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Notes from the Editor

The winter issue for 2022, the first of the year, is coming a bit late due to the retirement of my longtime layout editor (see my Notes from the Editor in issue 107-3 for more info). But thankfully, due to the willingness of some amazing CDFW employees, I now have the help I need to complete layouts for the Journal.

This issue contains six excellent articles on topics varying from elk to snails to fish and fire. The first article, a joint venture between UC-Davis and CDFW scientists, explores an approach for estimating the abundance of tule elk using spatially explicit capture-recapture (SCR) models combined with a less time-intensive single-visit survey to collect fecal pellets. The authors compared this single-visit approach to an earlier multi-visit survey and found that it worked well given the high density of elk in a concentrated area. The next two articles cover the use of both macro- and micro-habitat suitability models for the Trinity bristle snail. Dr. Sullivan, a CDFW scientist, discusses the results of his modeling for the management of these endangered snails. Articles four and five provide important information on the population density and habitat of the San Pedro Mártir rainbow trout and the status and distribution of Arroyo chub, respectively. The issue concludes with a study that examined machine learning to understand patterns of burn severity from a complex of fires that occurred in the Diablo Range of northern California in 2020.

We have two new and one leaving Associate Editor this issue. We are losing a long-time editor, Neil Clipperton. Neil has worked as a biologist for CDFW since 2006 and has served as California's statewide bird conservation coordinator since 2013. He has collaborated with conservation partners through leadership on interagency teams, technical working groups, and policy teams, including the Pacific Flyway Council, Central Valley Joint Venture, and Tricolored Blackbird Working Group. Neil has worked with Department staff across the state to identify high priority monitoring and research needs, secure funding for project implementation, and collaborate with research partners. He has also conducted status reviews for bird species petitioned for listing under the California Endangered Species Act (CESA), led policy development for birds in California, consulted on management of special status bird species, and ensured large-scale conservation plans adequately consider the needs of birds. Neil recently accepted a new position in the Department as the supervisor of a new CESA Conservation Unit in the Wildlife Branch. Neil served as an associate editor for five years.

Replacing Neil as our non-game bird expert is Matt Toenies. Matt is an Environmental Scientist in CDFW's Wildlife Diversity Program and Cannabis Program. In 2014, he received a B.S. in Natural Resources–Wildlife Management from the University of Minnesota in Crookston. He then completed a M.S. in Ecology at Penn State University in 2017, where he researched shifts in avian community composition following die-off of eastern hemlock forests due to non-native insect invasion. Before joining CDFW, Matt worked in a variety of wildlife positions with diverse taxa, including mammals, waterfowl, herpetofauna, and passerines. In his two years with CDFW, he has worked with his team to develop methods for efficient bird and herpetofauna monitoring and data processing using recent technological

advances and machine learning-based species identification. Matt has coauthored papers on research conducted both outside and within his CDFW work and has served as a reviewer for other researchers' manuscripts. He is excited to be joining as an Associate Editor for the California Fish and Wildlife Journal.

Also joining the Journal staff is Mark Gard. Mark is a Senior Hydraulic Engineer in the Conservation Engineering Branch, specializing in fish passage, hydraulic modeling, and anadromous salmonid habitat restoration. Mark has a BS and MS in Civil Engineering and a PhD in Ecology, where he studied conservation of native fish in the South Yuba River. Prior to joining CDFW, Mark was a Fish and Wildlife Biologist with the U.S. Fish and Wildlife Service, working on instream flow studies, including collecting data for and developing habitat suitability criteria, and monitoring habitat restoration projects. Mark has published 20 articles in peer reviewed journals, largely focusing on habitat modeling of anadromous salmonids and fish passage assessments.

The Journal will have two special issues this year, both covering the proceedings of earlier conferences. The first will be the proceedings of the 14th Biennial WAFWA Deer and Elk Workshop. The Workshop brings together biologists from governments, universities, tribes, non-governmental organizations, and beyond to share research and discuss common challenges to conservation of deer and elk across western North America. Information shared during this biennial meeting is invaluable to conservation and management. This special issue will serve as a conduit for archiving the important work, discussions, and scientific advances shared during the Workshop. The other will cover the recent biennial CDFW Science Symposium—a conference for CDFW scientists statewide to share and discuss the research being conducted throughout the organization. The proceedings will serve to chronicle the important research, discussions, and scientific advances shared during the Symposium as well as provide this information to those outside of CDFW so the public can see the amazing work that CDFW scientists accomplish.

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RESEARCH NOTE

Testing a single-visit sampling approach for fecal DNA abundance estimation of tule elk in the Lake Pillsbury Basin

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Key words: abundance estimation, capture-recapture, *Cervus canadensis nannodes*, tule elk

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Estimating abundance (*N*) in ungulate populations is fundamental to their management. Fecal DNA provides a noninvasive basis for estimating *N* in ungulate populations through capture-recapture-based methodologies (Brinkman et al. 2011; Lounsberry et al. 2015). Most recently, application of spatially explicit capture-recapture (SCR) methods have proven especially powerful, particularly in more solitary species such as deer (*Odocoileus* spp.; Brazeal et al. 2017; Furnas et al. 2020). These SCR methods also appear relatively robust to spatial clustering in more gregarious species such as elk (*Cervus canadensis*), particularly when both sexes are incorporated into models (Batter 2020; Bischoff et al. 2020). On the other hand, some populations of elk congregate at especially high densities, particularly females (i.e., cow groups). Elk aggregations can become even greater during the mating season (the "rut"), when bull elk, typically sexually segregated, join cow groups to compete for mates (Bowyer 2004; Weckerly 1998) providing an opportunity to estimate their group sizes with less time-intensive non-spatial approaches (Mena 2019). Large numbers of samples also can be collected in a single visit, which, if analyzed appropriately, may provide a more efficient means of estimating *N* than multi-sample non-spatial or SCR approaches.

In the present study, we tested such a non-spatially explicit single-visit approach (hereafter, single-visit) to estimating tule elk (*C. c. nannodes*) abundance at Lake Pillsbury, California, where females occur at very high density year-round, almost exclusively within a 5-km^2 basin (Batter 2020). The Lake Pillsbury Basin (hereafter, the Basin) is located in Lake County, California (39.450, -122.956) and encompasses a discrete patch of suitable tule elk habitat composed primarily of grassland, lacustrine, and mixed hardwood habitats at approximately 270 m above sea level surrounded by less hospitable (to tule elk), higher elevation coniferous forest (Batter 2020). Although the range for males of this population extends well beyond the Basin, high densities of bull elk are routinely

observed engaging in rut activity within the Basin during Sept–Oct yielding the greatest aggregate group sizes. We therefore conducted a single-visit survey in the Basin during the rut to determine if abundance estimates of congregated elk were comparable to those generated from a range-wide (i.e., encompassing both sexes year-round) SCR estimate prior to the rut (Batter 2020).

We compared abundance estimates derived from the present single-visit survey to an independent one from an SCR study conducted earlier the same year (Jun–Aug) over a much wider spatial extent (189 km^2) that included the 5-km^2 Basin (Batter 2020). We also examined overlap between the two studies (i.e., single-visit and SCR) in detections of both female and male individuals to verify that females were comprehensively sampled within the Basin and to investigate the extent to which males may have been under-sampled by restricting our single visit survey to the Basin.

Five personnel conducted a single-visit survey on 14 October 2019 within the Basin, which involved collecting fecal pellets along transects through randomly selected plots (Fig. 1). Specifically, we divided the Basin into 150 250-m × 250-m sample plots and randomly selected 57 of them (approximately 40%) for sampling. We began sample transects at the mid-point of each plot's northern or southern boundary and traversed through the plot centroid, ending at the mid-point of the opposite edge (Brazeal and Sacks 2021). We stored fecal pellets in >95% ethanol prior to laboratory analysis. We analyzed fecal DNA using 20 microsatellites and a sex marker and assigned genotypes to individuals as described previously (Sacks et al. 2016; Batter et al. 2021). Because samples were collected in a single visit, we opted to use an urn model implemented in program Capwire to estimate N for capture-recapture data (Miller et al. 2005). We employed the likelihood ratio test in Capwire to select between the two innate rates model (TIRM), which allows some individual variation in detection probability, and the equal capture probability model (ECM), which does not. Methods used in the earlier SCR study were detailed elsewhere (Batter 2020). Briefly, we established 11 transects (4–6 km each) throughout the known range of the Lake Pillsbury population (189 km^2) based on random selection of 4-km^2 plots stratified by habitat quality; sample processing and genetic identification were conducted the same as for the single-visit survey.

We collected 280 pellet groups during the single-visit survey, from which 151 samples (54%) were successfully genotyped. Although this overall success rate was relatively low, the figure masked a spatial heterogeneity that ranged from <20% in the northern portion of the Basin to >80% success in the southern portion of the Basin, closer to the lakeshore (Fig. 2). During the day of sampling, we only observed elk on the southern edge of the basin, where we also experienced the highest genotyping success, suggesting the fecal pellets collected there tended to be fresher than those collected to the north. Because genotyping success is highest in fresh samples, restricting sampling to locations where elk are observed immediately prior to sampling could increase the efficiency of future single-visit surveys. The success rate in a fecal DNA study of Roosevelt elk (*C. c. roosevelti*) in northern California that sampled pellets only from locations in current use by telemetered individuals was 82% (Mena 2019), which is comparable to ours in the southern portion of our study area.

The 151 genotypes obtained from our single-visit survey included 103 from females (67 individuals) and 48 from males (30 individuals). Using the recapture profiles of the 103 genotypes of 67 females, a likelihood ratio test implemented in Capwire indicated a better fit of the TIRM over the ECM, which resulted in an estimate of $N = 159$ females (95% CI: 106–189) in the Basin. This estimate was statistically indistinguishable from the spatially more extensive SCR estimate of female abundance for the Lake Pillsbury population (136 females, 95% CI: 100–172; Batter 2020). The concordance of these estimates, which were based on independent samples and methods of analysis with different assumptions, supports their general accuracy for estimating female elk abundance

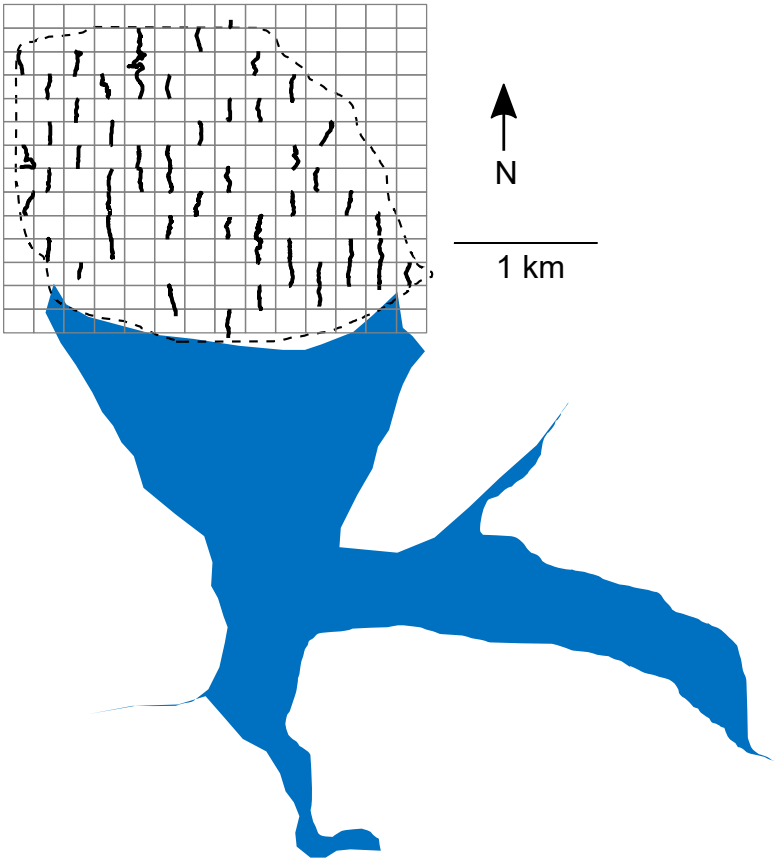

Figure 1. Sampling grid (grey) superimposed over the Lake Pillsbury Basin (black dashed polygon) in Lake County, California, USA, showing 57 transects in randomly selected plots sampled during a single-visit survey (14 Oct 2019).

in the Lake Pillsbury population. Using the recapture profiles of the 48 genotypes of 30 males, the likelihood ratio test similarly indicated a better fit of the TIRM over the ECM. In contrast to females, however, the abundance estimate for males in the Basin ($N = 71$, 95% CI: 41–96) was less than half that of the SCR estimate for the entire Lake Pillsbury population (148 males, 95% CI: 108–187; Batter 2020). Thus, our findings suggest that the single-visit survey was not appropriate for estimating the population abundance of males.

To further verify these conclusions, we investigated overlap in detections of individuals between the two studies (single-visit, SCR). The spatially broader SCR survey yielded a similar number of fecal pellet genotypes ($n = 155$), including 97 from females (49 individuals) and 58 from males (30 individuals) (Batter 2020). Based on 200 fecal genotypes from females sampled in the two surveys combined, all 85 individuals (100%) were sampled at least once in the Basin (Fig.3). Only two females were sampled outside the Basin during the SCR survey (one 4 times, the other 2 times), and both were additionally sampled within the Basin during the single-visit survey. Thus, the spatially broader SCR survey did not improve on the sampling of females over the single-visit survey restricted to the Basin, suggesting the latter approach was representative of the entire female population (i.e., sampling the Basin alone did not result in systematic under-detection of females). The single-visit survey restricted to the Basin also resulted in >70%

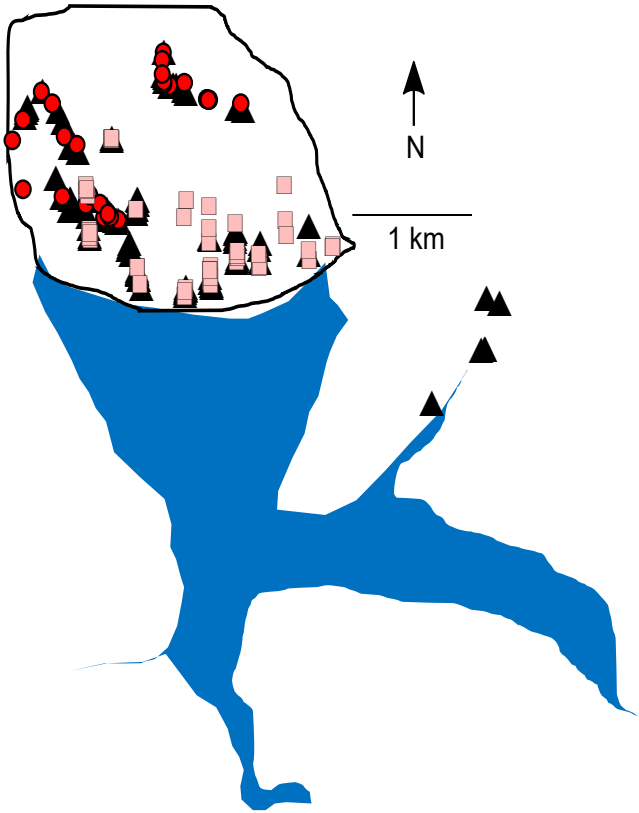

Figure 2. Locations of 280 elk fecal pellet groups (filled black circles) collected on 14 October 2019 from Lake Pillsbury Basin, Lake County, California, USA, superimposed upon an interpolated surface representing genotyping success. The high spatial heterogeneity in genotyping success rates presumably reflects recency of elk deposition of fecal pellets. The freshest elk pellets associated with highest genotyping success rates tended toward the south of the Basin, whereas older elk pellets associated with lowest genotyping success rates tended toward the north of the Basin. Interpolation was based on ordinary kriging using a variable search radius to include the 30 nearest fecal pellet groups.

more individuals sampled, suggesting it was more efficient than the broader SCR survey at sampling the female component of the population.

In contrast to females, however, many of the 106 fecal genotypes sampled from 51 males in the two 2019 surveys combined were of individuals sampled only outside the Basin during the SCR survey (Fig. 4). Of the 30 males sampled during the SCR survey, 15 were sampled only outside the Basin, 12 were sampled only within the Basin, and 3 were sampled both in and out of the Basin (1 male was sampled in both locations during SCR surveys). Of the 30 males sampled during the single-visit survey, 9 had been previously sampled during the SCR survey, and only 2 of these had been sampled outside the Basin. Thus, both abundance estimates and distributions of individual detections between the two studies indicate that for males the single-visit survey of the Basin was not representative of the broader population.

To the extent that monitoring of the female segment of the population is desirable, our results suggest that the single-visit survey protocol can substantially increase the efficiency of efforts to monitor the female component of the Lake Pillsbury Basin population. This approach was effective for this particular population because females

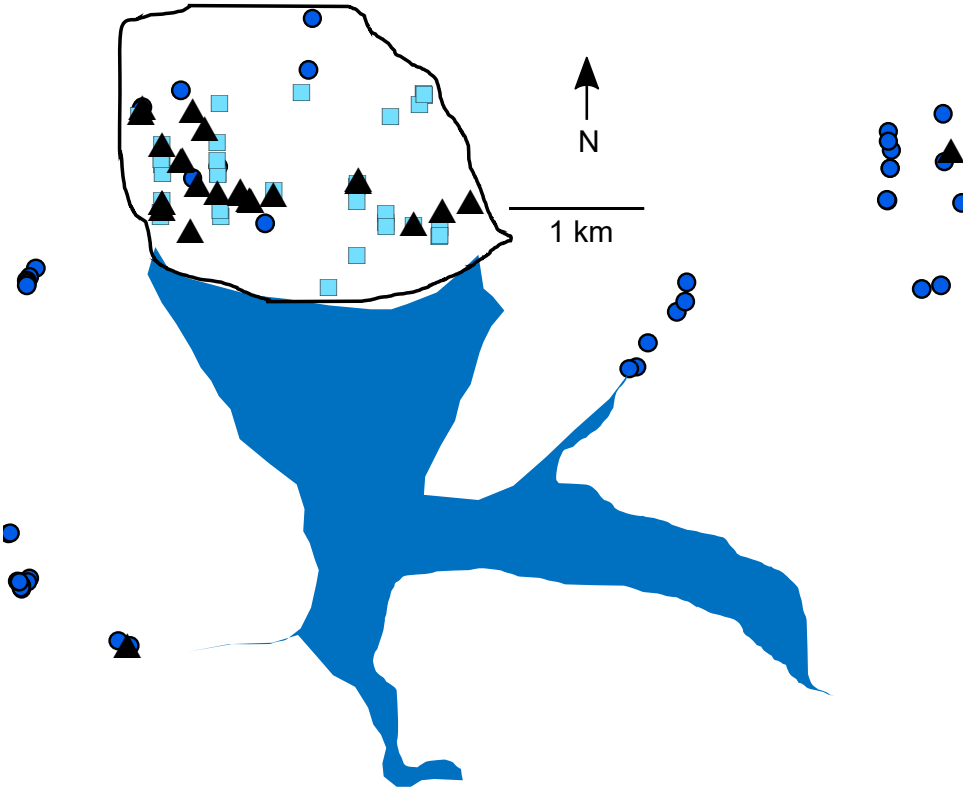

Figure 3. Successfully genotyped female tule elk pellets (n = 200) sampled from the Lake Pillsbury population, Lake County, California, USA, during the SCR survey (1 Jun–31 Aug 2019) throughout the range and the single-visit survey (14 Oct 2019) concentrated in the Lake Pillsbury Basin (circumscribed by black line), indicating samples from individuals that were sampled only during the SCR survey (red circles), only during the single-visit survey concentrated in the Lake Pillsbury Basin (light red squares), or during both surveys (black triangles), indicating that all females were sampled at least once in the Basin.

congregate in a single location, rather than being distributed across multiple spatially separated cow groups, as, for example occurs to the southeast in the Cache Creek population (Batter 2020). Thus, where efficiency is paramount and estimation of females alone is sufficient, this approach may be gainfully applied to other populations where females are concentrated in dense aggregations over relatively small spatial extents, such as the Potter Valley and Little Lake Valley tule elk populations in neighboring Mendocino County. We caution, however, that this approach would have been inappropriate for males in the Lake Pillsbury population and likewise would be inappropriate for other populations where the sampling site cannot be reasonably assumed to include all individuals during the sampling period.

