poisson error-structure (family = Poisson [link = “log”]) with each GLM regression when comparing habitat affected by categories of both habitat suitability and SBS to graphically establish the relationship between the response variables (i.e., suitability and SBS) and smoothed functions of the predictor variable (i.e., ha of habitat). I used this error structure because data consisted of categories (i.e., suitability and SBS) and counts (ha). I used the residual deviance statistic (χ^2) to evaluate the difference between null and residual deviances to evaluate if the model was “useful” in fitting the data in each environmental subset assessed by GLM (i.e., $\text{pchisq} = \text{null deviance} - \text{residual deviance}$, with degrees of freedom [df] = number of predictor variables in the model (<https://www.statology.org/null-residual-deviance>)).

I constructed plots of the relationships among the six categories of macrohabitat suitability using linear discriminant function (DFA) analyses on log-transformed environmental variables for those attributes found to be significantly correlated with suitability criteria based on GLM analyses. DFA uses linear combinations of the predictors to create new axes for the final classification. DFA strives to find the linear combinations of the original environmental variable subsets (i.e., forest stand, monthly minimum and maximum temperature, precipitation) that gives the best possible separation between subsets of the original HSM dataset. This process maximizes component axes for class-separation and provides a visual assessment in 2-dimensional space of major variable-driven differences between each category of suitability for both partitions of the original HSM. I used confusion statistics (ConfusionMatrix function, Program “caret”; Accuracy and Kappa values) to assess the “fit” of the DFA model for each category of habitat suitability. Accuracy refers to the “success” rate of the model expressed as a percent. The Kappa statistic is a normalized statistic that compares the accuracy of the observed model to the accuracy of an expected random model; its value never exceeds 1.0.

Results

Comparison of Environmental Variables between Subsets of the HSM

The primary concentration of the Monument Fire occurred in the northeast section of the species range on both sides of the Trinity River, which included the southernmost sectors of tributaries of the North Fork Trinity River and New River near the confluence with the mainstem Trinity River. My analysis showed that the Monument Fire encompassed 44.5% (47,962 ha) of the total available area of suitable macrohabitat for the species (~107,913 ha). A comparison of the total ha within the CWHR cover-type classification found similar patterns in the proportion of each vegetation type between the Monument Fire and Non-fire partitions of the original HSM ([Table 1](#)). For each subset of the HSM the predominant vegetation type was Douglas fir forest followed by montane hardwood conifer, and Sierra mixed conifer, which was slightly more prevalent in the Monument Fire HSM compared to the Non-fire HSM ([Table 2](#)). Blue oak-foothill pine and montane hardwood were virtually nonexistent for each subgroup of the original HSM.

Table 1. Standard statistics based on ha of various vegetation types contained within the California Wildlife Habitat Relationship System (CWHR) cover-type Geographic Information System (GIS) layer for each subset of the habitat suitability model (HSM for the Monument Fire (MF) and the Non-fire (NF) HSMs.

Table 1a. Monument Fire HSM

Vegetation type	Polygon count	Min.	Max.	\bar{x}	n	%	SD	S²
Blue oak-foothill pine	52	0.1	14.3	1.5	77	0.7%	2.2	4.7
Douglas fir	2,131	0.0	57.3	2.8	5,912	55.1%	4.1	16.7
Montane hardwood conifer	1,783	0.0	38.5	1.8	3,137	29.2%	2.3	5.3
Montane hardwood woodland	23	0.7	8.7	2.6	60	0.6%	2.2	4.9
Sierra mixed conifer	679	0.0	21.5	2.3	1,541	14.4%	2.8	7.5
Total	4,668	—	—	—	10,728.70	100%	—	—

Table 1b. Non-fire HSM

Vegetation type	Polygon count	Min.	Max.	\bar{x}	n	%	SD	S²
Blue oak-foothill pine	50	0.0	5.2	1.1	53	0.4%	1.0	0.9
Douglas fir	3,664	0.0	46.0	2.1	7,820	60.0%	3.0	9.2
Montane hardwood conifer	2,642	0.0	25.8	1.5	4,042	31.0%	1.8	3.1
Montane hardwood woodland	13	0.4	8.6	2.1	28	0.2%	2.1	4.4
Sierra mixed conifer	602	0.0	16.1	1.8	1,100	8.4%	2.0	3.9
Total	6,971	—	—	—	13,042	100%	—	—

Table 2. Perimeter and area of suitable habitat categories for the Monument Fire (MF) and the Non-fire (NF) HSMs.

Suitability	MF Perimeter	MF Perimeter %	MF	MF ha %	NF Perimeter	NF Perimeter %	NF ha	NF ha %
Low	1,250,610	34.8%	18,576	38.7%	1,789,364	40.6%	27,209	45.4%
Low-moderate	1,001,335	27.9%	12,668	26.4%	1,337,894	30.4%	18,508	30.9%
Moderate	747,140	20.8%	9,100	19.0%	796,398	18.1%	9,312	15.5%
Moderate-high	403,232	11.2%	5,469	11.4%	324,685	7.4%	3,513	5.9%
High	154,146	4.3%	1,702	3.5%	96,437	2.2%	869	1.4%
Critical	38,254	1.1%	448	0.9%	59,098	1.3%	539	0.9%
Total	3,594,716	—	47,962	—	4,403,876	—	59,951	—

Results of the Kruskal-Wallis non-parametric ANOVA showed that 73.9% (n = 46) of all environmental attributes were significantly different between the two HSM subsets (**Table 3**). All metrics describing forest stand elements within the boundaries of the Monument Fire HSM had significantly larger values compared to the Non-fire HSM. Similarly, except for averaged monthly minimum temperatures in March and April, all other values were significantly warmer for the Monument Fire HSM compared to the Non-fire HSM. This pattern was also evident for the months of June, July, September, and October for averaged maximum monthly temperatures. For all other months averaged maximum temperatures were warmer within the Non-fire HSM. In average monthly precipitation the Monument Fire-HSM received significantly less precipitation in every comparison that was significant with the Non-fire HSM.