In the present study, we opted to conduct a single-visit survey to estimate tule elk abundance in a high-use concentrated area necessitating a one-sample method of analysis, in our case use of Capwire. Although the approach worked well in the present case for the female population segment, protocols based on multiple surveys could also be used if desired to enable use of traditional multi-session methods such as the Huggins closed capture model (Huggins 1989; Mena 2019). Spatial capture-recapture models also

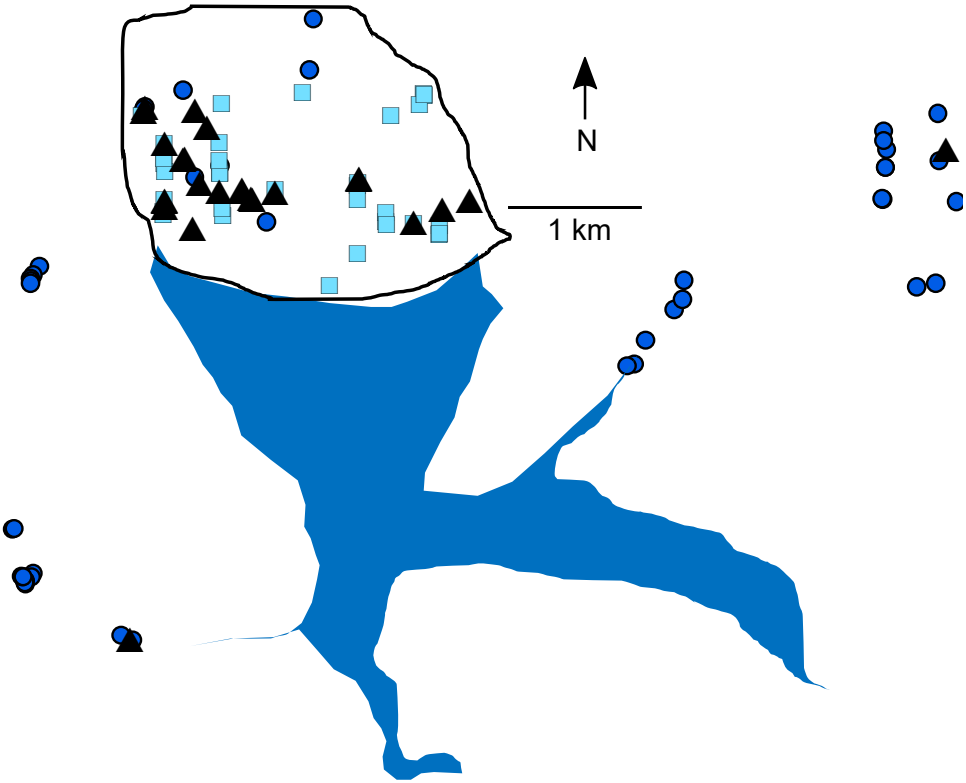

Figure 4. Successfully genotyped male tule elk pellets (n = 106) sampled from the Lake Pillsbury population, Lake County, California, USA, during the SCR survey (1 Jun–31 Aug 2019) throughout the range and the single-visit survey (14 Oct 2019) concentrated in the Lake Pillsbury Basin (circumscribed by black line), indicating samples from individuals that were sampled only during the SCR survey (blue circles), only during the single-visit survey (light blue squares), or during both surveys (black triangles), indicating that most males were sampled in the Basin or outside the Basin, but rarely (n = 2 individuals) both.

may perform well as long as the population is composed of multiple cow groups or both sexes are included. Because male space use accords more closely with SCR assumptions of independence, their inclusion in multisex SCR models helps offsets violations of this assumption by the female component of the population (Batter 2020). In cases such as the present one, however, where females essentially share a single home range and activity center, use of SCR to estimate female abundance in isolation from males entails severe violations to the assumption of independence, which could potentially bias point estimates and precision (Efford and Fewster 2013; Bischoff et al. 2020).

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FULL RESEARCH ARTICLE

Macrohabitat suitability model for the Trinity bristle snail in the Greater Trinity Basin of northern California

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Analytical methods used to identify species-specific suitability of habitat include statistical habitat distribution models. Habitat type is the most reliable predictor of species occurrence in a particular area. Here, I developed a spatially explicit landscape-level suitability framework using metrics derived from forest, climatic, and topographic criteria for the Trinity bristle snail (*Monadenia setosa*). I conducted surveys to document locations of Trinity bristle snails and then performed spatial analysis of ecological variables in a geographic information systems (GIS) framework using point density estimators to produce a spatially explicit habitat suitability model; a geographic map reflecting the total area of hypothesized suitable macrohabitat within the known geographic range of the species; and a set of density surfaces showing where point features were concentrated that defined habitat suitability ranging from low to critical. This model provides resource managers with a distributional framework and overlay useful in anticipating where suitable macrohabitat for the species may be found across the landscape and serves as a foundation for updating and expanding population-level surveys and site-specific microhabitat assessments.

Key words: landscape, macroscale, microhabitat, *Monadenia setosa*, terrestrial gastropods, threatened species

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The first stage of successful wildlife conservation requires effective evaluation of habitat suitability of the area in which a particular species resides (Kushwaha and Roy 2002). Habitat suitability models help to identify critical elements to the survival and viability of a species throughout its geographic range as well as potential threats to habitat (Pearce et al. 1994; Guisan and Zimmermann 2000; Rushton et al. 2004; Hein et al. 2007; Franklin 2010). Habitat suitability models function by formalizing the relationship between the occurrence of the focal taxon and environmental characteristics measured at sites sampled (Austin 2002; Hatten et al. 2005). Development of predictive habitat suitability models at a macroscale helps to identify factors that influence species persistence across multiple scales (Brown and Maurer 1989; Pereira and Itami 1991; Burnside et al. 2002; Root et al.

2003). This methodology also facilitates follow-on site-specific microhabitat assessments, discovery of new populations, range extensions, options for species translocation, and other applications related to management and conservation planning (Larson et al. 2004; Leathwick 2009; Guisan et al. 2013; Villero et al. 2017). Suitability models may also be used to predict increases or decreases in populations of listed species based on the distribution of suitable habitat potentially impacted by climate change (Thuiller 2003). Additionally, corridors of suitable habitat between fragmented populations are vital for dispersal in many species (Fahrig and Merriam 1994; Brooker et al. 1999; Sullivan 1995; Sullivan 1996; Christie and Knowles 2015). Once suitable habitat is located, it is important to assess its connectivity to avoid problems such as inbreeding depression (Greenwood et al. 1978; Willoughby et al. 2019).

Additionally, landscape-level suitability models are useful for predicting quality habitat for species that are endangered, rare, or have patchy distributions (Wu and Smeins 2000; Dayton and Fitzgerald 2006). One such species is the Trinity bristle snail (*Monadenia setosa*). This taxon is a rare and large terrestrial forest-dwelling gastropod endemic to the Southern Klamath Mountains of the Greater Trinity Basin (Fig. 1). The California Fish and

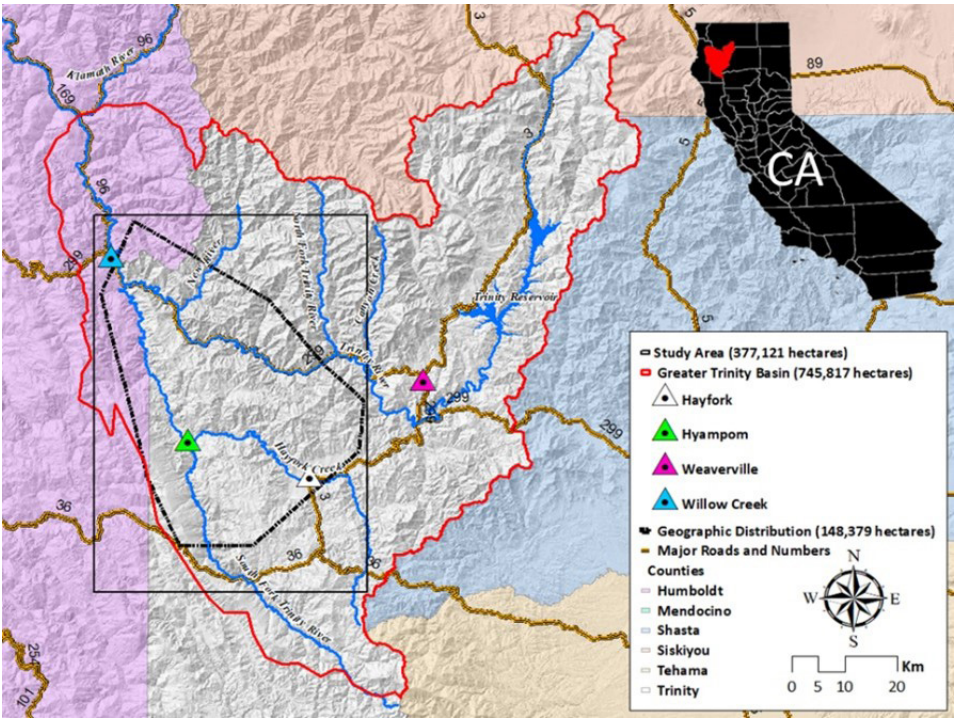

Figure 1. Study area and known geographic range of the Trinity bristle snail in the Greater Trinity Basin of northern California.

Game Commission listed this species as Threatened in 1984 under the California Endangered Species Act (CESA 1970). Populations of Trinity bristle snails are thought to be relicts of the late Pleistocene epoch when the local climate was much cooler and more mesic than current conditions (Talmadge 1952). Its current range is estimated to be ~1,484 km^2, or ~18% of the total area encompassed by Trinity County jurisdictional boundaries (8,307 km^2). The species consists of five subspecies separated by geographic discontinuities, riparian watershed

corridors, and major riverine barriers (Sullivan 2021). Populations of this species occur in isolated and highly fragmented locations along both sides of the western-most segment of the Trinity River, New River, South Fork of the Trinity River, Hayfork Creek, and along the east slope of South Fork Mountain along the Trinity-Humboldt County divide.

The biogeography, ecology, and systematics of large forest-dwelling terrestrial gastropods in the Pacific Northwest are poorly documented (Dunk et al. 2004) and the Trinity bristle snail is no exception. Historically, qualitative habitat for the species characteristically included mixed conifer, hardwood forest, and riparian forests, with large quantities of shaded, dead wood, thick leaf litter, moss covered forest floors, and decomposing large woody debris (Fig. 2; Talmadge 1952; Roth 1978; Roth and Eng 1980). To date, there is no

Figure 2. Example of characteristically high-quality habitat for the Trinity bristle snail (inset). Typical primary vegetation includes Pacific madrone, big leaf maple, white alder, tan oak, and sword fern (*Polystichum munitum*) in association with a thick carpet of leaflitter and decaying large and small fragments of wood from various plant species.

published literature that has quantified large-scale macrohabitat or microhabitat selection by the species or subspecies within the Trinity bristle snail complex. Previous studies of this species have lacked the fine-scale ecological detail (i.e., ground cover, vegetation, surface substrate, subsurface structure and composition, etc.) and geographic scope necessary to assess habitat requirements for purposes of management and conservation (Talmadge 1952; Walton 1963; Roth 1978; Roth and Eng 1980; Roth and Pressley 1986). Moreover, there are

no landscape-level habitat evaluations that identify blocks of suitable macrohabitat, which could support viable source populations and facilitate gene flow among disjunct populations throughout the range of this species. In a diverse landscape, macrohabitat analysis provides essential information on potential habitat areas of occupancy by uncovering specific vegetation structures or environmental conditions important to the focal taxon (Morrison et al. 1992; North 1996).

Given the lack of information on availability suitability of available habitat for Trinity bristle snail and the need to develop recommendations for management, my objectives in this study were two-fold. The first objective was to create a predictive landscape-level model of habitat suitability based on forest, climatic, and topographic criteria using a geographic information system (GIS) format. This process was necessary to identify, quantify, and map suitable macrohabitat throughout the known geographic range of the species. The second objective was to develop species-specific management recommendations based on evaluation of factors posing imminent threats to relict populations. Understanding how special status species respond to both natural and anthropogenic alterations in the landscape is vital to efficient implementation of future conservation strategies (Sanderson et al. 2002). Results of this study can function as a baseline and methodological approach for future management, conservation, and assessment of the listing status for the Trinity bristle snail. It may also serve as a template for other large terrestrial gastropods with similar ecologies potentially threatened by natural and anthropogenic habitat degradation in the region.

METHODS

Study Area

The study area in the Greater Trinity Basin watershed (~7,600 km^2) includes geographic regions throughout the northwestern segment of the Trinity River and its tributaries in Trinity and Humboldt counties (Fig. 1). The watershed is almost entirely covered by mountains, with the only level land in a few narrow valleys (i.e., Weaverville Basin, and Hoopa, 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 willow (*Salix* spp.). Whereas upland environs are characterized by a deciduous hardwood understory of Pacific madrone (*Arbutus menziesii*), giant chinquapin (*Castanopsis chrysophylla*), tanoak (*Lithocarpus densiflorus*), and canyon live oak (*Quercus chrysolepis*). The overall climate 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 around 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. Large volumes of rocks and sediment carried by floods are spread along the rivers forming wide alluvial channels.

Survey Methods

Field surveys focused on historical qualitative accounts of suitable ("high quality") habitat for the species based on documented occurrences and past survey data (Talmadge 1952; Walton 1963; Roth 1978; Roth and Eng 1980). I sampled for active bristle snails during warm wet, foggy, or rainy conditions during the months of March, April, May, September, and October. Surveys were conducted opportunistically at the surface of the soil,

under objects large enough to accommodate a large-bodied 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 associated with a well-developed organic soil base. Snails were hand-picked in focal areas using the visual search method, which was rapid and entailed neither degradation nor soil removal (Gotmark et al. 2008; Raheem et al. 2008). Because land snails are dependent on microhabitat, different search images were required to prevent bias depending upon what substrate was encountered (boulder vs. tree vs. depression vs. flat ground; Fontaine et al.

Table 1. Biotic and abiotic environmental predictors, classifications, codes, and plants species assemblages used in development of the macrohabitat suitability model for Trinity bristle snail across the species known geographic range. Data were derived by use of existing geographic information systems (GIS) data layers.

Category of predictor variable	Description
	Forest cover-types
1. Regional dominance cover-type	CALVEG REGIONAL DOMINANCE COVER-TYPE a forest cover-type that mapped regional dominance categories to describe common vegetation of dominant alliances or land-use categories. Cover-type elements: DF = Douglas fir (*Pseudotsuga menziesii*), DP = Douglas fir- Ponderosa pine [*Pinus ponderosa*], DW = Douglas fir-white fir (*Abies concolor*), QG = Oregon white oak (*Quercus garryana*), QC = Canyon live oak, QT = Tanoak-Pacific madrone, and MP = mixed conifer pine.
2. SAF cover-type	CALVEG SAF COVER-TYPE a western forest cover-type (Eyre 1980) that mapped: white fir = 211, Douglas fir = 229, Oregon white oak = 233, Sierra Nevada mixed conifer = 243, Ponderosa pine-Douglas fir = 244, California black oak (*Q. kelloggii*) = 246, and blue oak (*Q. douglasii*)-digger pine (*P. sabiniana*) = 250.
3. Vegetation cover-type	CALVEG VEGETATION COVER-TYPE a forest cover-type that mapped vegetation corresponding to: conifer forest = CON, mixed conifer and hardwood forest stands = MIX, and hardwood forest stands = HDW.
4. Cover-type	CWHR COVER-TYPE a forest cover-type that mapped relative cover of conifer and hardwood trees for mixed conditions: DFR = Douglas fir, MHW = montane hardwood, SMC = Sierra mixed conifer, WFR = white fir; MCP = montane chaparral, AGS = annual grass, and BOP = blue oak-foothill pine (*P. sabiniana*).
5. Life-form	CWHR LIFE-FORM COVER-TYPE a forest cover-type that mapped standard life forms consisting of tree dominated forest and woodland habitats that did not differentiate non-vegetated from sparsely vegetated locations; > 10% cover was used for map unit: CWHR-CON = conifer forest, CWHR-HDW = hardwood forest-woodland, CWHR-MIX = mixed conifer-hardwood forest, CWHR-HEB = herbaceous dominated habitats, and CWHR-SHB = shrub dominated habitats.

Table 1. (continued)

Category of predictor variable	Description
	Individual forest stand attributes
6. Aggregation type	CALVEG AGGREGATION TYPE mapped the forest aggregation-type describing the arrangement of vegetation condition found within a polygon: G = group compositional consisted of alliances or dominance types with similar community composition and physiognomy; H = a homogeneous condition of map units was composed of a single alliance or dominance type > 85% of area within polygon.
7. Conifer cover from above 8. Hardwood cover from above	CALVEG VEGETATION COVER FROM ABOVE (CFA mapped vegetation (%) cover [crown] from above as delineated by aerial photos). Conifer and hardwood tree cover was mapped as a function of canopy closure in 10% cover classes for conifer tree (CON-CFA) and hardwood tree (HDW-CFA) cover-types from above: 0 (< 1%), 5 (1 – 9%), 15 (10 – 19%), 25 (20 – 29%), 35 (30 – 39%), 45 (40 – 49%), 55 (50 – 59%), 65 (60 – 69%), 75 (70 – 79%), 85 (80 – 89%,) and 85 (90 – 100%).
9. Over-story tree diameter	CALVEG OS-TREE DIAMETER CLASS mapped the over-story tree diameter class of mixed tree types using mean diameter at breast height (DBH = 1.37 m above ground) for trees forming the uppermost canopy layer (Helms 1998) using average basal area (Quadratic Mean Diameter or QMD; Curtis and Marshall 2000) of top story trees: 1 = seedlings (0 – 2.3 cm QMD), 2 = saplings (2.5 – 12.5 cm QMD), 3 = poles (12.7 – 25.2 cm QMD), 4 = medium sized trees (50.8 – 76.0 cm QMD), and 5 = large sized trees (> 76.2 cm QMD).
	Climate, topography, and distance to nearest stream
10. Monthly maximum temperature 11. Monthly minimum temperature 12. Monthly annual precipitation	Climate attributes were derived from the PRISM Climate Group (https://prism.oregonstate.edu/), where long-term average datasets were modeled using a digital elevation model (DEM) as the predictor grid. Data for average minimum and maximum monthly temperature were obtained from raster data using the PRISM model (Parameter-elevation Regressions on Independent Slope Model; Daly et al. 1994), which analyzed spatially gridded average monthly, and annual minimum and maximum temperatures for specific climatological periods. PRISM is an analytical model that uses point data and an underlying DEM grid or a 30-year climatological average (1980-2010 average) to generate gridded estimates of monthly and annual temperature. It is well suited to regions with mountainous terrain and incorporates a conceptual framework that addresses spatial scale and pattern of orographic processes.

Table 1. (continued)

Category of predictor variable	Description
	Topographic and distance to nearest stream
13. Aspect 14. Elevation 15. Hill-shade 16. Slope 17. Distance to nearest stream	Maps of aspect, elevation, hill-shade, and slope were all derived from a United States Geological Survey (USGS) Digital Elevation Model (DEM) based on a 1:250,000-scale/3-arc second data resampled to 10 m resolution. Information on aspect was obtained from a raster surface that identified down-slope direction of maximum rate of change in value from each cell to its neighbors. Aspect equates to slope direction and values of each cell in the output raster show compass direction of surfaces measured clockwise in degrees from zero (due north) to 360° (Burrough and McDonell 1998). Degrees of aspect in relative degrees in direction were: north (0°), east (90°), south (180°), and west (270°). Values of cells in an aspect dataset indicate direction cell's slope faces. Flat areas having no down slope direction were given a value of -1 in the model. Aspect was quantified by use of aspect degrees binned into one of eight 45° ordinal categories (N, NE, E, SE, etc.). Elevation consisted of vertical units of a spaced grid with values referenced horizontally to the Universal Transverse Mercator (UTM) projection referenced to North American Datum NAD 83. Hill-shade was obtained from a shaded relief raster (integer values ranging from 0 – 255) in which the source of illumination was considered to be at infinity. The output raster only considered local illumination angle. Analysis of shadows considered effects of local horizon at each cell. Shadowed raster cells received a value of zero. Slope was obtained from a raster surface that identified gradient or rate of maximum change in z-value from each cell of a raster surface. Slope relates maximum change in elevation over distance between a cell and its eight neighbors, thus identifying the steepest downhill descent from the cell (Burrough and McDonell 1998). For degrees, range of slope values was: flat (0°), steep (35° – 45°), moderate (5° – 8.5°), to very steep (> 45°). Distance to the nearest stream was obtained from the California Department of fish and Wildlife GIS Clearing house (https://wildlife.ca.gov/Data/GIS/Clearinghouse and ftp://ftp.wildlife.ca.gov).

2007; Cucherat and Demuynck 2008).

Data Collection

Macrohabitat attributes were derived from metric-based regional biotic- and abiotic-data layers at a geographic scale consistent with the range of the species. Therefore, it was assumed that this process resulted in relatively little impact to predicted estimates of suit-

ability as the functions were fitted to the modeled location. Selected variables were derived from qualitative ecological descriptions and recommendations of preferred habitat based on historical accounts of this and other species in the genus *Monadenia* (Talmadge 1952; Roth 1978; Roth and Eng 1980; Roth 1982; Roth and Pressley 1986; Duncan et al. 2003; Furnish et al. 2007; Table 1). Model variables were evaluated in accordance with the distribution of existing mesic forest and woodland plant communities. Metrics derived from empirical data based on actual Trinity bristle snail sample sites were purposely used in preference to other habitat diversity scoring methods (Huber et al. 2011). Sampling did not rely on "expert" opinion from non-quantified site descriptions or hypothetical presence-absence data. Similarly, absence of snails at sites was not part of the sampling design.

In the GIS analysis the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG; USFS 1981) and the Wildlife Habitat Relationship System (CWHR; Airola 1988; Mayer and Laudenslayer 1988; Garrison et al. 2002) cover-type layers were used to assess geographic variation in forest type and stand structure at each sample site based on UTM coordinates (Parker and Matyas 1979; Goodchild et al. 1991; Sawyer and Keeler-Wolfe 1995). Each GIS classification system used a minimum mapping size of 2.5-hectare pixels for contrasting vegetation based on cover-type, vegetation type, tree cover from above, and over-story tree diameter. Searches were implemented at several sites to check the condition of the site and to see if snails were active. Life-forms were derived from a classification of Landsat Thematic Mapper imagery. Non-forest abiotic environmental attributers were obtained from geo-rectified raster data sets for Northern California. Evaluation of forest-type attributes (e.g., forest cover-type, and forest stand, and tree structure variables) were compared to values within the geographic boundaries of Trinity County as a base of reference within the region. Climate attributes were derived from the PRISM Climate Group (https://prism.oregonstate.edu/), where long-term average datasets are modeled using a digital elevation model (DEM) as the predictor grid. Topographic variables (i.e., elevation, aspect, slope, hill-shade, and distance to nearest stream) were generated from 10-meter digital elevation models in GIS.

Statistical Analyses

I conducted all analyses using Program R (R Core Team 2020) and statistical significance was set at $\alpha < 0.05$. For comparative purposes, univariate and multivariate analyses of geographic attributes were assessed for both Trinity County as a whole and simultaneously for all 2.5-hectare sites where snails were sampled ($n = 333$). I also used principal components analysis (PCA) in variable selection, to examine the extent of association among habitat attributes, and to assess the relative ability of attributes to explain variation among sites (Smartt and Sullivan 1990; Sullivan and Smartt 1995; Sullivan 1996; Sullivan 1997). This process minimized multicollinearity between model predictors, with the goal of identifying a smaller subset of variable components that capture the majority of variance in predictors (Everitt and Hothorn 2011). I used the nonparametric 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 the Kolmogorov–Smirnov two-sided test (KS) to compare the percent frequency distributions between two samples. This test is sensitive to differences in both location and shape of the cumulative distribution functions of each sample (Marozzi 2013).

Habitat Suitability

Random point model.— Suitable habitat for the Trinity bristle snail has not been modeled from a geographic perspective using forest vegetation cover-type, topography, or other special-location covariate GIS overlays in combination with digital orthoquads. Here, habitat suitability was modeled based on multiple macrohabitat variables parameterized by theoretical point-density functions. Mixed sources of information used in the model had similar geographic scale-dependent background data. Suitability modeling was conducted by use of GIS Spatial Analyst functions (ArcMap; ESRI 2021). Modeling was based on a spatially explicit systematically derived landscape-scale habitat evaluation. This process was combined with a macrohabitat framework of biotic and abiotic metrics obtained from forest, topographic, and climatic data layers. A concerted effort was made to emphasize the biological plausibility of the model by use of relevant environmental preferences based on the species natural history characteristics. This effort allowed development of a more complex model that included specific variable plot parameters. A GIS-based geographic suitability framework was then developed using metrics linked to key macrohabitat attributes collected at 333 site-specific UTM coordinates (Table 1) as follows. First, Spatial Analyst extracted values from CALVEG and CWHR forest vegetation cover-types and other GIS environmental base layers to the 333-point samples. The composite cover-type base layer was clipped to a map of the study area (3,771 km^2; Fig. 1). The resulting map encompassed the current geographic range of the species as determined from previous surveys and recent molecular DNA analyses, which encompassed 1,484 km^2 or 39.4% of the research area. Second, macrohabitat attributes measured at each sample site were used as selection criteria (Query Builder tool) to query a set of nonoverlapping random points (n = 80,000) generated from within the boundaries of the study area. Values for each GIS environmental base-layer were extracted to each of these random points. Selection criteria derived from the 333 sample sites were used to query areas within the set of random points, which resulted in a newly "selected" random-point layer. Third, the Point Density tool calculated the density of point features around each output raster cell ("neighborhood"). Points that fell within the neighborhood were totaled and divided by the area of the neighborhood to which a smoothly tapered surface was fit. Default values used in the density model (henceforth called the "Random Point Model") were: Population = None, Output cell = 206, Neighborhood = circle, Radius = 1715, Units = Map, Area units = km^2, and Classes = 6. Fourth, raster density values generated from the Random Point Model were converted into integers, which provided acreage values for comparison with estimates of macrohabitat suitability. The resulting density surfaces showed where point features were concentrated with values ranged from 1 to 6. When plotted these values represented a set of hypothetical limits that defined relative macrohabitat suitability ranging from: 1) Low, 2) Low – Medium, 3) Medium, 4) Medium – High, 5) High, and 6) Critical.

Validation of the suitability model.—The validation procedure attempted to identify the utility in strengths and weakness of remotely sensed macroscale metrics to assess habitat suitability for the long-term viability of the species. Absence data across the range of the species does not currently exist so modeling using pseudoabsence or nonexpert-identified absence data to compare variation in macrohabitat to the subset of habitat conditions found at sample sites was not possible (Guisan and Zimmermann 2000; Engler et al. 2004; Franklin 2010; Barrett et al. 2014). Lacking true absence data to define the physical environment of

the study area does not necessarily allow a precise estimate of the probability of presence and may not be proportional to it (Phillips et al. 2009; Zarnetske et al. 2007). Consequently, model validation using generalized linear, machine-learning, or maximum entropy modeling were not used (MaxEnt; Phillips et al. 2006; Phillips et al. 2009; Crawford et al. 2020). Therefore, a fundamental assumption of the present study was that habitat suitability model accurately referenced suitable macrohabitat and that significant correlations between model outputs and observed macrohabitat corridors would be found. As such, relative validity of the suitability model relied on the ability to delineate suitable macrohabitat based on the following considerations:

- Internal validation was used to determine robustness and generality of the model by simply comparing the ability to include existing sample sites for the species based on previous research and sampling.
- Landscape-level distribution patterns and composition were evaluated for consistency with previous historical sampling, research, and field inventories.
- Predicted areas of highly suitable macrohabitat were highlighted based on known species strongholds, which likely represent centers of population viability that have persisted and flourished to date.
- Landscape patterns in macrohabitat provide a realistic historical glimpse into habitat corridors that facilitated gene flow throughout the region. This criterion is supported by patterns of genetic differentiation following Pleistocene-Holocene warming in response to forest fragmentation and isolation of populations coincidental with topographic and riverine barriers (Whittaker 1961; Sullivan 2021).

RESULTS

Forest Cover-types

Although the overall percent frequency distributions of cover-type categories for Trinity County versus where snails were sampled were significantly different (KS = 0.40, p = 0.016, n = 30; Table 2), the ranked correlation between the two cover-type distributions was highly significant (r_s = 0.860, p = < 0.001, n = 30). For sites sampled for snails' individual pair-wise ranked correlations showed that except for the CALVEG REGIONAL DOMINANCE COVER-TYPE versus the CWHR LIFE-FORM COVER-TYPE (r_s = 0.020, p = 0.719, n = 333) and the CALVEG SAF COVER-TYPE versus the CWHR LIFE-FORM COVER-TYPE (r_s = -0.080, p = 0.155, n = 333), all other comparisons were significantly correlated (p < 0.001). Yet the strength of each correlation was not robust between any pair of forest cover-types (min: r_s = -0.180 vs. max: r_s = 0.600, n = 333). Principal components analysis of forest cover-types accounted for 86.5% of the total dispersion among samples along the first three vectors (Appendix I). The CWHR COVER-TYPE followed by the CALVEG REGIONAL DOMINANCE COVER-TYPE had the highest loadings along PC I and were considered marginally more informative as suitable macrohabitat for the species. Proportionally these two variables contained a more diverse plant species assemblage ("community") compared to other categories of forest cover-types.

Summary relationships based on sample site location indicated that the dominant macrohabitats for the Trinity bristle snail were: 1) conifer forest (Douglas fir [*Pseudotsuga menziesii*]-white fir [*Abies concolor*]), 2) mixed conifer (fir and pine), in combination with 3) mixed conifer and hardwood plant assemblages (Table 3). Pure stands of hardwood,

Table 2. Percent summary of plant species assemblages by forest cover-type based on the CALVEG and CWHR systems for Trinity County compared to percent forest cover-types at locations where Trinity bristle snails were sampled.

Plant community/species	CWHR Code	Trinity County acres hectares	%	Snail sample sites n	%
Regional dominance cover type (CALVEG REGIONAL DOMINANCE COVER-TYPE)					
Douglas Fir-white fir	DW	37,526	9.4%	179	53.8%
Douglas fir	DF	154,283	38.6%	87	26.1%
Mixed conifer-pinel	MP	86,255	21.6%	39	11.7%
Douglas fir-ponderosa Pine	DP	57,583	14.4%	16	4.8%
Canyon live oak	QC	14,866	3.7%	2	0.6%
Oregon white oak	QG	19,548	4.9%	2	0.6%
Tanoak-Pacific madrone l	QT	2,601	0.7%	4	1.2%
White fir	WF	27,352	6.8%	4	1.2%
Total		400,013		333	1.2%
Western Forest Cover-Type (CALVEG SAF COVER-TYPE)					
Douglas fir	DF (229)	191,810	46.9	269	80.8%
Sierra Nevada mixed Conifer	SNMC (243)	86,414	21.1%	38	11.4%
Ponderosa pine-Douglas-fir	PPDF (244)	57,583	14.1%	15	4.5%
California black oak	CBO (246)	8,926	2.2%	4	1.2%
White fir	WF (211)	40,640	9.9%	4	1.2%
Oregon white oak	OWO (233)	19,548	4.8%	2	0.6%
Black oak-digger pine	BODP (255)	4,082	1.0%	1	0.3%
Total		409,002		333	
Vegetation cover from above (CALVEG VEGETATION COVER FROM ABOVE [CFA])					
Conifer	CON	304,091	65.0%	276	82.9%
Mixed conifer-hardwood	MIX	119,294	25.5%	49	14.7%

Table 2. (continued)

Plant community/species	CWHR Code	Trinity County acres hectares	%	Snail sample sites n	%
Hardwood	HWD	44,131	9.4%	8	2.4%
Total		467,516		333	
California Wildlife Habitat Relationship Standards for Life-form (CWHR LIFE FORM)					
Conifer forest-woodland	CON	360,183	69.3%	303	91.0%
Mixed conifer-hardwood	MIX	47,930	9.2%	14	4.2%
Hardwood forest-woodland	HDW	45,968	8.8%	8	2.4%
Herbaceous dominated habitats	HEB	12,266	2.4%	6	1.8%
Shrub dominated habitats	SHB	53,536	10.3%	2	0.6%
Total		519,883		333	
Wildlife habitat relationship vegetation type (CWHR TYPE)					
Sierra mixed conifer	SMC	172,036	41.0%	223	67.0%
Douglas fir	DFR	119,455	28.4%	74	22.2%
Montane chaparral	MCP	43,508	10.4%	15	4.5%
Montane hardwood	MHW	45,229	10.8%	8	2.4%
Annual grass	AGS	10,632	2.5%	8	2.4%
White fir	WFR	25,100	6.0%	4	1.2%
Blue oak-foothill pine	BOP	4,010	1.0%	1	0.3%
Total		419,969		333	

Table 3. Percent summary of all forest cover-type classifications derived from the CALVEG and CWHR systems. CALVEG REGIONAL DOMINANCE COVER-TYPE = RDC; CALVEG SAF COVER-TYPE = SAF; CALVEG VEGETATION COVER-TYPE = VGC; CWHR COVER-TYPE = COV; and CWHR LIFE-FORM COVER-TYPE = LIFE. Codes for plant species: DF = Douglas fir, DFWF = Douglas fir-white fir, WF = white fir, PPDF = Ponderosa pine-Douglas-fir, SMCP = Sierra Nevada mixed conifer pine, MHC = montane hardwood conifer, MHW = montane hardwood, TOK = tanoak, OBOP = Oregon and blue oak and digger pine, CLO = canyon live oak, CBO = California black oak, and BAR = barren (rock, soil, sand, snow, and urban). Dashed lines = cover-type not present.

		CALVEG cover-types			CWHR cover-types	
Cover-type classifications	Plant species code	RDC	SAF	VGC	COV	LIF
Douglas-white fir forest (72%)	DF	24.9%	79.9%	--------	21.9%	91.9%
	DFWF	55.0%	--------	82.9%	--------	--------
	WF	1.3%	1.2%	--------	1.2%	--------
Mixed conifer (24%)	PPDF	4.8%	4.5%	--------	--------	--------
Mixed conifer hardwood (2%)	SMCP	11.7%	11.7%	14.7%	67.3%	3.9%
	MHC	--------	--------	2.4%	3.9%	2.4%
	MHW	--------	--------	--------	3.0%	--------
Oak woodland (1%)	TOK	1.3%	--------	--------	--------	--------
	OBOP	1.0%	0.9%	--------	--------	--------
	CLO	0.0%	0.6%	--------	--------	--------
	CBO	--------	1.2%	--------	0.3%	--------
Non-forest (1%)	BAR	--------	--------	--------	2.4%	--------

riparian shrub, and herb cover-types were not important stand components at sample sites. These habitat elements are known to be important to the species (Roth and Pressley 1986). However, they were entirely subsumed within conifer and mixed conifer-hardwood forest cover-types, which effectively relegates discovery of these cover-type elements to detailed follow-on microhabitat surveys and site-specific assessments.

Individual Forest Stand Attributes

A comparison of the combined individual forest stand attributes between Trinity County and sites where snails were sampled was not significant (KS = 0.21, p = 0.564), as the frequency distributions of each sample were highly correlated (r_s = 0.920, p = < 0.001, n = 29; Table 4). Assessment of the extent of forest tree aggregation at sample sites showed that the arrangement of forest stands was mostly homogeneous (82.3%) compared to compositionally aggregated (17.7%). Percent overstory tree cover from above for both Trinity County and sample sites for snails ranged from 30.0–79.9% for conifer trees (CON-CFA). Hardwood crown-cover was virtually nonexistent in both groups (69.9% and 83.2%, respectively). Diameter of over-story conifer trees consisted of habitat dominated by small (25.4–50.6 cm quadratic mean diameter (QMD)) and medium sized trees (50.8–76.0 cm QMD) for both Trinity County and sample sites for snails. In contrast, the few stands of hardwood identified consisted of overstory tree diameters mostly associated with pole trees (15.0%; 12.7–25.2 cm QMD).

Principal components analysis of forest stand attributes accounted for 84.6% of the total dispersion among sample locations on the first three principal components (PC). Loadings (correlations of each component with each variable) on PC I (36.7%) were positive for all variables (Appendix I). Component loadings for PC II (31.3%) were positive and moderate to high for over-story tree diameter and conifer cover from above, but negative for hardwood cover from above and aggregation type. Lack of a strong correlation among variables was evident in the discordant vector trajectories shown in a plot of PC I versus PC II (Fig. 3A–D). Collectively, these data suggest that the sites where snails were sampled were strongly affiliated with mixed conifer stands containing medium to large sized trees, which provided abundant over-story cover (shade) in association with homogenous forest stands. However, individual hardwood stand elements were rare even at the level of the county, which supports the preceding analysis of hardwood forest cover-types.

Seasonal Climatic Attributes

Temperature.—At sites where snails were sampled seasonal variation in the annual minimum temperature fluctuated between -3.3°C in January ($\bar{x}$ = -0.8°C) and 12.8°C in July ($\bar{x}$ = 11.7°C), with the largest fluctuations occurring in September ($\bar{x}$ = 9.7°C) and October ($\bar{x}$ = 6.2°C; range = 5.6; Fig. 4A; Appendix I). Seasonal variation in annual maximum temperature ranged from 6.1°C in December ($\bar{x}$ = 7.4°C) to 34.4°C in July ($\bar{x}$ = 32.1°C), August ($\bar{x}$ = 32.1°C), and September ($\bar{x}$ = 28.9°C), with the largest variance occurring in September (range = 7.2; Fig. 4B; Appendix I). The correlation among average monthly temperatures explained 94.3% of the total dispersion among sample sites on the first three PCs for monthly minimum temperature, and 96.5% of the total dispersion for monthly maximum temperature (Appendix I). Average monthly maximum temperature explained more total variation among samples on PC I (89.2%) than did average monthly minimum

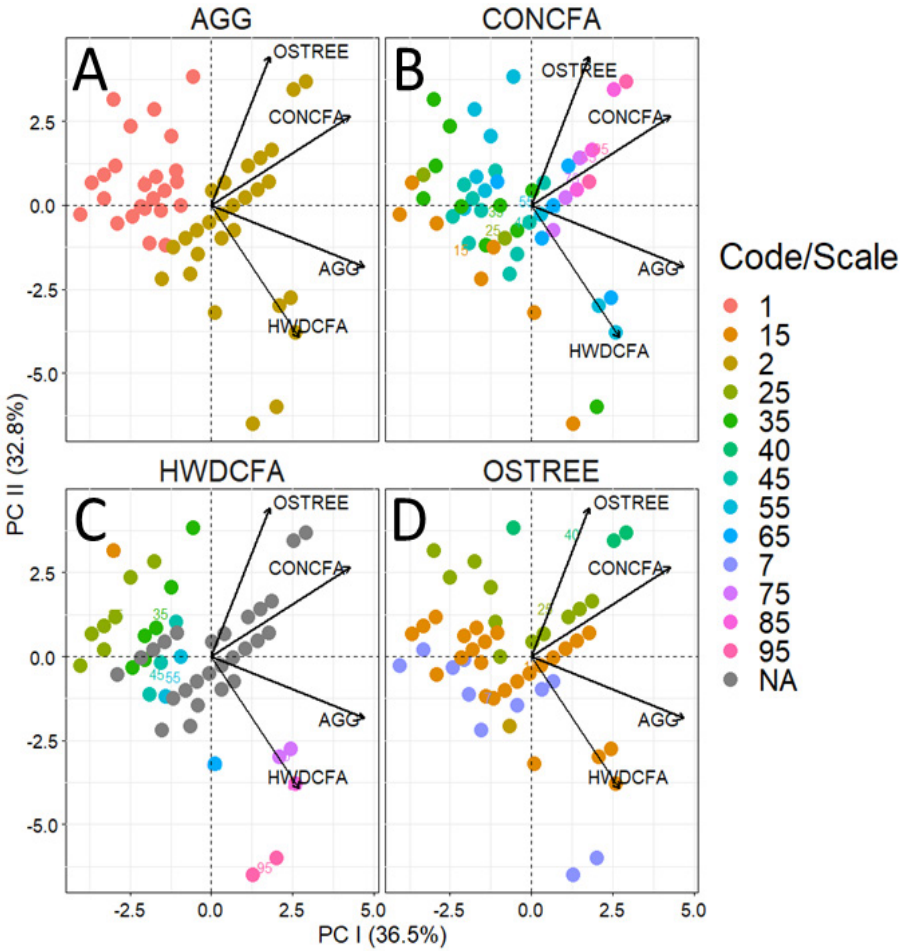

Figure 3. Two-dimensional distribution of factor scores along the first two principal component (PC) axes for individual forest tree stand variables. Vector directions (black colored arrows) show the direction that each variable plotted along PC I and PC II. Codes corresponding to scales for each variable are: A) forest aggregation (AGG; compositional group = 1, homogenous condition = 2); B) conifer forest cover from above (CONCFA); C) hardwood cover from above (HWDCFA); and D) over-story tree diameter class (OSTREE) at breast height (DBH). Percent overstory cover from above for both CONCFA and HWDCFA stands was: 0 (< 1%), 5 (1 – 9%), 15 (10 – 19%), 25 (20 – 29%), 35 (30 – 39%), 45 (40 – 49%), 55 (50 – 59%), 65 (60 – 69%), 75 (70 – 79%), 85 (80 – 89%,) and 85 (90 – 100%); and OSTREE was: 1 = seedlings (0 – 2.3 cm QMD), 2 = saplings (2.5 – 12.5 cm QMD), 3 = poles (12.7 – 25.2 cm QMD), 4 = medium sized trees (50.8 – 76.0 cm QMD), and 5 = large sized trees (> 76.2 cm QMD). NA (not available) refers to DBH size classes that were missing from HWD-CFA data.

temperature (70.5%). For both monthly minimum and maximum temperature all other PCs accounted for minor amounts of variation. For monthly minimum temperatures, the highest component loadings along PC I occurred for the annual average temperature, and the months of June, December, and January (> 0.900). However, for average monthly maximum temperatures all component loadings on PC I were high and positive (> 0.860), especially annual maximum, and the months of June, July, May, and April (> 0.971). In both PCAs, annual monthly minimum and maximum temperatures had the highest loadings along PC

Table 4. Percent summary of individual forest stand attributes based on the CALVEG classification system for Trinity County compared to sites where Trinity bristle snails were sampled. NA = not present.