Table 3. Summary of mean values for each GIS macrohabitat variable and results of the Kruskal-Willis (KW) nonparametric analyses (df = 2) of variance for the Monument Fire HSM (n = 4,668) versus the Non-fire HSM (n = 6,971). Variables not significant different between subsets are not shown. CFA = cover from above, OTD = over-story tree diameter, DBH = diameter breast height; P = 0.5*, P = 0.01**, P = 0.001***.

Table 3a. Forest stand, stream, and elevation variables

Variables	Monument Fire HSM \bar{x}	Non-fireHSM \bar{x}	χ^2	P-value
1.Total tree CFA	78.4	76.3	70.0	0.001***
2. Conifer CFA	40.7	39.8	18.0	0.001***
3. Hardwood CFA	32.7	31.5	45.0	0.001***
4.OTD (DBH)	21.6	22.1	16.0	0.001***
5. CWHR size	4.0	3.9	36.0	0.001***
6. Elevation	803	794.2	10.0	0.01***

Table 3b. Average monthly minimum temperature (°C)

Variables	Monument Fire HSM \bar{x}	Non-fireHSM \bar{x}	χ^2	P-value
11. March	0.3	0.3	12.0	0.001***
12. April	1.5	1.5	12.0	0.001***
13. May	4.7	4.6	97.0	0.001***
14. June	8.0	7.9	155.0	0.001***
15. July	11.3	11.0	310.0	0.001***
16. August	10.7	10.3	323.0	0.001***
17. September	8.3	8.1	72.0	0.001***
18. Annual total	4.0	3.9	69.0	0.001***

Table 3c. Average monthly maximum temperature (°C)

Variables	Monument Fire HSM \bar{x}	Non-fire HSM \bar{x}	χ^2	P-value
22. January	8.3	8.5	293.0	0.001***
24. March	13.8	13.9	11.0	0.001***
25. April	17.2	17.3	14.0	0.001***
26. May	22.3	22.4	6.0	0.050*
27. June	27.5	27.5	7.0	0.020*
28. July	32.7	32.6	40.0	0.001***
30. September	29.2	29.1	52.0	0.001***
31. October	22.1	21.9	129.0	0.001***
32. November	12.2	12.4	231.0	0.001***
33. December	8.2	8.4	366.0	0.001***

Table 3d. Average monthly precipitation (cm) and total annual evapotranspiration.

Variables	Monument Fire HSM \bar{x}	Non-fire HSM \bar{x}	χ^2	P-value
35. January	199.4	219.6	1,563.0	0.001***
36. February	161	178.9	1,791.0	0.001***
37. March	151.5	169.5	1,844.0	0.001***
38. April	66.8	74.2	1,056.0	0.001***
39. May	33.7	36.7	699.0	0.001***
40. June	17.8	18.0	20.0	0.001***
43. October	78.1	82.7	465.0	0.001***
44. November	184.0	202.8	1,328.0	0.001***
45. December	208.2	228.6	1,394.0	0.001***
46. Evapotranspiration	1,147.6	1,257.5	1,353.0	0.001***

Comparison of Categories of Suitable Habitat between Subsets of the HSM

In both perimeter and area, the Monument Fire HSM had a somewhat smaller proportion of Low and Low-moderate suitability habitat, but a somewhat larger proportion of Moderate and High suitability habitat

than the Non-fire HSM ([Table 1](#); [Fig. 3A-3D](#)). Paired Wilcoxon signed rank exact tests showed no significant difference between HSMs in the proportion of suitable habitat categories when measurements of polygon perimeters and ha of habitat were combined in the paired comparison ($V = 34.0$, $P = 0.965$, $n = 12$); whereas pairwise correlations between categories were highly significant ($r_s = 0.980$, $P < 0.001$, $n = 12$).

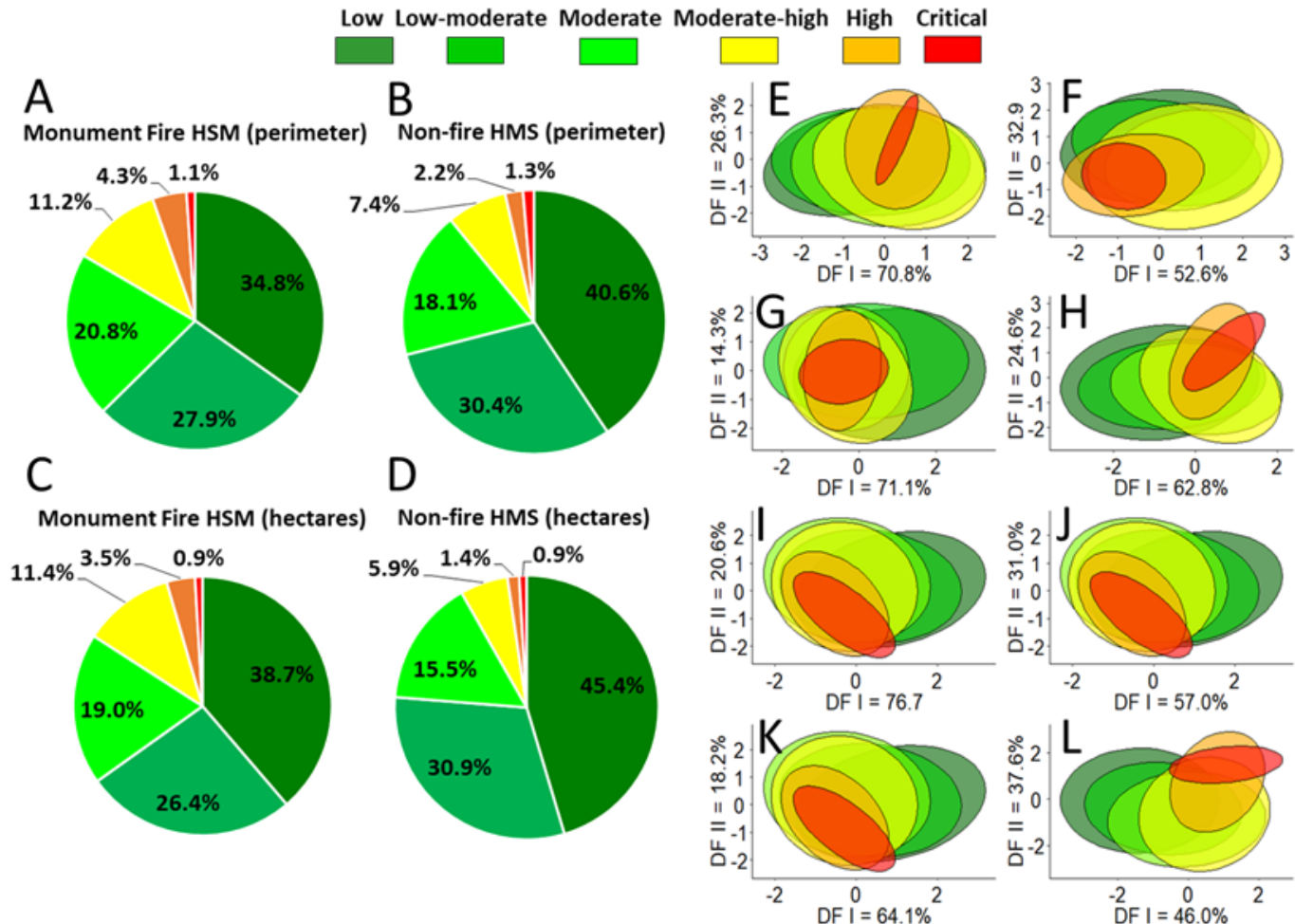


Figure 3. Pie diagrams showing proportional differences in GIS-based macrohabitat suitability categories (perimeter [m] and ha) between the Monument Fire (A and C) and Non-fire segments (B and D) of the original Trinity bristle snail macrohabitat suitability model (HSM). Linear discriminant function analysis (DFA) plots in 2-dimensional space of the relationship between categories of macrohabitat suitability in each set of log-transformed environmental variables for both the Monument Fire HSM and the Non-fire HSM. Individual forest stand attributes = E and I; averaged minimum monthly temperature = F and J; averaged maximum monthly temperature = G and K; and averaged monthly precipitation = H and L, respectively.

Comparisons among Categories of Habitat Suitability in Each Subset of the HSM

Mean values for High and Critical suitability values for each subcomponent of the original HSM were generally larger or smaller than any of the other macrohabitat suitability categories ([Table S2](#)). Among forest stand site attributes, GLM identified significant correlations between categories of suitability and

total tree CFA, overstory tree diameter, WHR size, elevation, evapotranspiration, and distance to the nearest stream ([Table S3](#)). Average monthly minimum temperature suitability was significantly correlated with the months of January and February, April through June, and September through annual averaged monthly values. Categories of suitability were significantly correlated with averaged monthly maximum temperature for the months of January and February, May through July, and October through annual averaged monthly values. For averaged monthly precipitation all months were significantly correlated with suitability, annual averaged values. In all GLM regressions the residual deviance statistic (i.e., χ^2 -P-value test) was significant, indicating that each regression model was “useful” in fitting the data in each subset of environmental attributes.

For both the Monument Fire and Non-Fire HSMs, forest stand characteristic and maximum monthly temperature explained the greatest amount of variation along DF I (70.8% and 76.7% versus 71.1% and 64.1%, respectively; [Table S4](#)). Along DF II the greatest amount of variation explained in the Fire HSM was for average minimum monthly temperature (32.9%) and forest stand characteristics (26.3%). For the Non-fire HSM it was average monthly precipitation (37.6%) and minimum monthly temperature (31.0%). Evaluation of the coefficients of linear discriminants (i.e., variable loadings) for DF I showed that for the Monument Fire HSM monthly: 1) evapotranspiration, 2) August, September, and annual minimum temperatures, 3) April maximum temperature; and 4) November precipitation had the strongest positive loadings on this discriminant vector, respectively. For the Non-fire HSM evaluation of variable loadings for DF I showed that: 1) elevation and average monthly, 2) annual minimum temperature, 3) maximum June temperature, and 4) November precipitation had the strongest positive loadings on DF I, respectively).