	Trinity County		Snail sample sites	
Variable (CWHR code)	Hectares	%	n	%
Percent Aggregation Type (AGGREGATION-TYPE)				
Compositional group (1)	132,418.0	24.9%	59	17.7%
Homogeneous condition (2)	399,947.0	75.1%	274	82.3%
Total	532,365.0		333	
Percent over-story cover (crown) from above (CON-CFA)				
Conifer tree cover (CON-CFA)				
10 – 19.9% (15)	21,934.0	5.4%	14	5.0%
20 – 29.9% (25)	39,023.1	9.6%	7	2.0%
30 – 39.9% (35)	56,557.3	13.9%	34	10.0%
40 – 49.9% (45)	56,852.8	13.9%	84	25.0%
50 – 59.9% (55)	74,805.0	18.4%	88	26.0%
60 – 69.9% (65)	57,947.4	14.2%	54	16.0%
70 – 79.9% (75)	58,747.1	14.4%	33	10.0%
80 – 89.9% (85)	35,677.1	8.8%	16	5.0%
90 – 100.0% (95)	6,062.2	1.5%	3	1.0%
Total	407,606.1		333	
Percent Hardwood tree cover from above (HDW-CFA)				
None (NA)	368,931.1	69.9%	277	83.2%
10 – 19.9% (15)	19,336.7	3.7%	1	0.3%
20 – 29.9% (25)	43,580.3	8.3%	15	4.5%
30 – 39.9% (35)	43,101.1	8.2%	22	6.6%
40 – 49.9% (45)	14,298.8	2.7%	8	2.4%
50 – 59.9% (55)	12,141.8	2.3%	2	0.6%
60 – 69.9% (65)	9,806.0	1.9%	2	0.6%
70 – 79.9% (75)	8,912.0	1.7%	3	0.9%
80 – 89.9% (85)	5,286.0	1.0%	1	0.3%
90 – 100.0% (95)	2,074.8	0.4%	2	0.6%
Total	527,468.5		333	
Percent diameter (DBH) of over-story trees (OS-TREE-DIAMETER-CLASS)				
Conifers:				
Sapling 2.5 – 12.5 cm QMD (2)	17,750.8	3.9%	7	2.1%
Pole 12.7 – 25.2 cm QMD (7)	95,200.8	21.0%	22	6.6%
Small size tree 25.4 – 50.6 cm QMD (15)	160,411.2	35.4%	249	74.8%
Medium size tree 50.8 – 76.0 cm QMD (25)	162,065.5	35.7%	48	14.4%
Large size tree > 76.2 cm QMD (40)	17,995.6	4.0%	7	2.1%
Total	453,423.9		333	
Hardwoods:				

Table 4 (continued)

None (NA)	413,090.0	80.1%	286	86.3%
Pole 12.7 – 25.2 cm QMD (7)	80,073.7	15.5%	39	11.5%
Small tree 25.4 – 50.6 cm QMD (15)	22,825.9	4.4%	8	2.2%
Total	515,989.6		333	

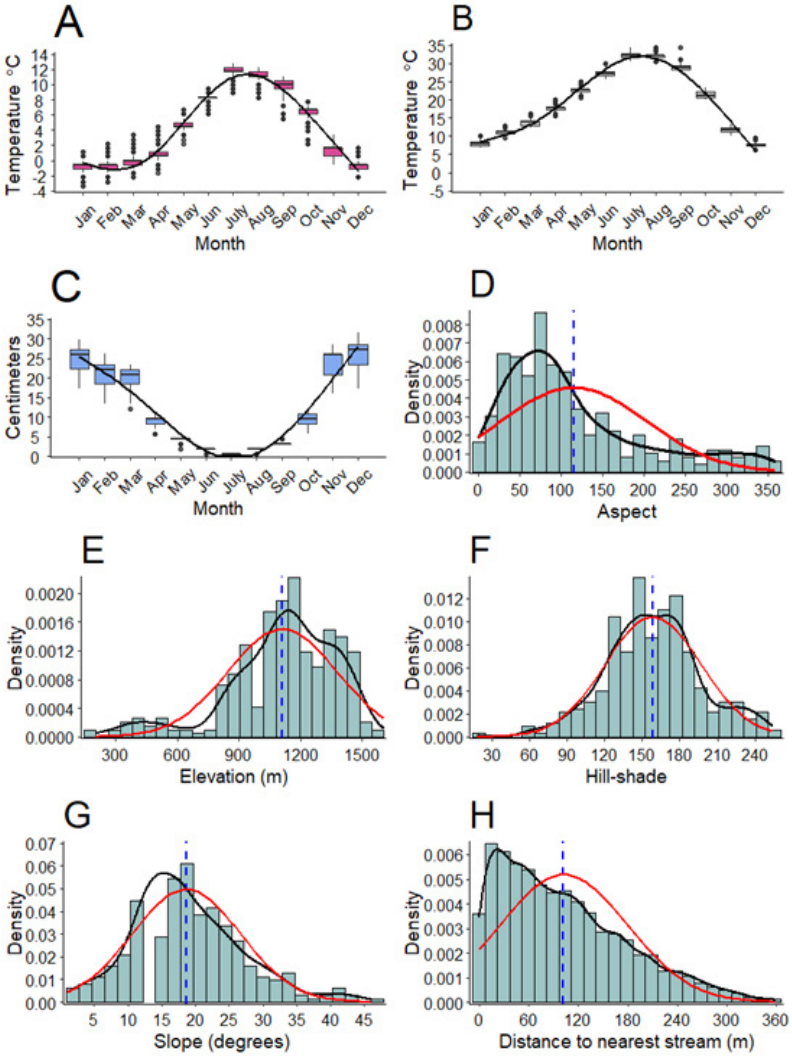

Figure 4. Boxplot and bar graph summaries of monthly variation in: A) minimum and B) maximum air temperature (C°), and 3) precipitation (cm); and the shape and extent of variation in frequency distributions of D) aspect°, E) elevation (m); F) hill-shade and G) slope° at sites where Trinity bristle snails were sampled, and H) distance (m) to the nearest stream. Data are based on n = 333 locations evaluated using geographic information systems. Smoothed frequency distribution compared to a normal distribution (black lines) or Gaussian distribution (red lines) for each continuous variable. The mean for each distribution is shown by a vertical blue dashed line. Exact values for each monthly variable are found in Appendix I.

I (0.974 and 0.992, respectively).

Precipitation.—Seasonal variation in monthly precipitation fluctuated from 0.6 cm in June ($\bar{x}$ = 1.9 cm), July ($\bar{x}$ = 0.6 cm), and August ($\bar{x}$ = 1.8 cm) to 31.8 cm in December ($\bar{x}$ = 26.3 cm). The largest variance in precipitation occurred in December ($\bar{x}$ = 26.3 cm), January($\bar{x}$ = 25.0 cm), February ($\bar{x}$ = 20.9 cm), and November ($\bar{x}$ = 24.1 cm; Fig. 4C; Appendix I). As expected, the relationship between minimum and maximum monthly precipitation was highly positive and significant. Both monthly temperature variables showed a significant negative relationship with precipitation. Principal components analysis of monthly variation in precipitation explained 83.2% of the total dispersion among mapped sites on the first three vectors (Appendix I). Except for the month of July all other monthly component loadings were positive and high along PC I (65.8%); whereas all other PCs accounted for only minor amounts of variation in monthly precipitation. As in the previous analysis of monthly minimum and maximum temperature, total annual precipitation loaded highest of all variables along PC I (0.991).

Topographic Attributes

A summary of the extent of variation in the frequency distributions of topographic attributes at sites where snails were sampled compared to expectations based on normality is illustrated in Fig. 4D through 4G. Average aspect was 115° (min = 0°, max = 358°) with most (70.3%, n = 333) samples occurring at < 132° in association with mesic (shaded, cool, moist) north-, northeast-, and east-facing slopes. Few snails were found on more arid facing slopes (S, SW, W, SW) unless there was abundant shade and shallow sloping surfaces. Average elevation was 1,112 m (min = 204 m, max = 1,605 m) but most (82.3%, n = 333) snails were found at elevations > 900 m. Average hill-shade was 158.7 (min = 18.0, max = 254.0) but most values (82.0%, n = 333) were < 189.0. These data suggest that sample sites occurred mostly at low sun angles in shaded relief as opposed to sites with open illumination. Average slope was 18.6° (min = 1°, max = 45.7°). Most sites (80.8%, n = 333) had slopes ranging from gentle (1–3°) to slightly stronger slopes (< 25°).

Lightly shaded areas of exposed side hills with steep upper slopes yielded no specimens. Occasionally Trinity bristle snails were found on both east- and west facing canyon exposures, but not on south facing slopes fronting the Trinity River or Hayfork Creek. Average distance to the nearest stream measured at sites where snails were sampled was 81.3 m (range 0.1–357.8 m; n = 333; Fig. 4H); and 95.2% of the samples were within 200 m of a stream corridor. There was no significant relationship between distance to the nearest stream and length of the stream corridor (r_s = 0.020, p = 0.746; n = 333). Principal components analysis of all topographic attributes simultaneously accounted for 76.9% of the total dispersion among samples along the first three vectors. Aspect and slope loaded high along PC I (37.7%; Appendix 1); whereas elevation and distance to the nearest stream loaded high but negative along this vector. Collectively, this analysis found that sites where Trinity bristle snails were sampled occurred in: 1) mesic forest conditions, 2) on landscapes dominated by shaded north-, northeast-, and east-facing exposures, 3) at moderate to higher elevations in associated with steep to gentle slopes, and 4) within 200 m of a riparian corridor.

Random Point Habitat Suitability Model

The point density algorithm (Point Density Tool) applied to the 80,000 random points

predicted a range of suitable macrohabitat totaling 107,913 hectares. Of this 21.5% (30,951 hectares) consisted of medium to critically suitable macrohabitat, or ~20.9% of the geographic range of the species (Table 5). The Random Point Model described suitable macrohabitat as highly fragmented across the entire geographic range of the species. Appendix I shows the abiotic and biotic categories and GIS selection criteria used in the composite GIS selection query that defined the Random Point Model selected 6,187 (7.7%, n = 80,000) random points (Fig. 5). Use of all abiotic and biotic variables simultaneously was better at predicting the landscape-level map produced by the model than if each variables were used individually (Fig. 6A), or in composite macrohabitat categories (Fig. 6B).

Table 5. Estimates of the total, percent, and average hectares of potentially suitable macrohabitat categories from throughout the known range of the Trinity bristle snail as predicted by the Random Point Model. Total acreage of all suitable habitat combined was 143,726 hectares.

Habitat suitability score	Total	Percent	Average	Minimum	Maximum
Low suitability	45,783	42.4%	22,893	20,199	25,586
Low-medium	31,176	28.9%	15,588	13,479	17,697
Medium	18,412	17.1%	9,206	8,037	10,375
Medium-high	8,982	8.3%	4,491	2,880	6,102
High	2,570	2.4%	1,285	1,148	1,423
Critical	987	0.9%	247	68	589

In other words, the relative "information" content of the model increased as macrohabitat attributes were added one-by-one into the analysis. This pattern was also evident when several categories of combined variables were independently applied to the model. To illustrate, aspect accounted for 100% of all 80,000 random points but comprised only 7.7% of the points selected in the final model. By contrast, over-story tree diameter accounted for 28.7% of all random points and 26.9% of the points selected in the final model. Use of individual or composite subsets of variables selected so many random points as to be uninformative in identifying where suitable macrohabitat might occur. Information content improved as variables, even highly redundant ones, were added to the model starting with: 1) various forest cover-types, followed by 2) average maximum monthly temperature, 3) hardwood cover from above, and finally 4) overstory tree diameter (Fig. 6C). The category consisting of monthly maximum temperatures was the most "informative" composite set of variables when applied as a single unit. However, even these data were highly inefficient in mimicking the final model (34.4%; Fig. 6B).

DISCUSSION

Results of the GIS analysis of ecological metrics using point density estimators to generate a set of density surfaces showed where random point features were concentrated, which resulted in a spatially explicit habitat suitability model for the Trinity bristle snail. At the macroscale level, this model reflected the hypothesized distribution of suitable macrohabitat within the known geographic range of the species. Quantitative analysis of environmental variables used in the Random Point Model to determine the potential occurrence of the Trinity bristle snail resulted in new macrohabitat parameters previously not analyzed within the current literature (i.e., Table 1; Figure 3). These new environmental

metrics were highlighted in shaping the current "macrohabitat niche" of the species (Emery et al. 2012; Candeiro et al. 2018; Quin et al. 2018). Use of a multitude of remotely sensed environmental metrics at similar macroscales allowed delineation and quantification of

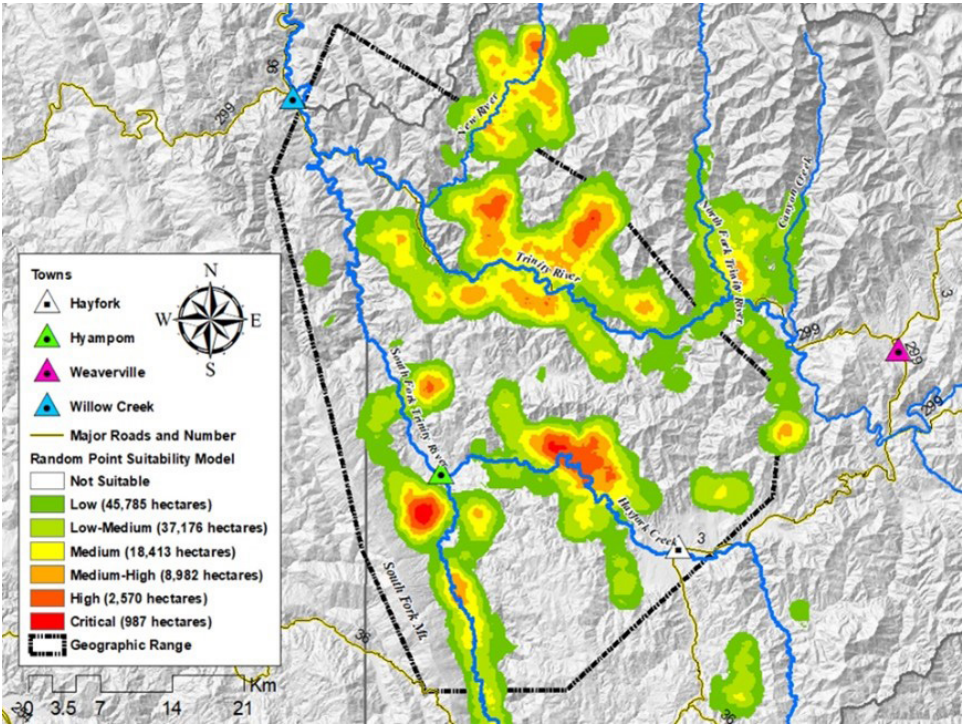

Figure 5. Final Random Point Model including predicted acreages of hypothesized macrohabitat suitability that ranged from Low to Critical within and in some areas outside the known geographic range of the Trinity bristle snail. Note the relative macrohabitat barriers to potential gene flow through high quality habitat along the mainstem Trinity River, New River, and lower reaches of the North Fork Trinity River and Hayfork Creek, as opposed to upriver segments and headwater areas where higher quality habitat surrounds both sides of riverine corridors.

a continuum of low to critically suitable macrohabitat (Wiens 1989). Model predictions were a good indicator of suitability based on site-specific macroscale criteria. This method provides a practical strategy and overlay for identifying geographic regions where applied management and conservation efforts may be focused on the level of jurisdictional watersheds and stream corridors.

The Random Point Suitability model (Fig. 5) suggests that within the administrative boundaries of Trinity and Humboldt counties potential suitable macrohabitat for the Trinity bristle snail occurs: 1) west of Evans Bar and Carr Creek along the Trinity River, and 2) north to the North Fork of New River, Guinby Creek, and Waterman Ridge northeast of Willow Creek to the Humboldt County line. In Humboldt County, potential suitable macrohabitat appears to include only a small geographic area at the eastern edge of the county boundary west of the South Fork Trinity River and east along the western slope of South Fork Mountain, Panther and Deadman creeks in the south, north to near China Creek, and ~2 miles south of Willow Creek.

Additionally, several highly or critically suitable macrohabitat areas were predicted

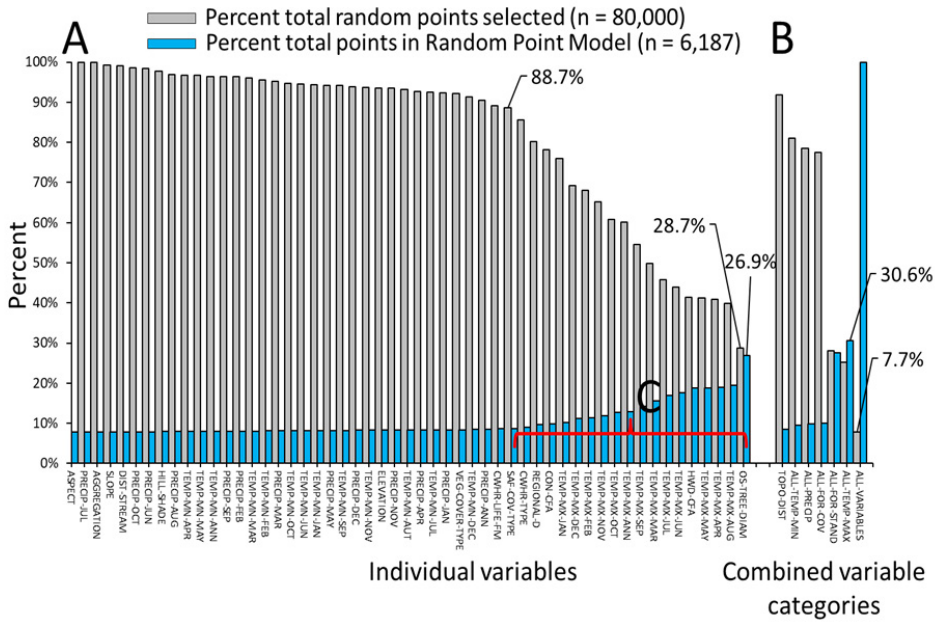

Figure 6. A) Individual abiotic and biotic variables and B) combined variable categories used in the Random Point Model. Illustration shows what percentage that each attribute contributed to the total number of random points (n = 80,000) selected versus their relationship to the final Random Point Model (n = 6,187), both in terms of percent contribution and relative "information" content. Information content increased as attributes were selected one-by-one. C) Region in the graph that identifies the brake-point beginning with most all forest cover-types followed by maximum monthly temperature, hardwood cover from above (HWD-CFA), and over-story tree diameter (red horizontal line). These later variables selected the random points most consistent with the final model. Abbreviations are consistent with names of variables presented in Appendix I.

on both the north and south sides of the Trinity River at higher elevations: 1) Hennessy and McDonald creeks west of Burnt Ranch, 2) Bidden and Mill creeks, 3) Cedar Flat and Stetson creeks south of Don Juan Point on the Trinity River, 4) Smoky Camp, Don Juan, and Big creeks, 5) Underwood and Eltapam creeks, 6) Hay Fork Creek and the area surrounding Dinner Gulch, 7) Deer and Monkey creeks northwest of Big Bar, 8) Bell Creek near the town of Daily, 9) Devils Canyon east of Denny, and 10) Barney Gulch near the Ozark Mine on North Fork of Trinity River.

Not surprisingly, several small areas of potential suitable habitat mapped outside the known geographic range of the species (Fig. 5). These areas (NE, E, SE) are predicted to contained small amounts of high-quality habitat. Thus, the possibility of extant populations in these areas suggests that Trinity bristle snails may be more widely distributed than previously reported. Given this prediction additional surveys and site assessments in these areas seems warranted.

Further, the geographic map produced by the model showed that the distribution of suitable macrohabitat for the Trinity bristle snail is not continuous or homogeneous macrohabitat structure . Instead, the pattern reflects a patchwork of mixed-conifer and hardwood forests, and riparian corridors isolated by topography and major southeast-to-northwest

flowing riverine barriers. These corridors are not always contiguous to maintain connectivity among snail populations even through low suitability habitat. This landscape pattern was consistent with the latitudinal orientation of montane corridors and coniferous forest vegetation in the central Greater Trinity Basin and the northwest flow pattern of water in the Trinity River, South Fork Trinity River, and Hayfork Creek.

Historical biogeography predicts that potential dispersal through connecting macrohabitat corridors ranging from medium to low suitability may be inferred from the various suitability levels shown in the model (Whittaker 1961). Notably, from a dispersal and topographic standpoint the Random Point Model further predicts that existing populations occupying high-quality suitable macrohabitat at higher elevations are largely distributed in areas separated by three major riverine systems. These potential riverine barriers included: 1) North Trinity River Area (type locality at Swede Creek), 2) Middle Trinity River-South Fork Trinity River-Hayfork Creek area, Hayfork Creek-South Fork Trinity River area, and 3) the South Fork Trinity River area (Fig. 5). Importantly, there are no obvious connections between blocks or corridors of highly suitable macrohabitat along opposite sides of the southeast-to-northwest flow of the central reach of the Trinity River. Such connections only occur at headwater regions of the New River, South Fork Trinity River, and especially along Hayfork Creek.