Subsets of environmental variables that were significantly correlated with suitability in the GLM regression analyses were used as input into the DFA plots of habitat suitability. Plots of the first two discriminate functions for both the Monument Fire HSM ([Fig. 3E-3H](#)) and Non-fire HSM ([Fig. 3I-3L](#)) showed that High and Critical macrohabitat suitability exhibited the least amount of variation along DF I and DF II. The extent of separation among categories of suitability graded from moderately negative to moderately positive along DF I for both subsets. Inspection of individual coefficients of linear discriminants and discriminant function plots showed that no environmental attribute definitively separated High and Critical from other categories of suitability at the 95% confidence level.

The greatest extent of overlap in variance occurred in Low, Moderate-low, and Moderate suitability, which encompassed the largest total acreages among categories of suitability for each HSM subset. Based on the 2-dimensional DF plots, the greatest separation between categories of both High and Critical suitability from other categories appeared to be in averaged monthly precipitation ([Fig. 3H and 3L](#)). For example, in the Fire HSM DF I (62.8%) was dominated by a positive November vs. negative September precipitation ratio; and DF II (34.6%) was dominated by a positive January versus a negative February-October precipitation ratio. For the Non-fire HSM DF I (46.0%) was dominated by a positive November vs. a negative annual-September precipitation ratio; and DF II (37.6%) was dominated by a positive December-September-April vs. a negative January-February precipitation ratio. This interpretation was also substantiated by the observation that the average monthly precipitation subset had somewhat higher Accuracy and Kappa statistics for both the Monument Fire (Accuracy = 36.4%, Kappa = 0.17) and Non-Fire HSMs (Accuracy = 40.2%, Kappa = 0.17) compared to other environmental data.

Soil Burn Severity

Of the 90,195 ha of the Monument Fire evaluated in the SBS model 19.7% (n = 17,765) had Unburned-very low SBS, 47.1% (n = 42,472) had Low SBS, 29.1% (n = 26,260) had Moderate SBS, and 4.1% (n = 3,662) had High SBS. These proportions were virtually identical to those found in the 47,942 ha of the SBS map that encompassed the Monument Fire HSM ([Fig. 4](#)). Unexpectedly in terms of total ha of habitat, my analysis showed that each SBS category had virtually the same proportional degree of soil burn on each category of suitability in the Monument Fire HSM ([Fig. 5A-5D](#)).

Watersheds Encompassed by the Fire and Impacted by the Soil Burn Severity

There were 48 watersheds burned by the Monument Fire-HSM ([Fig. 4](#)). Of the 81,115 ha contained within the boundaries of these watersheds 59.3% (n = 46,071) were affected by the fire to some degree ([Table S5](#)). Minors, Canadian, Lower Big French, Don Juan, Middle Big French, Bear, Big creeks, and Dinner Gulch watershed had the largest concentrations of High and Critical suitable habitat for the Trinity bristle snail. Whereas, Rowdy Bar, Italian (type locality of *M. setosa*), Mill 1, Manzanita, and Dutch creek watersheds had Moderate-high habitat suitability. Although not every watershed contained large acreages of suitable habitat the relationship between total ha in the watershed and total ha of suitable habitat was significant ($r_s = 0.820$, $P < 0.001$, $n = 48$).

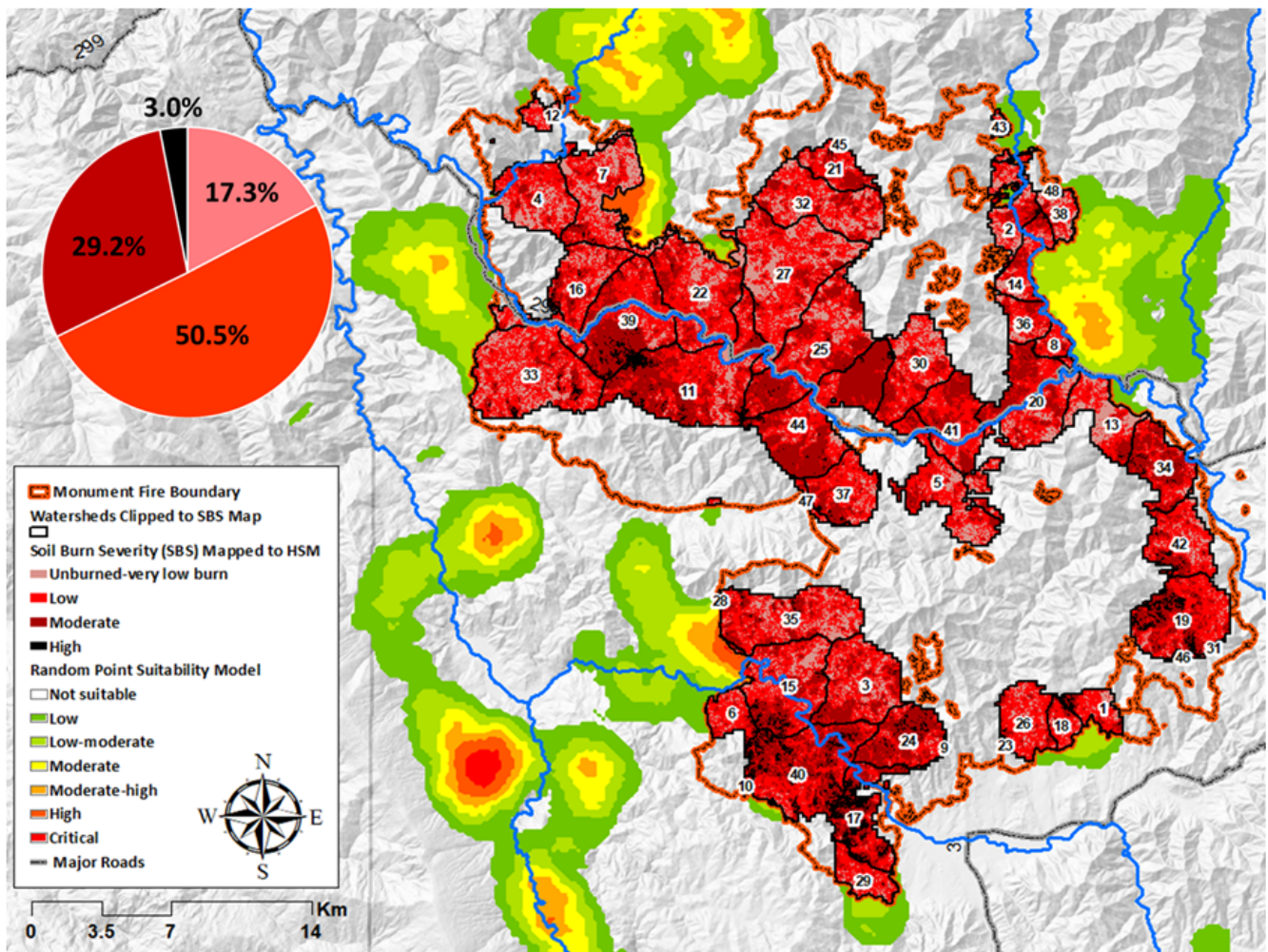


Figure 4. Map of the boundary of the Monument Fire showing the extent of the Soil Burn Severity (SBS) map that encompassed the Monument Fire HSM and impacted watersheds. Inset represents proportional differences in ha for each category of SBS. Numbers correspond to watersheds named in [Table S5](#) and [Table S6](#).

In general, the bigger the watershed the more likely it contained suitable habitat for the species. However, these significant relationships only held for Low to Moderate-high categories because in most watersheds there were few or zero ha of High or Critical suitable habitat even in the largest of watersheds ([Fig. 5E](#)). Also, each category of suitable habitat graded into each adjacent category in terms of total ha. For example, Low suitability was significantly correlated with Low-moderate suitability, Low-moderate suitability was significantly correlated with Moderate suitability, Moderate suitability was significantly correlated with Moderate-high suitability, Moderate-high suitability was significantly correlated with High and Critical suitability, and High suitability was significantly correlated with Critical suitability ([Table 4](#)).