Notably, the suitability map provides a macrohabitat envelope framed in a geographic perspective, defined as an ecological representation of a species observed distribution (i.e., realized niche) based on the spatial intersection of multiple attributes (Zarnetske et al. 2007). This framework outlines the location of potential dispersal corridors symbolized by a gradation in the level of habitat suitability from low to critical. Dunk et al. (2004) hypothesized that high-quality habitat zones for large forest-dwelling gastropods may be a function of the density of streams (> 2 km of stream/km^2) in an area. Herein, populations of Trinity bristle snails were all located < 357.8 m from the nearest stream. Historically, these disjunct blocks of "refugial" habitat were likely important "source" areas characterized by long-term population viability, which functioned as centers for dispersal and subsequent gene flow through corridors of less suitable macrohabitat. Notably, the independent landscape pattern of macrohabitat predicted by the suitability model is consistent with patterns of genetic differentiation and the historical biogeographic hypothesis developed for relict populations of the Trinity bristle snail based on recent molecular DNA analyses (Sullivan 2021).

As expected, several areas of gradation in macrohabitat suitability transcend the known range of the Trinity bristle snail and merge into the geographic range of other large-banded forest-dwelling gastropods (Sullivan 2021). Thus, the suitability model developed here likely reflects similar historical and ecological conditions at a macroscale within the range of other sympatric taxa (Futuma 2009). A notable exception being Church's sideband, which occupies a comparatively dryer ecological conditions to the south in Trinity and Tehama counties, and to the east in Shasta County, relative to the more mesic adapted forest-dwelling taxa described above (Dunk et al. 2004; Roth and Sadeghian 2006).

Although environmental suitability models may represent the fundamental ecological niche of a species, these models do not necessarily imply that the species is abundant at a particular location nor do these models necessarily reflect habitat quality. Habitat suitability models only describe the potential distribution of the species or the realized niche in response to current environmental conditions (van Horne 1983; Johnson and Seip 2008). Terrestrial gastropods exhibit low vagility and are unable to emigrate at distances > 50 m under condi-

tions that are suboptimal or ecologically degraded (van der Laan 1971; Roth and Pressley 1986; Dunk et al. 2004). For low-vagility species the area immediately surrounding them (microhabitat) should be a better predictor of survival and reproduction than more distant macroscale areas (van der Laan 1971; Roth and Pressley 1986). A hypothesis advocated by ecological niche theory suggests that habitat suitability may reflect the adaptive landscape of the species (Nagaraju et al. 2013; Mammola et al. 2019). Logically, long-term population viability of should be higher at the core of a taxon's most suitable macrohabitat niche. This is where conditions are assumed to be optimal, rather than at the edges of the range where suitability is assumed to be less optimal (Pulliam 2000). For Trinity bristle snail areas of high and critical habitat suitability predicted by the model connotes conditions that are assumed to be optimal for survival and long-term population viability.

An implicit assumption of all habitat-suitability models is that the predicted ecological niche of a species reflects its adaptive landscape (Futuyma 2009). Accordingly, fitness of individuals of a given species would be expected to increase with increasing habitat suitability (Nagaraju et al. 2013). Validating the functional accuracy of suitability models (i.e., fitness increases with increasing habitat suitability) requires assessing fitness of individuals occupying habitats of differing quality (Tytar and Baidashnikov 2020). Such an effort would necessitate initially identifying the "best quality" habitat for the species, follow-on field investigations of key ecological attributes in natural populations, detailed reproductive and population genetic studies, and should be the focus of future work on Trinity bristle snails.

With climate changing rapidly, terrestrial ectotherms are expected to be extremely vulnerable to changes in temperature and water regimes, which are worsened by an increase in extreme weather events, particularly in temperate regions (Nicolai and Ansart 2017). Herein, the highest loadings obtained in the PCA were a function of average monthly measurements of temperature and precipitation compared to forest stand and topographic variables as predictors. Yet, metrics describing seasonal variation in temperature and precipitation were not informative individually or as composite categories compared to the use of all attributes simultaneously. This outcome suggests that climate may be only one of several factors influencing the species distribution at a macroscale level. Nevertheless, given that terrestrial gastropods are ectotherms, their survival and viability are unquestionably dependent on optimal moisture and temperature regimes for movement, breeding, feeding, and estivation during inclement weather. As cautioned by Beale et al. (2008) and Dunk et al (2014), correlations between climate and the distribution of suitable habitat may only reflect the spatial structure of climate rather than real biological phenomena.

Throughout California, annual average air temperatures have increased since 1895, with temperatures rising at a faster rate beginning in the 1980s (Field et al. 1999; Milanes et al. 2018). Conifers forests occupy less area statewide and in certain regions oaks cover larger areas than in the past (Field et al. 1999). A decline in large conifer trees at higher elevation and an increase in the abundance of shrublands are projected due to statewide increases in regional climatic water deficits. Moreover, because many forest ecosystems in northern California are effectively isolated geographically (Whittaker 1961), even modest climate change increases the vulnerability of disjunct forest and woodland gastropod communities. These predations are particularly ominous given the massive fuel loadings found in forest and woodland ecosystems of California and the realistic prospect of annual uncontrolled forest fires (Sugihara et al 2006).

In a rapidly changing climate terrestrial snails are vulnerable to alteration in the

variance of thermal and water regimes in temperate regions (Nicolai and Ansart 2014). This is because body temperature and basic physiological functions depend upon environmental temperature within narrow limits of tolerance (Gillooly et al. 2001; Deutsch et al. 2008). For example, terrestrial gastropods are susceptible to climate change with minimal physiological resilience to temperature extremes for several reasons. First, their activity and physiology are highly sensitive to fluctuations in local temperatures, inducing many species to enter a state of dormancy when conditions are unfavorable for activity on the soil surface (Cameron 1970; Heller and Ittiel 1990; Iglesias et al. 1996). Second, they depend on a highly dispersed "subterranean niche" that can accommodate temperature, humidity, and space requirements for moving a large adult shell thought interstitial spaces within a saxicolous matrix. Third, their moist skin and secretion of a mucus trail for locomotion make snails sensitive to low hygrometric conditions (Nicolai and Ansart 2014). Fourth, their slowness and high cost of movement greatly limits their ability to actively and timely escape the onset of hostile environments (Denny 1980).

Although extreme variance in future climatic regimes may not portend bioregional extirpation of a species, it does attest to the need for greater exploration of climate related phenomenon for Trinity bristle snails. This effort requires continuing research on the relationship of climate to persistence of this and other forest-dwelling gastropods in the ecoregion and throughout California. Given their life history attributes, the rapidity and severity of extreme future climatic regimes requires that vulnerable populations and their critical spatial regions be identified if conservation is to succeed (Urban 2015; Nicolai and Ansart 2017; Prugh et al. 20180).

Given potential vulnerability of Trinity bristle snail to climate change as discussed above, I predict that climate change will have the following impacts on Trinity bristle snails: 1) densities of snails will decrease as a function of increased variability in the physical macro- and micro-environment; 2) populations will retreat to higher elevations encompassed by dwindling acreages of highly suitable habitat that will degrade or disappear entirely over time; 3) corridors of low suitability connecting high quality macrohabitat will shrink, become less suitable, or disappear; 4) populations at the edge of their range will be at a high risk of extirpation (Wiens 2016); 5) existing topographic and riverine barriers to dispersal will be more effective at facilitating isolation, inbreeding depression, and extinction (Sullivan 2021); and 6) there will be a dramatic reduction in the taxonomic diversity of species at the community-level.

Considerations and Management Recommendations

Development of management and conservation plans for terrestrial gastropods in ecologically impacted regions of the Pacific Northwest is key to successful management of Special Status Species (Duncan et al. 2003; Dunk et al. 2004). This effort is in its infancy and will require a profound understanding of the natural history of endemic terrestrial snails and their preferred habitat at multiple scales. My study identified important range-wide suitable macrohabitat relationships for the Trinity bristle snail that can inform conservation and planning decisions and serves as a defensible method for conducting similar habitat assessments for the ~117 other special status species of gastropods in California. Like the Trinity bristle snail, many of these taxa are rare and at risk to land management activities within forests in northern California and the Pacific Northwest (Duncan et al. 2003; Dunk et al. 2004; Furnish et al. 2007). Some of these are likely to be designated for future status

assessments and conservation planning initiatives (i.e., Shasta chaparral snail [*Trilobopsis roperi*], Tehama chaparral snail [*Trilobopsis tehamana*], and Big Bar Hesperian snail [*Vespericola pressleyi*]).

Like all habitat suitability models, future iterations should include additional new data on the species distribution. Knowledge of habitat suitability is critical to identify and conserve important habitats for species and information provided from this study will allow resource managers to intervene and prevent or mitigate effects of anthropogenic landscape or climate change on Trinity bristle snails, including from forest timber harvesting, highway construction projects, stream-bed alteration or degradation, marijuana cultivation, and perpetual changes in climate that are management concerns in California (Cabeza et al. 2004; Strauss and Biedermann 2005). Importantly, a macrohabitat suitability assessment like this one for Trinity bristle snails provides guidance in determining the need for follow-on population-level microhabitat assessments prior to any land management action. Such knowledge facilitates and expedites more efficient survey, assessment, and budgetary processes (Hirzel and Guisan 2002).

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Appendix I. Summary of the Principal Components Analysis for the first three principal components (PCs) of selection criteria used in modeling macrohabitat at Trinity bristle snails sample sites (n = 333) based on the CALVEG and CWHR systems. Abbreviations for forest cover-types and tree stand structural elements within each category are: 1) CALVEG REGIONAL DOMINANCE COVER-TYPE (DF = Douglas fir, DP = Douglas fir-Ponderosa pine [*Pinus ponderosa*]), DW = Douglas fir-white fir, QG = Oregon white oak [*Quercus garryana*], QC = Canyon live oak, QT = Tanoak-Pacific madrone, MP = mixed conifer pine); 2) CALVEG SAF COVER-TYPE (white fir = 211, Douglas fir = 229, Oregon white oak = 233, Sierra Nevada mixed conifer = 243, Ponderosa pine-Douglas fir = 244, California black oak [*Quercus kelloggii*] = 246, blue oak [*Quercus douglasii*]-digger pine [*P. sabiniana*) = 250); 3) CALVEG VEGETATION COVER-TYPE; 4) CWHR COVER-TYPE (DFR = Douglas fir, MHW = montane hardwood, SMC = Sierra mixed conifer, WFR = white fir; MCP = montane chaparral, AGS = annual grass, BOP = blue oak-digger pine; 5) CWHR LIFE-FORM COVER-TYPE (WHR-CON = conifer forest, CWHR-HDW = hardwood forest, CWHR-MIX = mixed conifer-hardwood forest, CHDW = Hardwood forest-woodland, CHEB = herbaceous dominated habitats, CSHB = shrub dominated habitats); 6) CALVEG AGGREGATION TYPE (G = grouped aggregations, H = homogeneous aggregations); 7) CALVEG CON-CFA = conifer forest); 8) CALVEG HDW-CFA = hardwood forest); and 9) CALVEG OS-TREE DIAMETER CLASS (overstory tree diameter breast height [DBH]).

Category and GIS selection criteria	Principal components		
Forest cover-type variables (total variance explained = 86.5%)	PC I (43.9%)	PC II (29.0%)	PC III (13.6%)
1. CALVEG REGIONAL DOMINANCE COVER-TYPE	0.750	0.103	0.584
2. CALVEG SAF COVER-TYPE	-0.514	0.679	0.380
3. CALVEG VEGETATION COVER-TYPE	-0.646	0.620	-0.023
4. CWHR COVER-TYPE	0.819	0.389	-0.029
5. CWHR LIFE-FORM COVER-TYPE	0.531	0.665	-0.440
Forest stand and tree structure (total variance explained = 84.6%)	PC I (36.7%)	PC II (31.3%)	P III (16.6%)
6. CALVEG AGGREGATION-TYPE	0.757	-0.275	-0.427
7. CALVEG CON-CFA > 4.8 m	0.692	0.454	-0.159
8. CALVEG HWD-CFA > 4.8 m	0.581	-0.568	0.578
9. CALVEG OS-TREE DIAMETER CLASS > 2.1 m	0.227	0.806	0.352
Minimum monthly temperatures C° (Total variance explained = 94.3%)	PC I (70.5%)	PC II (20.3%)	P III (3.5%)
10. January > -3.3 and < 1.1	0.900	0.062	0.307
11. February > -2.7 and < 2.2	0.887	-0.392	0.109
12. March > -2.8 and < 3.3	0.824	-0.532	0.021
13. April > -2.2 and < 4.4	0.637	-0.732	-0.162
14. May > 2.2 and < 6.7	0.891	-0.331	0.155
15. June > 6.1 and < 9.4	0.951	0.072	0.132
16. July > 8.9 and < 12.8	0.817	0.497	-0.047
17. August > 8.3 and < 12.2	0.836	0.451	0.077
18. September > 5.6 and < 11.1	0.636	0.737	-0.175
19. October > 2.2 and < 7.8	0.697	0.678	-0.052
20. November > -0.6 and < 3.3	0.827	-0.236	-0.489
21. December > -2.2 and < 1.7	0.942	-0.178	0.013
22 Annual average > 2.2 and < 6.1	0.974	0.062	-0.038

Appendix I (continued)

Maximum monthly temperature C° (total variance explained = 96.5%)	PC I (89.2%)	PC II (4.1%)	P III (3.2%)
23. January > 6.7 and < 10.0	0.914	-0.040	-0.386
24. February > 9.4 and < 12.8	0.860	-0.492	-0.073
25. March > 12.2 and < 16.1	0.910	-0.396	-0.024
26. April > 15.6 and < 20.0	0.971	0.007	0.174
27. May > 20.6 and < 25.0	0.972	0.019	0.201
28. June > 25.6 and < 30.0	0.980	0.027	0.126
29. July > 30.6 and < 34.4	0.975	0.090	0.151
30. August > 30.6 and < 34.4	0.961	0.025	0.250
31. September > 27.2 and < 34.4	0.910	0.161	0.001
32. October > 20.0 and < 23.3	0.956	0.126	-0.123
33. November > 10.0 and < 13.3	0.956	0.111	-0.118
34. December > 6.1 and < 9.4	0.914	0.246	-0.255
35. Annual average > 17.8 and < 21.7	0.992	0.061	0.026
Monthly precipitation cm (total variance explained = 83.2%)	PC I (65.8%)	PC II (8.2%)	PC III (8.2%)
36. January > 16.8 and < 30.5	0.952	0.058	0.057
37. February > 13.2 and < 26.2	0.970	0.023	0.030
38. March > 11.9 and < 23.6	0.985	0.011	0.019
39. April > 5.7 and < 10.9	0.954	-0.010	-0.068
40. May > 1.9 and < 4.6	0.911	0.129	0.082
41. June > 0.6 and < 2.0	0.318	0.144	0.853
42. July > 0.6	-0.085	0.786	-0.083
43. August > 0.6 and < 2.0	0.593	0.094	-0.546
44. September > 3.2 and < 4.6	0.285	-0.720	0.045
45. October > 5.7 and < 12.2	0.891	-0.090	-0.109
46. November > 15.9 and < 29.7	0.966	0.016	0.015
47. December > 17.2 and < 31.0	0.958	0.037	0.007
48. Annual total > 99.1 and < 170.2	0.991	0.017	0.005
Topographic/distance to stream (total variance explained = 76.9%)	PC I (37.7%)	PC II (24.9%)	P III (14.4%)
49. Aspect < 60°	0.665	0.453	-0.080
50. Distance to nearest stream (m) > 0.114 < 357.8	-0.589	0.560	0.255
51. Elevation (m) > 204 and < 1605	-0.803	-0.042	0.347
52. Hill-shade > 18 and < 254	0.275	0.772	0.201
53. Slope < 46°	0.611	-0.355	0.699

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FULL RESEARCH ARTICLE

Microhabitat Characteristics and Management of the Trinity Bristle Snail in the Greater Trinity Basin of Northern California

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Microhabitat assessment of the Trinity bristle snail (*Monadenia setosa*), a state threatened species, was conducted at 88 randomly selected sites throughout its known geographic range in northern California. Nineteen abiotic and biotic environmental variables were measured for each site. Results of univariate and multivariate analyses indicate that sample sites were dominated by physical parameters of air and soil temperature, and elevation and exposure in association with habitat structure consisting of the presence, size, and nearness of large woody debris, rocky surface and subsurface structure, and riparian stream corridors, respectively. No individual or small suite of attributes defined microhabitat suitability for the species based on site-specific characteristics. Instead, a robust combination of physical and biological variables was key to the distribution of specimens at the population-level, most of which were allied with structural elements of the sample site.

Key words: ecology, assessment, *Monadenia setosa*, threatened species, terrestrial gastropod

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An important aspect of species management and conservation is knowledge of the habitat on which a species depends (Noss et al. 1997). Variance in abiotic and biotic parameters across the landscape enable a species to preferentially select features and conditions at multiple spatial scales (Orians and Wittenberger 1991; Morris 2003). Combined with general habitat characteristics, knowledge of spatial and temporal habitat selection can aid in management and protection of microhabitat and landscape-level features required by a species (Morrison 2001; Miller and Hobbs 2007). For terrestrial gastropods, selection of microhabitat features is predominantly static. Unlike highly mobile species, terrestrial mollusks do not alter their preferred habitat based on daily or seasonal variances. Instead, natural habitat alterations affecting terrestrial snails are generally a function of historical events involving major geologic, topographic, or ecological transformations of the landscape (Foster and Ziegltrum 2013). Terrestrial gastropods preferentially select areas based on microhabitat parameters, which are often more important than macroscale features for thermoregulation, foraging, and predator avoidance (Brown and Maurer 1989; Nicolai and Ansart 2017). Yet little is known about the microhabitats or fine-scale structural features

(i.e., ground cover, vegetation, surface substrate, subsurface structure and composition) within large-scale macrohabitat selected by this diverse invertebrate group.

In northern California, the Trinity bristle snail (*Monadenia setosa*) is a rare and large terrestrial forest-dwelling gastropod found entirely within the Southern Klamath Mountains of the Greater Trinity Basin (Fig. 1). The species range is estimated to be ~1,484 km² or ~17.9% of the total area encompassed by Trinity County jurisdictional boundaries (n = 8,307 km2). This taxon is a California threatened species consisting of five subspecies (Sullivan 2021). Populations of this taxon are considered relicts of the Late (Upper) Pleistocene Epoch (~ 129,000 and c. 11,700 years ago). when local climate was much cooler and more mesic than today (Talmadge 1952). These populations are currently separated by topographic discontinuities, corridors of riparian vegetation, and major riverine barriers. Extant populations inhabit isolated and highly fragmented locations along both sides of the western-most segment of the Trinity River, New River, South Fork of the Trinity River, Hayfork Creek, and along the east slope of South Fork Mountain along the Trinity-Humboldt County divide.

The ecology and habitat preferences of large forest-dwelling terrestrial gastropods in the Pacific Northwest are poorly documented and quantified, and habitat accounts are often anecdotal or based on a modest amount of research done on related taxa (Furnish et al. 1997; Kelley et al. 1999; Duncan et al. 2003; Foster and Ziegltrum 2013). In their analysis of rare forest mollusks of Northern California, Dunk et al. (2004) found that published information on the ecology of the three largest species in the genus *Monadenia* was practically

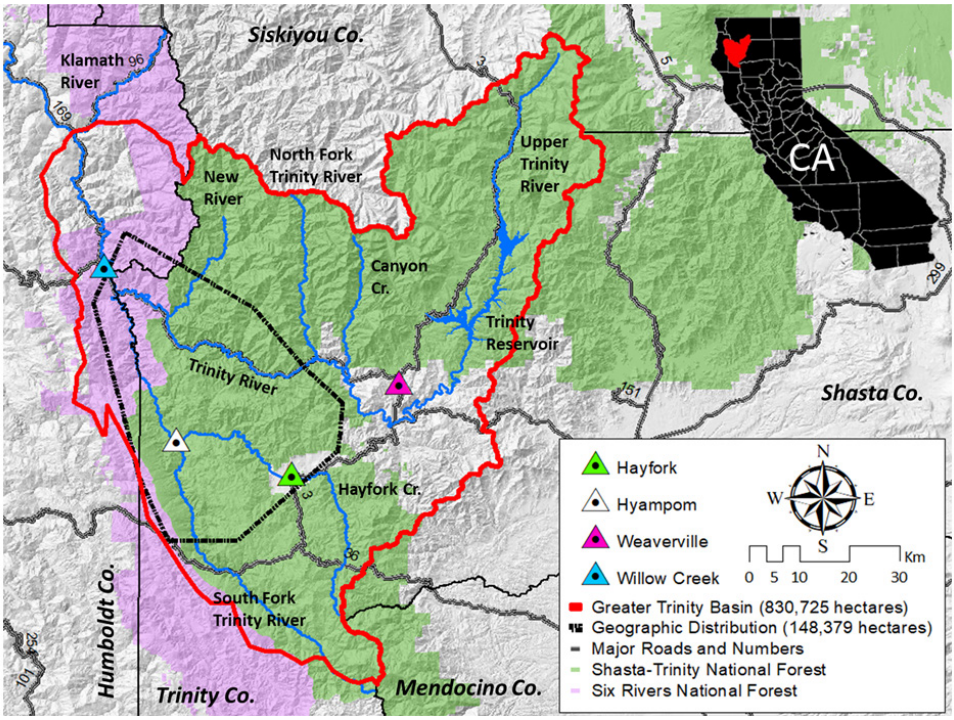


Figure 1. Map of the known geographic distribution of the Trinity bristle snail showing topographic relief, major river systems, distribution of national forests, referenced to major towns within the Greater Trinity Basin of Trinity and eastern Humboldt counties.

nonexistent. However, Dunk et al. (2004) did not identify or include the Trinity bristle snail in their predictive macroscale habitat modeling for taxa sensitive to management activities on public lands, even though the geographic distribution of the Trinity bristle snail is surrounded by all the species they studied (Sullivan 2021). Similarly, previous studies of the Trinity bristle snail also lack the ecological detail and geographic scope necessary to assess habitat requirements for purposes of management and conservation (Talmadge 1952; Walton 1963; Roth 1978; Armijo 1979; Roth and Eng 1980; Roth 1982; Roth and Pressley 1986). To date, there is no published literature that has quantified fine-scale structural features of the microhabitat within larger-scale macrohabitat selected by this species.