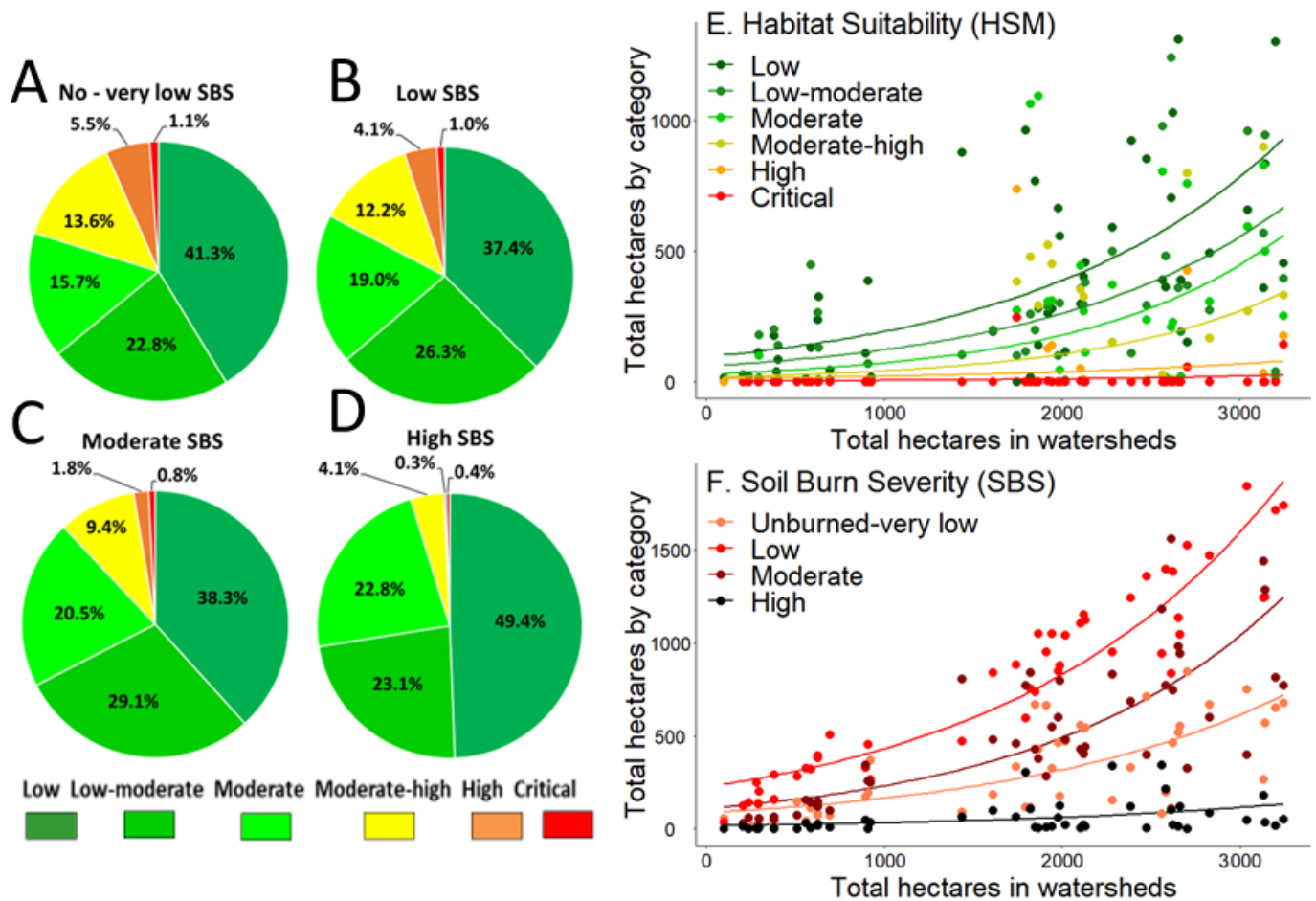


Figure 5. Figures A-D are the proportional relationships of the amount (ha) of various categories of suitable macrohabitat consumed by different levels of Soil Burn Severity (SBS). Results of Generalized Additive modeling (GLM) showing regressions between: E) total ha in watersheds versus total ha of each category of suitable macrohabitat in the same watersheds; F) total ha in watersheds versus total ha impacted by the Soil Burn Severity (SBS) as a result of the Monument Fire. Spearman rank correlations for each regression are found in [Table 3](#).

Table 4. Spearman rank (r_s) correlations between each pair-wise category of macrohabitat suitability (MS) and soil burn severity (SBS). Correlations are below the diagonal and P-values are above the diagonal; $P = 0.5^*$, $P = 0.01^{**}$, $P = 0.001^{***}$ (mod = moderate).

Category	Watershed ha	MS Low	MS Low-mod	MS Mod	MS Mod-high	MS High	MS Critical	SBS Unburned-very low	SBS Low	SBS Mod	SBS High
Total acres	—	0.001***	0.001***	0.001***	0.006**	0.300	0.298	0.001***	0.001***	>0.001**	0.006**
Low	0.650	—	0.031*	0.731	0.268	0.185	0.332	0.001***	0.001***	0.001**	0.104
Low-mod	0.590	0.310	—	0.001***	0.116	0.908	0.849	0.707	0.034*	0.001**	0.005**
Mod	0.480	-0.050	0.520	—	0.001***	0.135	0.466	0.222	0.019*	0.002**	0.084
Mod-high	0.390	-0.160	0.230	0.720	—	0.001***	0.024*	0.032*	1.015*	1.102	0.716
High	0.150	-0.190	-0.020	0.220	0.520	—	0.001***	>0.082	0.159	0.902	0.658
Critical	0.150	-0.140	-0.030	0.110	0.330	0.590	—	0.208	0.177	0.857	0.900
Unburned-very low	0.630	0.470	0.060	0.180	0.310	0.250	0.190	—	0.001***	0.932	0.199

Category	Watershed ha	MS Low	MS Low-mod	MS Mod	MS Mod-high	MS High	MS Critical	SBS Unburned-very low	SBS Low	SBS Mod	SBS High
Low	0.850	0.600	0.310	0.340	0.350	0.210	0.200	0.790	---	0.001***	0.146
Moderate	0.840	0.590	0.720	0.440	0.240	-0.020	0.030	0.250	0.580	---	0.001***
High	0.006	0.240	0.400	0.250	0.050	-0.070	-0.020	-0.190	0.210	0.600	---

The SBS map showed that Rusch, Dutch, Lower Big, Canadian, Little, Soldier, East Fork Big French, Rowdy Bar, and Baker creeks, and Drinkwater Gulch had the most ha impacted by the Monument Fire ([Table S6](#)). Here there was a significant relationship between total ha in the watershed and total acres of all categories of SBS ([Table 4](#); [Fig. 5F](#)). As in categories of habitat suitability, each SBS category also graded into each adjacent SBS class in terms of total ha of habitat affected. Unburned-to-very low burned soil was significantly correlated with Low burned soil, low burned soil was significantly correlated with Moderate burned soil, and Moderate burned soil was significantly correlated with Highly burned soil ([Table 4](#)). Ranked correlations between categories of suitable habitat and those of SBS revealed that ha of Low habitat suitability was significantly correlated with Unburned-very low, Low, and Moderately burned areas of SBS. Low-moderate and Moderate habitat suitability's were significantly correlated with Low, Moderate, and High areas of SBS. Moderate-high suitability was significantly correlated with Unburned-very low and Low burn areas of SBS. However, there was no significant relationship between ha of High or Critical suitability and any category of SBS ([Table 3](#)).

Discussion

Impacts of Wildfire and Soil Burn Severity on Habitat Suitability

My study showed that the Monument Fire engulfed a significant portion of the geographic range and suitable macrohabitat of *M. setosa* at both the landscape- and watershed-levels. This outcome was a function of both total acreage of suitable forest habitat and proportional differences in ha of habitat quality. Total area of forest cover-type vegetation and individual forest stand attributes impacted by the fire was not significantly different from areas that were not burned. Similarly, there were no significant proportional differences between burned and unburned areas in the categories of suitable macrohabitat (i.e., Low-Critical), and only minor differences in the percentages of forest cover-types. There were, however, significant differences in many environmental parameters measured at sample sites between unburned and burned subsets of the original HSM. These differences were a function of the geographic region encompassed by each subset of the original HSM. For example, the bulk of the Monument Fire HSM was located centrally along the northeast boundary of the species range. This region tends to be colder in the winter, and drier and warmer in the summer. By comparison, most of the Non-fire HSM included more southwestern regions of the species range characterized by more moderate temperatures and greater rainfall moving in a coastal westerly direction toward the boundary between Trinity and Humboldt counties.