Both geographic and microhabitat information are required for evaluation of species listing status, management, and conservation planning (Sanderson et al. 2002). Recently, I developed a macroscale habitat suitability model of the Trinity bristle snail in which macrohabitat was delineated throughout the known range of the species (Sullivan 2022). My study did not, however, address quantification of population-level microhabitat variables at each site sampled. Instead, I focused on delineating suitable habitat at a macroscale using a geographic information system (GIS) format. Importantly, microhabitat site assessments are necessary to refine determination of suitable habitat for a species once it is identified at the landscape-level. Therefore, the purpose of my study was twofold. First, I provide a proactive approach to microhabitat assessment aimed at preventing this unique endemic mollusk from being listed as a state endangered species. Second, I provide resource managers with a more complete understanding of the factors influencing the relationship between occurrence and microhabitat selection by the Trinity bristle snail. The specific objectives were to provide an update on the general ecology of the species, identify and describe microhabitat parameters characteristic of sites sampled for the species, provide a quantifiable and statistical basis for evaluating microhabitat metrics, and suggest population-level management recommendations for conservation purposes.

METHODS

Study Area

The study area was confined to the known geographic distribution of the species (Fig. 1) located within in the Greater Trinity Basin watershed (~7,600 km²). It includes geographic regions throughout the northwestern segment of the Trinity River and its tributaries in Trinity and adjacent eastern Humboldt counties, including portions of both the Shasta-Trinity and Six Rivers national forests (Fig. 1). The watershed is almost entirely covered by mountains, with the only level land in a few narrow valleys (i.e., Weaverville Basin, and Hoopa, Hyampom and Hayfork valleys; USFS 2005). These areas are dominated by mixed conifer and hardwood forest, with riparian corridors of white alder (*Alnus rhombifolia*), big leaf maple (*Acer macrophyllum*), and willow (*Salix* spp.), whereas upland environs are characterized by a deciduous hardwood understory of Pacific madrone (*Arbutus menziesii*), giant chinquapin (*Castanopsis chrysophylla*), tanoak (*Lithocarpus densiflorus*), and canyon live oak (*Quercus chrysolepis*). The overall climate is Mediterranean, with cool, wet winters and hot, dry summers. Annual precipitation over the Trinity River watershed averages ~1,400 mm. Annual precipitation ranges from 940 mm in lowlands around Weaverville and Hayfork, to as high as 2,200 mm at higher elevations (Barrett 1966). High rainfall combined with rugged geography results in extremely fast runoff and a high risk of flooding during winter

storms, which result in large volumes of rocks and sediment carried by floods spread along rivers forming wide alluvial channels (Barrett 1966).

Survey Method

A total of 88 sample sites were randomly selected from throughout the known range of the species focused on known ecological and microhabitat descriptions based on historical qualitative accounts (Talmadge 1952; Roth 1978; Roth and Eng 1980). Live active snails were sampled during warm wet, foggy, or rainy conditions during the months of March, April, May, September, and October over a two-year period (2008 – 2009). Snails were most active between dusk and dawn during the months of May and October when ambient air is cool and humid. Surveys were conducted after three days of saturating rains, two hours before and after sun-up, or during the first two hours after dark (Roth and Pressley 1986). Coastal species, such as adult Pomo bronze shoulderband snail (*Helminthoglypta arrosa*; van der Laan 1971), have been observed to emerge from estivation and begin mating within 24 hours after the first soaking rain in October, both at night and on overcast and rainy days. During cold winter or more arid summer months, inactive live Trinity bristle snails were found sealed in their subterranean estivation chambers well below the ground surface.

Surveys were conducted: 1) at the surface of the soil; 2) within the soil-laden leaf litter to a depth of > 3 cm; 3) under objects large enough to accommodate a large-bodied adult shell (i.e., large moss-covered boulders, slabs of thick sluffed-off bark from snags, dead wood, talus, etc.); 4) on tree trunks and dead standing branches; 5) at the base of Pacific madrone and tan oak root wads, and 6) in other crevices associated with a well-developed organic soil base. Snails were hand-picked in focal areas of a 10-m radius using by visually searching for individuals. This method was rapid and entailed neither degradation nor removal of the soil (Gotmark et al. 2008; Raheem et al. 2008). 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).

Although the shell of the Trinity bristle snail is one of the largest in the genus, it is thin and prone to rapid decomposition, which complicates the survey process (Appendix I). Shells in various stages of decomposition were found at all sites where accumulations of shells were found. Accretions of shells were particularly evident within large accumulations of buried boulders, well-developed and deep subterranean structure, and internal spacing within the saxicolous matrix. Buried intact shells were relatively rare given the thin nature of the shell, a condition likely a function of rapid decomposition under humid conditions, compared to thicker more mineralized shells found in other taxa (Sullivan 1996). Efforts to locate snails were facilitated when shells washed or drifted down from suitable habitat at higher elevations onto well-worn deer trails, catchments, or other depressions that prevented scattering.

Microhabitat Assessment

Nineteen microhabitat attributes were measured at each site (n = 88 sites) where live Trinity bristle snails were found and identified by use of molecular DNA analyses (Sullivan 2021; Table 1). These microhabitat attributes provided a detailed, proximate-level assessment of the surroundings associated with the physical and biological conditions found at each

Table 1. Microhabitat attributes measured at each site (n = 88) where live Trinity bristle snails were sampled; DBH = diameter breast height.

Component and variable	Component and variable
Physical component	**Substrate component**
1. Elevation (m)	10. Percent dominant substrate (< 10 m radius of sample)
2. Exposure/aspect (degrees)	11. Substrate upon which a snail was first observed
3. Slope (degrees) represented the average percentage slope for a 10 m radius around the sample site as measured by a clinometer	12. Type of large woody debris
4. Air temperature (°C)	13. Size large woody debris (cm
5. Soil temperature (°C)	14. Depth leaf litter (cm)
	15. Distance to nearest rock habitat (m)
	16. Size distribution of rock type (diameter cm)
Vegetation component	
6. Dominance ranking among plant species (< 10 m radius of sample)	**Riparian component**
7. Overstory vegetation (%)	17 Distance to nearest stream/drainage (m)
8. Distance to nearest tree (> 15.2 cm DBH) or shrub (< 15.2 cm DBH) in meters	18. Relative water availability (annual, ephemeral, perennial)
9. Distance to nearest large woody debris (m)	19. Stream classification (1 [fish bearing], 2, 3, 4)

sample location, which were considered "optimal" for terrestrial snails inhabiting mixed conifer, riparian, and hardwood forest communities (Sullivan 2022).

Statistical Analyses

All statistical analyses performed used R (R Core Team 2021) and statistical significance was set at $\alpha < 0.05$. Normality was evaluated in all microhabitat variables using distribution plots and Anderson-Darling tests (AD). The Akaike's Information Criterion (AIC; Akaike 1973) was used as a goodness of fit statistic to compare various theoretical distributions as applied to the data. Principal components analysis (PCA) identified variable selection, examined the extent of association among habitat attributes, and assessed the relative ability of attributes to explain variation among sites (Smartt and Sullivan 1990; Sullivan and Smartt 1995; Sullivan 1996; Sullivan 1997). This procedure minimized multicollinearity between model predictors, with the goal of identifying a smaller subset of variable components that capture the majority of variance in predictors (Everitt and Hothorn 2011). Kruskal-Wallis Chi-square rank sum tests ($\chi 2$) evaluated post-hoc delineations of clustered samples by PCA. Nonparametric Spearman's rank correlation (rs; 2-tailed test) was used to calculate the strength and direction of the relationship between any two variables expressed as a monotonic relationship, whether linear or not (Corder and Foreman 2014). Kolmogorov–Smirnov two-sided test (KS) was used to compare the percent frequency distribution between two samples because it is sensitive to differences in both location and shape of the empirical cumulative distribution functions of the two samples (Marozzi 2013).

Generalized additive models (GAM) were used in all regressions (Wood 2017). This method: 1) is a semi-parametric extension of Generalized Linear Models (GLM) that is less restrictive in assumptions about the underlying distribution of data, 2) is effective for assessing non-linear relationships between response and explanatory variables (Hastie and Tibshirani 1990; Madsen and Thyregod 2011), 3) generally gives the best mean square error performance and optimal smoother of any given basis dimension, and 4) avoids the

need to make prior assumptions about the shape of the function (Schluter 1988). Because all data were not normally distributed, a gamma error-structure was used to establish the relationship between response variables and the smoothed functions of predictor variables (Appendix II; Wood et al. 2016). Statistics reported from each GAM included the F-statistic (approximate significance of smooth terms), p-value, and 95% confidence bands for spline lines (Nychka 1988). Spearman's rank correlation coefficient was used as a follow-on statistic to assess strength and significance of trends in data delineated by smooth terms (Diankha and Thiaw 2016).

RESULTS

Microhabitat Assessment of Trees and Shrubs

The most common species of plants found within a 10-m radius of each site where Trinity bristle snails were sampled included: 1) Douglas fir (*Pseudotsuga menziesii*; 100%), 2) Pacific madrone (100%), 3) tanoak (90.9%), 4) big leaf maple (87.5%), and 5) sword fern (*Polystichum munitum*; 87.5%; Fig. 2A). An additional nine species of trees and shrubs were observed within these samples, but they occurred < 60.0% of the time. Poison oak (*Toxicodendron diversilobum*) was particularly common (59.1%) at sample sites where live snails and accumulations of shells were found. Assessment of the relative dominance ranking of plants indicated how prevalent each species of tree or shrub was within each 10-m radius sample. Douglas fir occurred in 100% of all samples. It was the most dominant species of plant in 52.3% of the samples, the second most dominant taxon in 36.4% of the samples, and the fourth most dominant plant in 11.4% of the samples. Oregon white oak (*Quercus garryana*) occurred in 31.8% of all samples yet compared to all other species of plants it ranked fifth, sixth, and seventh in abundance 8.0%, 13.6%, and 10.2% of the time, respectively. Within riparian habitat along lower Swede Creek, the type locality for the Trinity bristle snail (Talmadge 1952; Sullivan 2021), specimens were always found within the hardwood understory of big leaf maple, Pacific dogwood tree (*Cornus nuttallii*), California Hazel (*Corylus cornuta*), tan oak, and in the lowers reaches of the range, white alder. On riparian benches Trinity bristle snails were not found living farther from the stream than the growth of plant communities containing Pacific dogwood and big leaf maple (Roth 1978).

Microhabitat Assessment of Physical Parameters

Basic statistics and results of the Anderson-Darling (AD) tests for all continuously distributed microhabitat variables are found in Appendix II. These analyses showed that all variables were not normally distributed and that the distribution of each variable most closely (62.5%) approximated a Gamma distribution based on AIC goodness of fit criteria (Appendix III). In those variables that most closely followed a lognormal distribution (38.5%) the difference between the two theoretical distribution types was minimal. Follow-on rank correlation analyses showing the strength of association and the level of statistical significance between each pair of physical and ecological microhabitat variables are provided in Appendix IV.

Elevation, exposure, and slope.—Elevation averaged 782.0 m (n = 54; min = 310; max = 1,378) and most sites (64.0 %) were located above ~800 m in elevation. Among

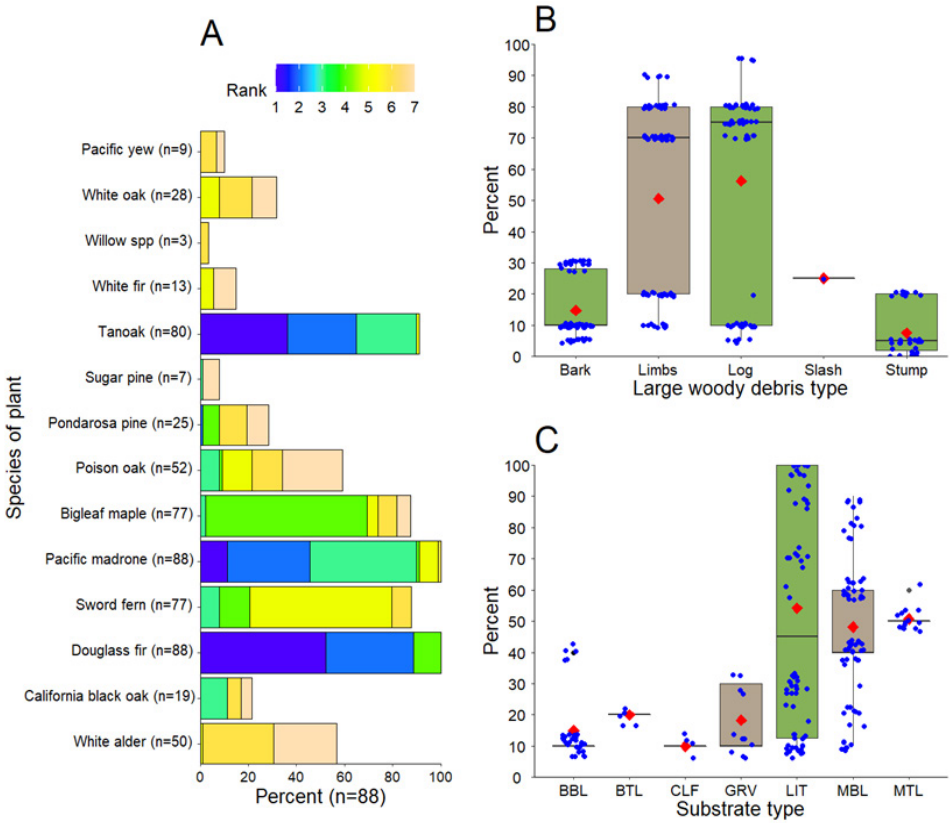


Figure 2. A) Bar graph of microhabitat attributes that summarize plant species composition within a 10-m radius of where each Trinity bristle snail was sampled (n = 88 sites). Sample size (n) of plants counted are surrounded by parentheses; and the rank of the species in the sample (1 = high, 7 = low) are indicated in the legend. Boxplots indicate the percent composition of the type of: B) large woody debris and C) substrate found at each sample site. Horizontal lines represent the median of each attribute, whiskers are the bounds of the minimum and maximum values, blue dots are values outside of the interquartile range, and red diamonds are mean values.

physical parameters, only slope was significantly and negatively correlated with the elevation of the sample site (Fig. 3A). Thus, as elevation increased slope decreased. Sites where live Trinity bristle snails were sampled had northern (37.5%), northeastern (17.0%), eastern (21.6%), or northwestern (23.9%) exposures, all of which were characteristic of shaded mesic environmental conditions ($\bar{x}$ = 102.8°; min = 1.0°; max = 315.0°; n = 88). None of the sites sampled had more arid facing slopes (S, SW, W). Occasionally shells were found on both east- and west-facing canyon slopes that had abundant shade with shallow sloping surfaces characteristic of small disjunct enclaves of suitable microhabitat. Snails were not found on south facing slopes fronting the Trinity River, Hayfork Creek, or windswept western exposures along the white fir (*Abies concolor*) dominated backbone of South Fork Mountain that runs east-to-west. There was no significant relationship between exposure and any of the other physical parameters measured (Appendix IV). Roth (1978) describes snails inhabiting areas of deep to moderate shade, but lightly shaded areas of exposed side hills and upper slopes yielded no specimens. Slope averaged 54.0° (min = 20°; max = 65°, n = 88) with 69.3% of the sample sites having a slope > 50°. Even at higher elevations,

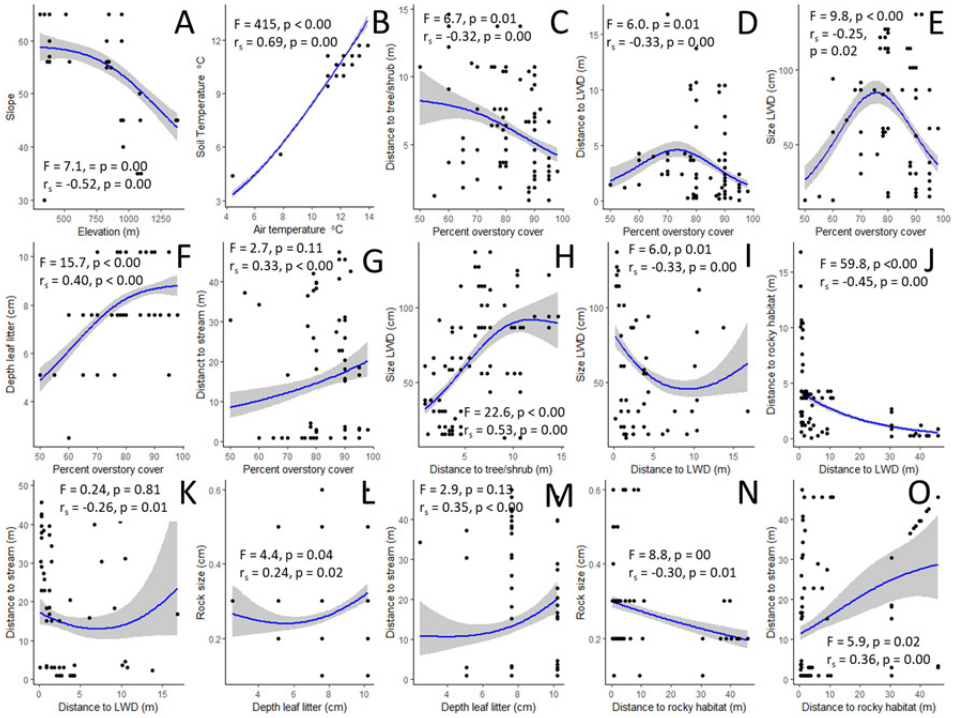


Figure 3. Generalized additive model (GAM) regressions of continuously distributed physical and ecological variables measured at each site where snails were sampled. Each GAM shows the F-statistic for the smooth and the Spearman rank correlation coefficient (r_s).

snails preferred shallower more stable slopes with less downward movement of the soil or substrate matrix. Both elevation and exposure exhibited the greatest degree of variation among all physical microhabitat metrics measured attributes (Appendix II).

Air and substrate temperature.—Air temperature averaged 11.3 °C (min = 4.1 °C; max = 13.9 °C), with 84.1% of all sample sites having an air temperature > 10 °C. This range of temperature facilitated diurnal and nocturnal activity by snails on the surface of a particular substrate as these conditions were generally associated with warm and often saturating rains. Similarly, 55.7% of all sample sites had a substrate surface temperature > 10 °C upon which live snails were first observed ($\bar{x}$ = 10.0 °C; min = 4.4 °C; max = 11.7 °C). As expected, air and substrate temperatures were significantly correlated (Fig. 3B), such that as air temperature increased so did the substrate temperature upon which snails were observed when sampled.

Microhabitat Assessment of Ecological Parameters

Percent over-story vegetation cover.—Percent over-story vegetation averaged 76.0% (45% – 95%) with 62.5% of all sites having > 80% overstory cover. This contrasts sharply with estimates derived from geographically mapped GIS sites of > 30% for conifers and > 15% for hardwood stands (n = 333; Sullivan 2022). In this comparison, the CALVEG

vector layer of cover-type information associated with macroscale measures of over-story cover likely underestimates the amount of over-story cover need by Trinity bristle snails. Among ecological attributes, overstory vegetation was significantly and negatively correlated with: 1) distance to the nearest tree or shrub, large woody debris, and size of large woody debris, but significantly and positively correlated with depth of leaf litter, and distance to the nearest stream, respectively (Figs. 3C, 3D, 3E, and 3F). Thus, as percent overstory cover increased distance to the nearest stream, distance to the nearest large woody debris, and size of large woody debris decreased, whereas the depth of leaf litter and distance to the nearest stream increased.

Distance to nearest tree or shrub.—Average distance to the nearest tree or shrub was 6.0 m (min = 0.9 m; max = 14.6 m); and 79.6% of all sample sites were within < 10 m of a tree or shrub. Structurally the most common species of trees (> 15.2 cm DBH) found at these locations were: 1) Douglas fir (44.4%), 2) tan oak (35.2%), 3) big leaf maple (11.1%), and 4) Pacific madrone (9.4%). The most common species of shrubs (≤ 15.2 cm DBH) were: 1) tan oak (27.8%), 2) Pacific madrone (20.4%), 3) sword fern (18.5%), 4) big leaf maple (11.1%), 5) poison oak (9.3%), 6) willow (9.3%), and 7) Douglas fir saplings (3.7%). Distance to the nearest tree or shrub was only significantly and positively correlated with the size of large woody debris (Fig. 3H).

Distance to the nearest large woody debris.—Average distance to the nearest large woody debris was 3.3 m (min = 0.1 m; max = 16.8 m). This variable was significantly but negatively correlated with size of large woody debris, distance to nearest rocky habitat, and distance to nearest stream (Figs. 3I, 3J, and 3K). Results of the correlation analysis showed that as distance to the nearest large woody debris increased, the size of large woody debris, distance to the nearest rocky habitat, and size of the rock substrate decreased.

Type and size of large wood debris.—Common types of large woody debris found within a 10-m radius of where snails were sampled included: 1) upright decomposing older-growth stumps (6.8%), 2) decomposing logs (28.4%), 3) limbs (50.0%), and 4) slabs of bark (14.8%) (Fig. 4). The full range of variation for both microhabitat attributes is illustrated in Fig. 2B. The average diameter of large woody debris within sample sites was 64.3 cm (min = 12.7 cm; max = 137.2 cm) and 81.8% of the debris < 100 cm in diameter. Size of the nearest large woody debris was significantly and negatively correlated with overstory vegetation and distance to the nearest largest woody debris, but positively correlated with distance to the nearest tree or shrub as reported above (Figs. 3E, 3H, and 3I). Therefore, as the size of large woody debris increased both percent overstory vegetation and distance to the nearest woody debris decreased. Distance to the nearest tree or shrub increased with increasing size of large woody debris, which was a function of the increased spacing pattern among large trees.

Predominant substrate type and depth of leaflitter.—Even during the most optimal suitable climatic conditions (warm early spring weather > 3 days of saturating rains) the number of snails observed on the surface of various substrates was few. For example, in an area of approximately 2.8 m² of Pacific madrone leaves and moss saturated by fog and rain a total of only eight adult Trinity bristle snails were observed moving on watered leaf surfaces (Figs. 4A and 4B). This was the maximum number of Trinity bristle snails encountered throughout all surveys. The averaged percent composition of the dominant substrate found within a 10-m radius of each site where live Trinity bristle snails were sampled consisted of: 1) moss-covered boulders ($\bar{x}$ = 58.0%), 2) leaf litter leaf litter ($\bar{x}$ = 54.2%), 3) bare talus

Figure 4. Photos of: A) a Pacific madrone hardwood stand where, B) a Trinity bristle snail traversing wet fog-drip madrone leaves, C) moss-covered Douglas fir tree stump, and D) a sugar pine stump with associated large sluffed-off slabs of bark where live snails found. The snail was moving on the surface of madrone leaves that were wet with rain and fog drip. Its fleshy foot is visible in upper photo on dead Pacific madrone leaves.

($\bar{x}$ = 20.0%), 4) gravel ($\bar{x}$ = 18.3%), 5) bare boulders (15.0%), and cliffs ($\bar{x}$ = 10.0%; Fig. 2C). At the surface, depth of leaf litter averaged 8.1 cm (min = 2.5 cm; max = 10.2 cm) and was only significantly correlated with overstory vegetation and rock size (Figs. 3F and 3L). Roth (1978), however, never found live specimens at depths > 5 cm in leaf-mold.

Substrate snails were most commonly found upon.—In contrast to the measure of predominant substrate, the substrate which live adult snails were first observed upon when sampled consisted of: 1) moss covered boulders or talus (44.3%), 2) on or within leaf litter (34.1%), 3) on live plants (10.2%, sword fern, white alder), 4) on bare gravel (3.4%), 5) on logs (2.3%), 6) on or under large slabs of bark (2.3%), 7) on bare soil (2.3%), or 8) on older growth stumps of Douglas fir and sugar pine (1.1%). Roth and Pressley (1986) found that of 92 observations of Trinity bristle snails in riparian habitat, 33% were found on soil or leaf-mold and 21% on bark of alders above ground. All of the other bristle snails (32%) found by these authors were found on objects including: 1) stalks or twigs (15%), 2) logs or deadfalls (9%), 3) rocks (8%), 4) under objects on the ground (4%), or 5) under bark of standing deadwood (3%). In contrast, of the 120 observations of Trinity bristle by Green Diamond Resources Company in upland hardwood and conifer forest habitats, 52% were found in association with large madrone trees, 28% with large conifer woody debris, 13% tan oak or canyon live oak, 4% with large conifer stumps, 2% with large conifer snags, and 1% in leaf litter in open areas (Early et al 2012; Fig. 5). Roth (1978) reported that juvenile

Trinity bristle snails were found inhabiting loose bark of standing broadleaf deadwood (big-leaf maple, white alder, canyon oak) from 0.5 to 3 m above ground level, but they were not found on or in logs on the ground, or in dead trunks of Pacific madrone or conifer species, despite the fact that all of these structural elements were abundant in the area.

Distance to the nearest rocky habitat and size distribution of boulders.—Average distance to the nearest rocky habitat where Trinity bristle snails were sampled was 9.5 m (min = 0.3 m; max = 45.7 m). The average size (diameter) of rock substrates was 25.2 cm (min = 7.6 cm; max = 61.0 cm). Distance to rocky habitat was significantly and negatively correlated with rock size, such that rock size decreased the further away the sample was from rocky habitat (Fig. 3N). Additionally, rock size increased significantly with increasing leaf litter depth and increasing distance away from the nearest stream (Figs. 3L and 3O). Roth (1978) found no obvious correlation between rock type and distribution of Trinity bristle snails, as all rocks in the regions sampled were highly fractured internally, yielding the talus character of the canyon slopes. He also did not find dead specimens (shells) at depths > 8 cm buried among rocks or the talus. Importantly, snails sampled herein were never observed in saxicolous outcroppings that consisted of smooth river rocks that were either buried or exposed, which indicates their absence from actively flowing riverine systems and larger drainages characteristic of fish-bearing streams.

Locating Trinity bristle snails during dry months often required extensive searching

Figure 5. Photographs of examples of upland habitats in which Trinity bristle snails were occasional found in association with: A) east facing slopes in shaded Douglas fir stands, B) shaded Pacific madrone woodlands, C) upslope from seeps in association with big leaf maple trees, saplings, and brush, and D) dense and shaded Douglas fir thickets on relatively flat terrain.

and excavation, particularly during the non-emergence period (i.e., summer, winter months). However, excavations of rocky habitat demonstrated the presence of live estivating individuals and shells within large, spacious, and humid catacombs of their "subterranean" microhabitat (Figs. 6A and 6B). Here, and at other locations within moss-covered boulder fields, estivating snails and accumulations of empty shells were found as deep as 1 m underground. Occupancy at this depth requires spaces that enabled large-shelled adults to migrate from deep within the recesses of boulder piles to the surface of the boulder field when moisture conditions permitted emergence. Snails burrowed deeper when "interstitial" spaces within the rock matrix were open enough for movement, particularly in more arid environs. In summer, snails retreated into deep and moist matrices of underground rock accumulations and retracted into their shells to avoid desiccation by adhering to rocks by secreting one or more epiphragms (seal), which consisted of a membranous partition between the animal and the aperture. Arousal of estivating snails was achieved by dissolving the protective mucus epiphragm, which caps-off the soft body inside the shell.

In all surveys the one composite microhabitat type that was always limiting consisted of large moss-covered boulders situated on cool mesic slopes, where humidity, space, and insulation were sufficient to allow large-shelled adult snails to estivate and overwinter during inclement weather and move vertically through a saxicolous matrix to emerge at the surface, rehydrate, feed, and reproduce. In some situations, not all "apparently" suitable

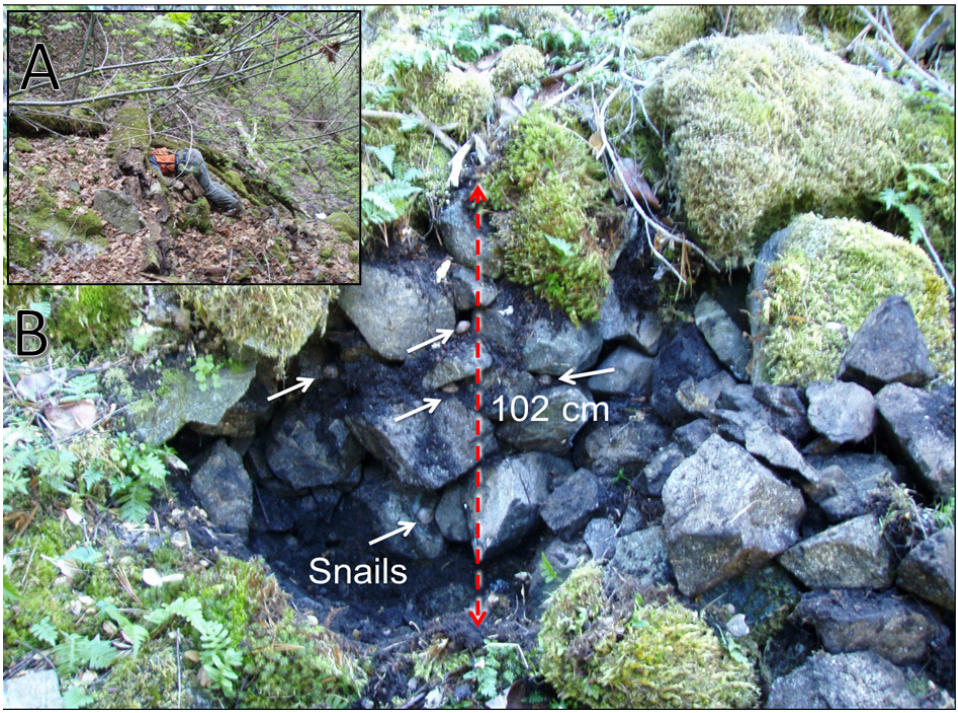


Figure 6. A) Example of an excavation site within big leaf maple and Douglas fir habitat above bank-full located on a shallow bench in a steep and rocky canyon. B) Typical sagittal profile through piles of moss-covered boulders located on a north-facing slope, which included estivating individuals and decomposing accumulations of shells (arrows). Live snails and shells were located within the interstitial matrix large enough to allow movement of large-shelled adults to and from the surface within the catacombs of their saxicolous subterranean niche.

sites were occupied by snails, which could be an indication of the narrow availability of microhabitat requirements within the subterranean recesses of presumed suitable habitat. I found that small-sized boulder fields did not have the combination of piled rock, abundant surface detritus, subterranean accumulations of organic materials, and shaded montane exposures. These areas typically were associated with steep unstable slopes that continue to erode or move down slope, preventing colonization by adjacent forest vegetation even when dispersal was facilitated by warm saturating rains. In these areas live adult snails were sparse in occurrence if they were found at all.

Distance to nearest stream.—Average distance to the nearest stream from each sample site was 15.4 m (min = 1.0 m; range = 47.5 m), compared to an average distance of 81.1 m (min = 0.12 m; max = 357.8) derived from GIS vector models of macrohabitat (Sullivan 2022). Most (80.8%) of the sample sites were affiliated with perennial riparian systems, 19.2% with annual streams, but no samples were collected in association with ephemeral stream-side habitat. In terms of fish-bearing streams, 50.0% were Class two streams, 26.9% were Class three streams, and 23.1% were Class four streams. No snails were found in association with Class one streams or rivers. Distance to the nearest riparian corridor or drainage was significantly correlated with overstory vegetation, depth of leaf litter, and distance to the nearest rocky habitat, but negatively correlated with distance to the nearest large woody debris (Figs. 3C, 3G, 3K, 3M, and 3O, respectively). Because of scale, landscape vector layers used to assess macrohabitat in GIS modeling likely overestimates distance of Trinity bristle snail sites to the nearest drainage basin and its relative proximity to riparian drainages.

In areas adjacent to streams where snails were found, they did not occupy locations below bank-full or directly adjacent to streams where organic materials wash out on a seasonal basis. These areas were typically subject to low frequency "sheet-wash" events resulting from heavy rainstorms that wash away essential leaf litter and organic materials from the soil (Benda et al. 2004). Instead, snails were commonly found in association with segments of the stream bed that wicked water perpendicular to channel migration and current flow typical of high-quality habitat. Areas below bank-full did not characteristically retain organic materials relative to areas above bank-full. Areas above bank full represented non-inundated portions of the drainage and in most conditions retained a soil profile in combination with a well-developed boulder field. These drainage bed conditions allowed persistence of spaces large enough for large-shelled adult snails to move through, while retaining moisture wicked from the nearby stream edge. Thus, steep slopes in more upland drier sites did not provide the quality of habitat found in more moderate slopes, with lush vegetation, and moist conditions.

Trinity bristle snails also used similar rocky habitats associated with the presence of nearby springs and seeps. A laterally narrower range of both hardwood plant species and bristle snails in drainages at lower elevations along the Trinity River, South Fork of the Trinity River, and Hayfork Creek, likely reflects a steeper moisture gradient away from the streambed and its critical organically rich subterranean interstitial spaces. Trinity bristle snails were absent from the wet banks of major rivers, tributaries to the Trinity River, and fast-moving stream systems. These conditions typically lacked well-developed organic leaf litter substrate to support snails and were largely composed of sand with willows subject to washouts during high water.

Principal Components Analysis

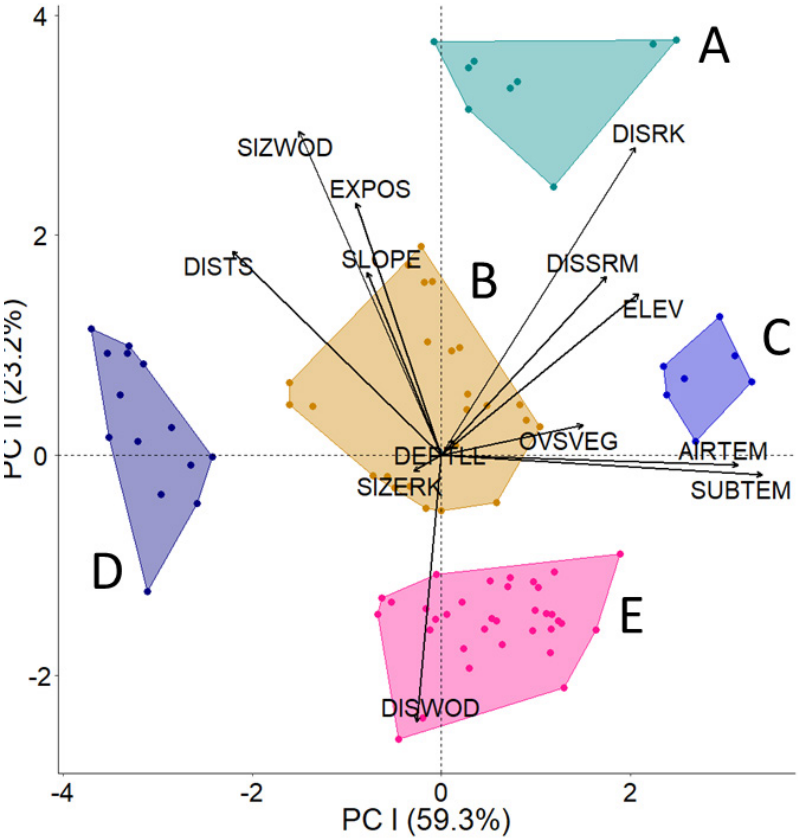
Principal components analysis on all 13 continuously distributed physical and ecological microhabitat parameters accounted for a cumulative 55.5% of the total dispersion (variance) among attributes on the first three factors (Table 2). As shown by vector loadings, relationship, and direction of each arrow, soil temperature followed by air temperature, elevation, distance to the nearest rocky habitat, distance to the nearest riparian corridor or drainage, and percent overstory vegetation had the highest positive loadings along PC I (21.8%; Fig. 7), whereas size of the nearest large woody debris, followed by distance to the nearest rocky habitat, exposure, distance to the nearest shrub or tree, slope, distance to nearest riparian drainage, and elevation vectored with the highest positive loadings along PC II (18.8%). Except for elevation and exposure all other attributes associated with sample sites were loaded negatively along PC III.

Among samples, there were five rather distinct clusters associated with one or more variable vectors based on their overall similarity (Fig. 7). Kruskal-Wallis rank sum tests identified significant differences among these post-hoc clusters along both PCI ($\chi^2 = 57.0$, df = 4, $p < 0.001$) and PC II ($\chi^2 = 70.0$, df = 4, $p < 0.001$). Clustered samples A (10.2%, n

Table 2. Results of the principal components analysis (PCA) of similarities and percent variance explained among environmental variables measured at each site where Trinity bristle snails were sampled.

	Vector		
Component statistic	PC I	PC II	PC III
Standard deviation	1.7	1.6	1.4
Percent of variance	21.4%	18.8%	15.3%
Cumulative percent variance	21.4%	40.2%	55.5%
	Loading		
Variable	PC I	PC II	PC III
1. Elevation	0.318	0.233	0.275
2. Exposure	-0.131	0.371	0.176
3. Slope	-0.112	0.267	-0.447
4. Air (°C)	0.472	-0.022	-0.044
5. Soil (°C)	0.511	-0.036	-0.053
6. Percent overstory vegetation	0.224	0.045	-0.261
7. Distance to nearest tree or shrub (m, < 6 in DBH)	-0.331	0.295	-0.068
8. Distance to nearest large woody debris (m)	-0.042	-0.393	-0.152
9. Size of nearest large woody debris (diameter cm)	-0.221	0.477	-0.023
10. Depth of leaf litter (m)	0.019	0.024	-0.535
11. Distance to nearest rocky habitat (m)	0.315	0.445	0.170
12. Size distribution of rocky type (diameter cm)	-0.049	-0.017	-0.358
13. Distance to nearest drainage (m)	0.268	0.255	-0.386

Figure 7. Principal components analysis of microhabitat attributes associated with each site where Trinity bristle snails were sampled. Clusters of samples are based on their overall similarity. Variable abbreviations are: 1. ELEV = elevation (m), 2. EXPOS = exposure, 3. SLOPE = slope, 4. AIRTEM = air temperature, 5. SUBTEM = soil/substrate temperature, 6. OVSVEG = overstory vegetation, 7. DISTS = distance to nearest tree or shrub, 8. DISWOD = distance to nearest large woody debris, 9. SIZWOD = size distribution of large woody debris, 10. DEPTLL = depth of leaf litter, 11. DISRK = distance to the nearest rocky habitat, 12. SIZERK = size distribution of nearest rock, 13. DISSRM = distance to nearest stream.



= 88) and C (23.9%) were closely aligned with vector variables consisting of nearest rock and stream habitats, elevation, and air and substrate temperatures. Clusters D (23.9%) and E (38.6%) aligned with vector variables associated with distance to the nearest tree and shrub, and large woody debris, respectively. Whereas cluster B (27.3%) aligned with vectors comprising size of the rocky substrate, depth of leaf litter, and overstory vegetation. Samples within this cluster also plotted positively along PC II in association with vectors consisting of slope, exposure, and size of large woody debris. Appendix V illustrates a series of high-quality microhabitats consisting of all shared characteristics described above in composite settings: 1) relatively flat terrain, 2) well-developed overstory vegetation, 3) stable moss- and leaf litter-covered boulder accumulations, 4) a stream side riparian corridor, 5) down and decomposing large woody debris, in association with 6) shaded and cool temperature effects of exposure and slope.

DISCUSSION

Critical Microhabitat

Models that identify potential areas of suitable habitat at a macroscale level generally lack site-specific field studies that quantify proximate-level microhabitat requirements (Dunk et al. 2004; Sullivan 2022). In my study, results of univariate and multivariate analyses indicate that sample sites for the Trinity bristle snail were dominated by physical parameters of air and soil temperature, elevation, and exposure, in association with habitat structure consisting of the presence, nearness, and size of large woody debris, rock surface and subsurface substrates, and riparian stream corridors. These results showed that no single or small suite of attributes defines suitable microhabitat for the species. Instead, a more robust combination of abiotic and biotic variables was key to the distribution of the species at the population-level, most of which were allied with structural elements of the local ecology. A summary of the hypothesized population-level critical microhabitat attributes for the species is provided in Table 3. These data can assist site-specific assessments at more proximate scales of resolution within preferred macrohabitats, facilitate a more focused and efficient pathway to management and conservation planning for the species, and provide a baseline for current and future environmental concerns regarding ecosystem management and conservation of the Trinity bristle snails on both public and private lands (Burke et al. 1999; Furnish et al. 1997; Duncan et al. 2003).