As expected, the extent to which the fire affected basin watersheds was highly variable. The relationship between total area of the watershed and area of suitable macrohabitat in the Monument Fire HSM was driven by Low to Moderate-high categories of suitability. Low model efficiency, combined with the fact that other variables (i.e., loadings) also influenced the distribution of suitability categories in the 2-

dimensional DF plots. Lack of a precise distinction between suitability measures complicated the significance of individual attributes in each set of environmental variables in evaluating the importance and distinctiveness of the suitability criteria modeled. Delineation of watersheds with Moderate-high, High, and Critical macrohabitat suitability provides new knowledge and identification of specific watersheds likely to be most important in post-fire inventory and conservation of the species, particularly as delineated in the analysis of SBS.

I also found significant correlations between levels of SBS and categories of macrohabitat suitability. Overlaying the SBS map onto the Monument Fire HSM revealed that the most extensive areas of soil burn (i.e., Low and Moderate SBS) occurred in areas of Low to Moderate-high habitat suitability. Low SBS generally equates to areas of partial consumption of fine fuels, while litter coverage remains relatively intact on the soil surface. Whereas Moderate SBS typically corresponds to areas in which nearly all soil cover of vegetative litter and fine fuels were consumed or converted to ash (BAER 2022). Conversely, there were few areas of High to Critical habitat suitability affected by high levels of soil burn (i.e., high heat and long burn time). The mosaic burn pattern in High to Critical habitat suitability was a direct function of the small area encompassed by these two “high quality” habitat categories exacerbated by their highly fragmented and widely dispersed geographic distribution. Further, these areas are mostly separated by major topographic and riverine discontinuities in the Greater Trinity Basin; a pattern supported by recent molecular and phylogenetic analyses of *M. setosa* from throughout its geographic range (Sullivan 2021). Importantly, as with most forest wildfires, it is generally not known to what extent the area and mosaic pattern of soil burn reflected in post-fire SBS maps are a function of regional topography, vegetative characteristics of the landscape, and climate, or the direct anthropogenic actions of fire suppression.

Impacts of Wildfire on Communities of Terrestrial Gastropods

Land snails that occupy layers of forest litter and duff with little or no protection from surface or buried saxicolous habitat are highly vulnerable to fire and changes to their microhabitats (Burke et al. 1999). Bros et al. (2011) found that postfire management produced variation in habitat structure according to different levels of wood removal related to the moist microhabitats provided by accumulation of wood debris on the ground (i.e., trunks, logs, stumps; [Appendix IA and IB \(PDF\)](#); see [Sullivan 2022b](#) [Fig. 4 and Appendix 5]). In contrast, taxa that occupied deep subsurface rock-laden fissures or root-wads of large conifer or hardwood trees (i.e., Pacific madrone, tanoak) withstood surface fire to a much greater degree than species that inhabit shallow leaf litter augmented by large woody debris (Burke et al. 1999; Bros et al. 2011; Gaines et al. 2011). For saxicolous species this applies even though high intensity fires may eliminate most individuals in local populations, and their microhabitat requirements and primary food sources. A subsurface rock-dwelling life history strategy is particularly true of *M. setosa*, in which the most abundant concentrations of individuals generally occupy shady mesic forest conditions that include buried boulder fields and stable slopes ([Appendix IC \(PDF\)](#)). Therefore, understanding the mechanistic causes of these varied responses by terrestrial gastropods is a conservation concern for the management of regional wildlife areas heavily affected by fire (Kiss and Magnin 2002; Santos et al. 2009; Driscoll et al. 2010).

Indeed, excavations of rocky habitat within mesic forest conditions often revealed the presence of live active or estivating snails (and shells) within the spacious and humid catacombs of their subterranean “niche.” Within these moss-covered boulder fields estivating snails and accumulations of empty shells

have been found as deep as 1 m underground (see [Sullivan 2022b](#) [Fig 6]). Habitation at this depth requires spaces that enabled large-shelled adults to migrate from deep within the recesses of boulder piles and to surface when moisture conditions permitted emergence. Thus, rock matrices may offer Trinity bristle snails protection even from high intensity surface burns, which make specimens less vulnerable to fire and changes to their critical subsurface habitat compared to species that live only amongst forest litter and large woody debris found on the forest floor.

Still, for all forest-dwelling terrestrial gastropods the effect of high levels of soil burn typically destroys (i.e., converts to ash) most vegetative cover, root systems, litter, fine soil fuels, and minerals down to several centimeters deep in the soil (BAER 2022). This process creates bare soil predisposed to the impacts of precipitation and subsequent water runoff and represents the most severe direct and indirect impacts to communities of soil-dwelling terrestrial snails. Modification of water repellency is a much-discussed fire effect because repellency is a natural soil property. Removal of leaf litter, in combination with vegetative cover, frequently results in compaction of soil surface, and alteration and potential destabilization of slope. As evidenced by Driscoll et al. (2021), high intensity fire can increase the severity and the thickness of the water repellent soil which has significant effects to post-fire water runoff in fire-prone areas.

Post-fire Colonization and Dispersal

Endemic populations of *M. setosa* have a geographic distribution within the Greater Trinity Basin that is highly fragmented topographically, hydrologically, and ecologically (Sullivan 2021 and 2022a). Regional landscape diversity in combination with small population size and low vagility act to restrict gene flow among relic populations. Recent molecular DNA analyses show that these attributes have functioned to facilitate allopatric differentiation leading to elevated levels of taxonomic diversity at the subspecies level (Sullivan 2021). This metapopulation structure of isolated subpopulations may result in altered population dynamics and over the millennium, has undoubtedly caused localized extinction. Colonization of post-fire habitat in mixed conifer forest and riparian ecosystems by relic populations of this species will likely proceed from the distribution of permanent subterranean accretions of large boulders and stable talus in combination with the spatial mosaic of unburned suitable habitat.

For example, densely vegetated areas are expected to create longer burn times, more intense heat, and greater subsurface soil penetration. This process creates a fine-scale mosaic across the landscape in which scattered land snail refugia are present as a result of both the widely distributed mosaic of subsurface rock and as a function of the mosaic pattern of fire behavior, intensity, burn time, and density of vegetation at the soil surface. Kiss and Magnin (2006) and Gongalsky (2011) described similar life-history survival strategies in snails occupying xerophilous boulder ecosystems of the Mediterranean and the Black Sea coast of the Caucasus, which led to lower intensity burns in those areas and higher snail survival. For *M. setosa* post-fire populations appear highly dependent upon post-fire habitat structure, fire behavior, and the pre-fire distribution of refugial subsurface habitat reflected in the geological and forest ecosystem site histories within the basin.

Suggestions and Recommendations for Post-fire Restoration

Restoration of natural wildfire regimes through fuels reduction and post-fire restoration has emerged as a prime management objective for forests prone to high severity burns within the interior western United

States (Huff et al. 2005). Yet such actions are not without their detractors when ostensibly in conflict with ecosystem approaches to conservation of listed, rare, or endemic taxa (Prather et al. 2007; Gaines et al. 2011). Huff et al. 2005 note that land management policies that accelerate fuel reduction using low intensity prescribed burning (e.g., light understory thinning of trees, removal of invasive shrubs; Biswell 1989; Gilliam et al. 2018) are currently being employed with limited scientific information on the ecological consequences for terrestrial animal species throughout the Pacific Northwest (Wright and Agee 2004; Hessburg et al. 2005, 2007). While studies of the effects of wildfire in forest ecosystems on vegetation communities are somewhat abundant for the Klamath Bioregion, research on the impacts of natural fire and prescribed burning on terrestrial gastropods is virtually nonexistent (Agee 2001; Dunk et al. 2004; Severns 2005; Halofsky et al. 2011; Ray and Bergey 2015; Collins et al. 2019; Brand et al. 2020).

Use of GIS-based fire, SBS, and debris-flow maps developed at the scale of drainage basins and stream segments may enable better identification of potential post-fire flashflood debris flows. This methodology is particularly relevant for use in areas of High to Critical suitable habitat (USGS 2022). For *M. setosa*, the spatial distribution of post-fire populations depends largely on post-fire habitat structure created by scattered refuges as a function of the spatial heterogeneity of the burn and the montage pattern of scattered refuges. Because detection of these subsurface enclaves will prove difficult to locate, increased planning and survey effort via ground-truthing will be required prior to and after prescribed burning, and for post-fire monitoring and mitigation (Hylander 2011). This methodology also applies to communities of terrestrial gastropods when assessing regional or forest-level mollusk biodiversity (Kiss and Magnin 2002). Thus, future post-fire evaluation, inventories, and research into subpopulations will require: 1) documentation of direct fire mortality on individuals and local population abundance; and 2) evaluation of the response of local populations to the effects of opening up the matrix of suitable habitat (i.e., vegetation), which alters fundamentally the levels of light and humidity essential for survival and long-term viability of populations over the next decade.

Across the landscape, fuel treatments that create firesafe conditions for rare or listed terrestrial snails may include a number of specific actions. For endemic populations of *M. setosa* the most important range-wide conservation actions include: 1) application of low intensity prescribed burning that will create a mosaic of burn conditions (i.e., small and unburned areas < 50 m²), which generally are not hot enough to kill individuals buried underground in their subterranean niches; 2) avoidance of areas of large moss-covered boulders in burning prescriptions that contain or potentially harbor *M. setosa* and their moist critical microhabitat; and 3) implementation of burns when snails are hibernating, preferable at or below freezing temperatures.

Conclusions

Understanding how special status species respond to both natural and anthropogenic perturbations in a heterogeneous landscape is vital to efficient implementation of future conservation strategies given the expectation that of future climate change will increase the frequency and extent of wildfire (Sanderson et al. 2002; Deguise and Kerr 2006). Understanding the mechanistic causes of this heterogeneous response is a conservation concern for the management of wildfire prone forests and the species that inhabit the Klamath Bioregion (Driscoll et al. 2010; Santos et al. 2009). Here, I present resource and land planners with a landscape-level perspective documenting the extent and potential impact of a major high-severity forest fire on the geographic range and differential extent of burning of suitable for *M. setosa*. This

analysis should prove useful at the watershed level in the development of post-fire surveys, future research, restoration, and conservation strategies given the unique ecology and life history strategy of this endemic species. Results may also serve as a template for evaluating biological diversity in other terrestrial gastropod communities with similar ecologies potentially threatened by wildfire and other anthropogenic habitat degradation within the Klamath Bioregion of northern California.

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