Although correlation and regression analyses do not imply causation of associations between occurrence and site-specific habitat factors, these procedures do provide initial insight into habitat features related to occurrence and are useful for understanding the habitat needs of a species (Anderson and Gutzwiller 1996). Nevertheless, a more complete understanding of the factors influencing the relationship between species presence at the local level is needed to better recognize the influence of microhabitat factors on the occurrence of Trinity bristle snails, particularly at the subsurface level. Future investigations of the life history information should focus on use of both surface and subsurface environments versus availability of habitat at different spatial scales. This effort will provide invaluable insight toward understanding the relationship between species occurrence, landscape-level patterns of distribution, and microhabitat factors, both in the context of short- and long-term environmental change.

Considerations and Recommendations

Regional climate models predict rates of warming in the Pacific Northwest ranging from 0.1 °C to 0.6 °C per decade with rainfall tending toward wetter autumns and winters with drier summers (Mote and Salathe 2010). As a result, this process may affect terrestrial gastropod communities in unforeseen ways (Foster and Ziegltrum 2013). Future work on terrestrial mollusks is a vital part of ecosystem management as they assimilate essential nutrients from the detritus and soil, which are then passed on to higher trophic levels (Barker 2004). Land snails are also studied for their capacity as ecological indicators (Shimek 1930) and as indicators of the effects of pollution and global climate change (Graveland et al 1994; Regoli et al. 2006). Many of these types of studies are in their early stages (Coppolino 2008). Results presented herein help to establish a baseline for assessment, evaluation, adaptive management of local and broad-scale environmental trends and threats to disjunct populations

Table 3. Summary table of hypothesized population-level guide to "critical" suitable microhabitat for the Trinity bristle snail throughout its known geographic range.

Microhabitat component and variable	Suitable microhabitat criteria
	Physical parameters
1. Elevation (m)	$\bar{x}$ = 782.0; min = 310; max = 1,378
2. Exposure (degrees)	$\bar{x}$ = 102.7; min = 1.0; max = 315.0
3. Slope (degrees)	$\bar{x}$ = 54.0; min = 20.0; max = 65.0
4. Air temperature (°C)	$\bar{x}$ = 11.3; min = 4.4; max = 13.9
5. Soil/substrate temperature (°C)	$\bar{x}$ = 10.0; min = 4.4; max =11.7
	Forest vegetation elements
6. Dominance ranking among plant species	Douglas fir = 100%, Pacific madrone = 100%, Tanoak = 90.9%, big leaf maple = 87.5%, sword fern = 87.5%, poison oak = (59.1%), in association with dogwood and white alder in riparian habitats.
7. Overstory vegetation (%)	$\bar{x}$ = 81.5; min = 50.0; max = 98.0
8. Distance to nearest tree or shrub (m)	$\bar{x}$ = 6.0; min = 0.9; max = 14.6
9. Distance to nearest large woody debris (m)	$\bar{x}$ = 3.3; min = 0.1; max = 16.8
	Substrate diversification
10. Percent dominant substrate	Moss-covered boulders ($\bar{x}$ = 58.0%), leaf litter ($\bar{x}$ = 54.2%), bare talus ($\bar{x}$ = 20.0%), gravel ($\bar{x}$ = 18.3%), bare boulders (15.0%), and cliffs ($\bar{x}$ = 10.0%).
11. Substrate upon which a snail was observed	Moss covered boulders or talus = 44.3%, on or within leaf litter = 34.1%, on live plants = 10.2%, on bare gravel = 3.4%, on logs = 2.3%, on or under large slabs of bark = 2.3%, on bare soil = 2.3%, or on older growth conifer stumps = 1.1%. Juveniles may be found on loose bark of standing broadleaf dead wood (bigleaf maple, white alder, canyon live oak).
12. Type of large woody debris	Upright decomposing older-growth stumps = 6.8%, decomposing logs = 28.4%, limbs = 50.0%, and slabs of bark = 14.8%.
13. Size large woody debris (cm)	$\bar{x}$ = 64.3; min = 12.7; max = 137.2
14. Depth leaf litter (cm)	$\bar{x}$ = 8.1; min = 2.5; max = 10.2
15. Distance to nearest rock habitat (m)	$\bar{x}$ = 9.5; min = 0.3; max = 45.7
16. Size distribution of rock type (diameter cm)	$\bar{x}$ =25.2; min = 7.6; max = 61.0
	Riparian corridor characteristics
17. Distance to nearest stream/drainage (m)	$\bar{x}$ =15.4; min = 1.0; max = 47.5. A buffer zone adjacent to streams springs, and wet seeps should be considered in any management scenario.
18. Relative water availability	Perennial riparian systems = 80.8%, annual riparian streams = 19.2%. No samples were collected in association with ephemeral stream-side habitat.
19. Stream classification	Class 2 streams = 50.0%, Class 3 streams = 26.9%, and Class 4 streams = 23.1%. No Trinity bristle snails were found in association with Class 1 (fish bearing) streams or rivers.

of Trinity bristle snails. As a practicable guide for resource management and conservation planning, population-level analysis of site-specific ecological conditions that quantify microhabitat attributes can complement macroscale assessments (Sullivan 2022), allow more accurate valuation of suitable habitat, and facilitate a more thorough understanding of life history requirements of the species.

In designing management programs, state and federal resource agencies should strive to: 1) obtain information on the presence and distribution of the Trinity bristle snail within a particular project area before implementing habitat alteration, 2) protect key habitats from land development or modification by stewardship activities, 3) ensure habitat connectivity to allow for movement of snails within and among suitable habitat patches, and 4) manage habitats so that habitat degradation is minimized to allow local populations to continue to persist at each project site for the long-term. These recommendations emphasize the importance of cooperative stewardship by government, industry, private landowners, and non-governmental organizations to ensure that high quality habitat is protected and rehabilitated for the long-term viability of the species. Adhering to these basic guidelines in addition to recognizing and considering the risks to the species will help demonstrate due diligence towards protection and recovery of this species. These recommendations are also applicable to other species of terrestrial forest and woodland dwelling gastropods being considered for protection under the federal Endangered Species Act (USFWS 2011), and whose critical suitable habitat may be affected by ongoing and future climate change, environmental degradation, and habitat fragmentation in northern California forest and woodland ecosystems.

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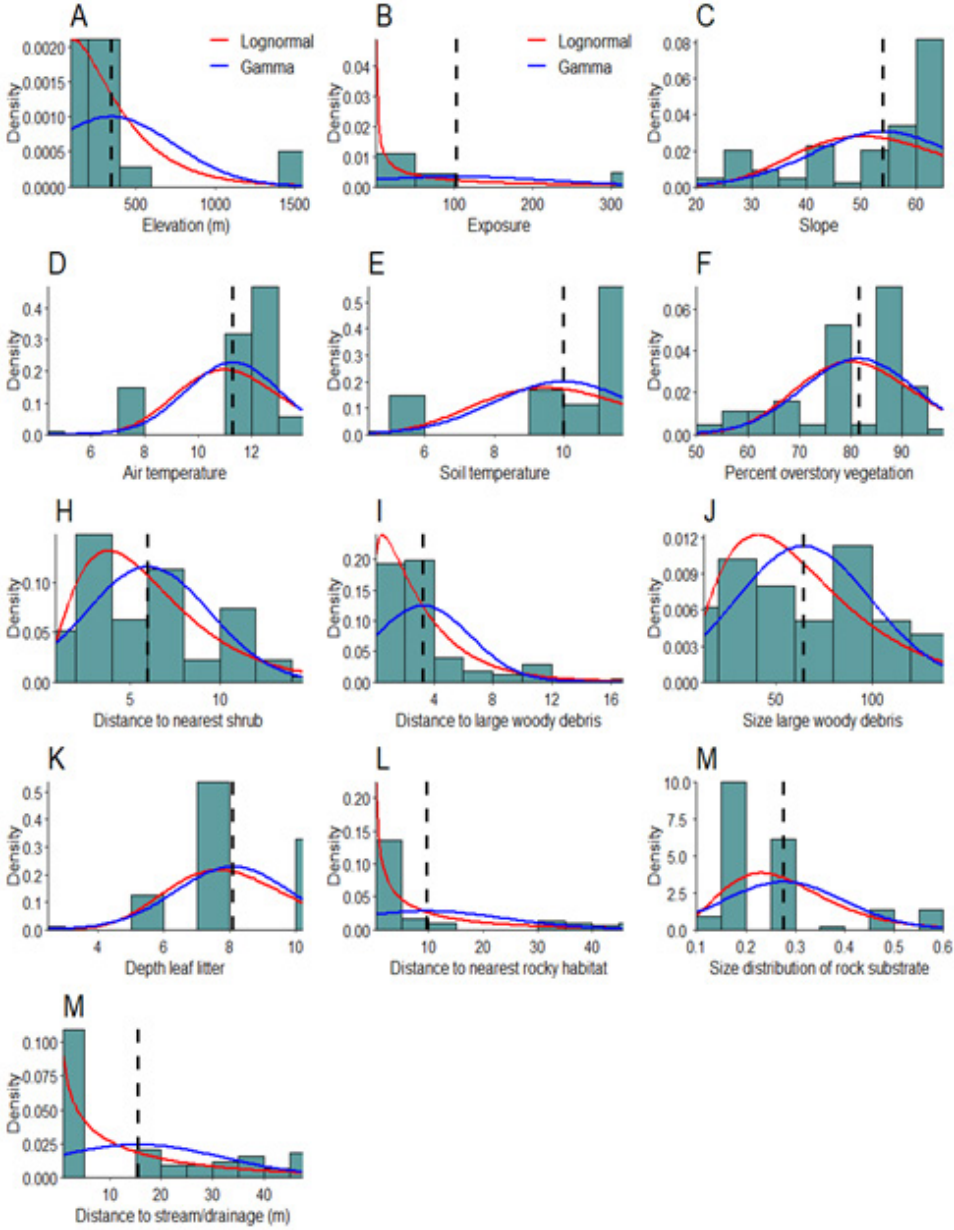
Appendix I. Example of the various stages of decomposition in shells of adult Trinity bristle snails typically found in accumulations of shells (dead snails) within saxicolous subterranean matrices of mesic conifer forest and woodland conditions.

Appendix II. Basic statistics and Anderson-Darling (A) normality tests for continuously distributed physical and ecological parameters measured at each site where Trinity bristle snails were sampled. Trees > 15.2 cm DBH and shrubs ≤ 15.2 cm DBH; n = 88 for all variables except elevation (n = 54); DBH = diameter breast height.

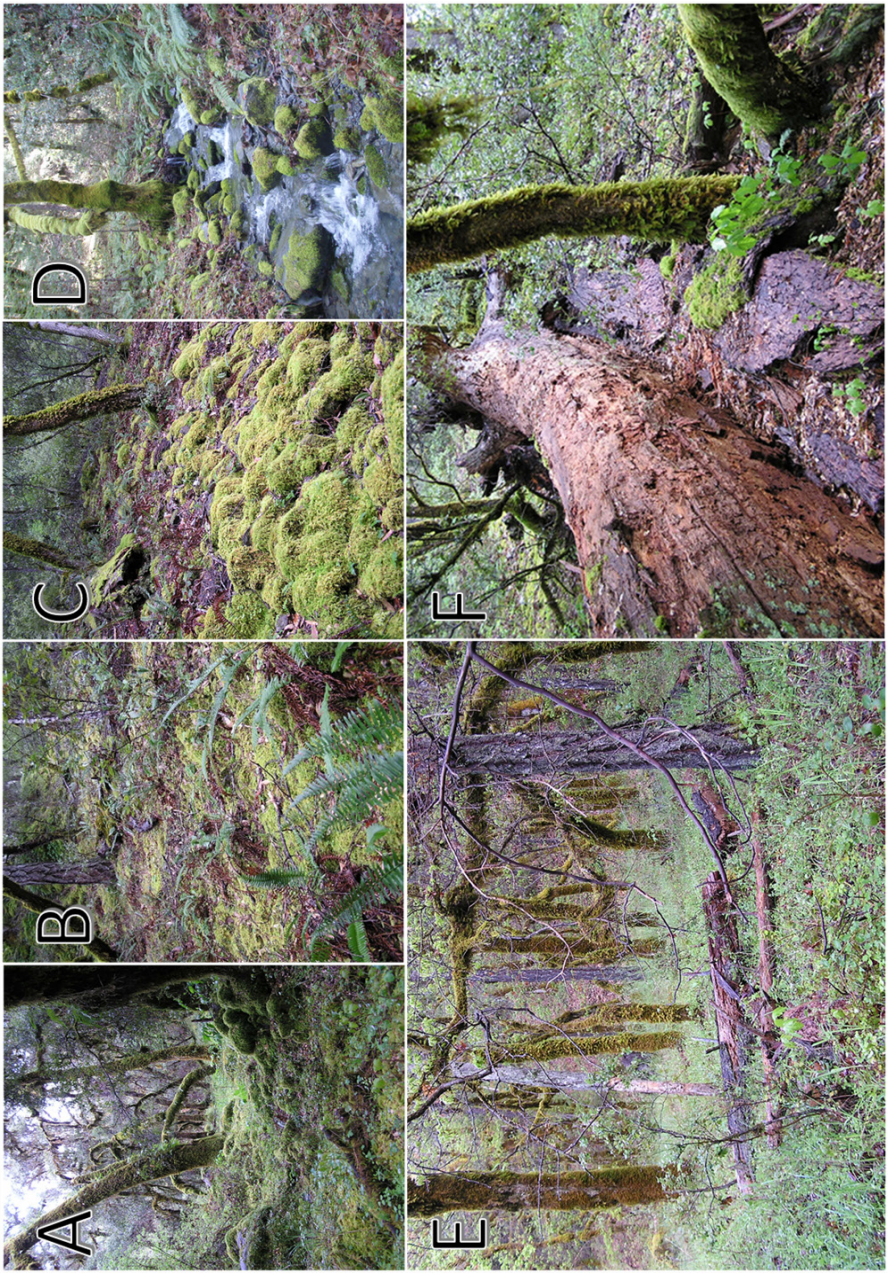
Microhabitat variable	$\bar{x}$	Min	Max	SD	S^2	A	p-value	AIC Lognormal	Gamma
Physical parameters									
1. Elevation (m)	782.0	310.0	1,378.0	331.5	109,905.7	15.2	< 0.001***	1307.9	1202.3
2. Exposure (degrees)	102.6	1.0	315.0	124.9	15,411.7	10.4	< 0.001***	1101.3	921.3
3. Slope (degrees)	54.0	20.0	65.0	13.1	172.0	6.7	< 0.001***	705.7	722.8
4. Air temperature (°C)	11.3	4.4	13.9	1.8	3.1	10.7	< 0.001***	352.4	371.8
5. Soil/substrate temperature (°C)	10.0	4.4	11.7	2.0	4.1	15.0	< 0.001***	376.0	398.9
Ecological parameters									
6. Overstory vegetation (%)	81.5	50.0	98.0	11.1	123.1	3.1	< 0.000***	676.2	683.2
7. Distance to nearest tree or shrub (m)	6.0	0.9	14.6	3.5	12.0	1.8	< 0.000***	471.7	457.1
8. Distance to nearest large woody debris (m)	3.3	0.1	16.8	3.2	10.3	5.7	< 0.001***	458.6	387.2
9. Diameter large woody debris (cm)	64.3	12.7	137.2	35.6	1,258.1	1.5	< 0.000***	880.9	875.2
10. Depth leaf litter (cm)	8.1	2.5	10.2	1.7	3.0	8.1	< 0.001***	352.4	362.5
11. Distance to nearest rock habitat (m)	9.5	0.3	45.7	14.5	208.4	14.0	< 0.001***	722.6	545.6
12. Size distribution of rock type (diameter cm)	25.2	7.6	61.0	13.8	1.9	9.0	< 0.001***	-114.5	-141.7
13. Distance to nearest stream (m)	15.4	1.0	47.5	16.8	279.6	7.1	< 0.001***	748.5	645.8

Appendix III. Goodness-of-fit density plots for log-normal (red smooth line) and Gamma (blue smooth line) theoretical distributions fitted to each physical and ecological microhabitat metric, which shows that each continuously distributed metric is not normally distributed as enumerated in Appendix I.



Appendix IV. Spearman rank correlations (r_s) of physical parameters measured at each site where Trinity bristle snails were sampled. Correlations are below the diagonal and probabilities are above the diagonal. Variables abbreviations are: 1. ELEV = elevation (m), 2. EXPOS = exposure, 3. SLOPE = slope, 4. AIRTEM = air temperature, 5. SUBTEM = soil/substrate temperature, 6. OVSVEG = overstory vegetation, 7. DISTS = distance to nearest tree or shrub, 8. DISWOD = distance to nearest large woody debris, 9. SIZWOD = size distribution of large woody debris, 10. DEPTLL = depth of leaf litter, 11. DISRK = distance to the nearest rocky habitat, 12. SIZERK = size distribution of nearest rock, 13. DISSRM = distance to nearest stream.

	Correlation and probability												
Microhabitat variable	ELEV	EXP0S	SLOPE	AIRTEM	SUBTEM	OVSVEG	DISTS	DISWOD	SIZWOD	DEPTLL	DISRK	SIZERK	DISSRM
1. Elevation (m)	------	0.090	0.000	0.594	0.326	0.439	0.851	0.018	0.059	0.073	0.000	0.002	0.214
2. Exposure	0.180	-------	0.399	0.081	0.584	0.005	0.021	0.000	0.000	0.006	0.046	0.738	0.322
3. Slope	-0.520	-0.090	-------	0.308	0.421	0.358	0.072	0.017	0.023	0.001	0.306	0.287	0.000
4. Air temperature (°C)	-0.080	0.190	-0.110	-------	0.000	0.848	0.071	0.063	0.289	0.104	0.000	0.376	0.000
5. Soil/substrate temperature (°C)	-0.140	0.060	0.090	0.690	-------	0.024	0.001	0.000	0.002	0.505	0.001	0.297	0.000
6. Overstory vegetation (%)	0.080	-0.300	0.100	0.020	0.240	-------	0.003	0.002	0.017	0.000	0.100	0.947	0.002
7. Distance to nearest tree/shrub (m)	-0.020	0.250	0.190	-0.190	-0.360	-0.320	-------	0.561	0.000	0.624	0.504	0.300	0.513
8. Distance to nearest large woody debris (m)	-0.250	-0.410	-0.250	-0.200	-0.400	-0.330	-0.060	-------	0.002	0.870	0.000	0.212	0.013
9. Diameter large woody debris (cm)	0.200	0.480	0.240	-0.110	-0.320	-0.250	0.530	-0.330	-------	0.945	0.114	0.540	0.343
10. Depth leaf litter (cm)	-0.190	-0.290	0.350	-0.170	-0.070	0.400	0.050	0.020	0.010	-------	0.667	0.024	0.001
11. Distance to nearest rock habitat (m)	0.570	0.210	-0.110	0.380	0.360	0.180	-0.070	-0.450	0.170	-0.050	-------	0.005	0.001
12. Size distribution of rock type (diameter cm)	-0.320	0.040	0.110	0.100	0.110	-0.010	0.110	-0.130	0.070	0.240	-0.300	-------	0.201
13. Distance to nearest stream (m)	-0.130	-0.110	0.480	0.560	0.540	0.330	-0.070	-0.260	-0.100	0.340	0.360	0.140	-------



Appendix V. Photographs and examples of moss-covered tree, shrub, rock, riparian corridor, large woody debris, and layered sluffed-off bark in mixed conifer forest and woodland plant community settings at sites where live Trinity bristle snails were sampled (A – F, respectively). Here sites were dominated by Pacific madrone, tan oak, and Douglas fir, and big leaf maple trees, saplings, and brush, as well as scattered sword fern, poison oak, and moss-covered plants and rocks.

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FULL RESEARCH ARTICLE

Population density and habitat selection in the San Pedro Mártir rainbow trout in mountain streams of northwestern Baja California, Mexico

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We assessed the population density and habitat selection of the southernmost rainbow trout subspecies, *Oncorhynchus mykiss nelsoni*, in three stream sites of the Sierra San Pedro Mártir, Baja California, Mexico. Habitat units (sections of the streams visually delimited on the basis of morphological and hydrological features) were sampled between February 2014 and April 2017, along a sample length of 2,980 m corresponding to 105 habitat units, which were classified into ten types. Mean population density (individuals/m²) was similar among the streams sampled (0.035–0.039/m²), as also over time for each stream, except for San Rafael Creek. Low gradient riffle was the habitat unit with the highest mean density of trout (0.151/m²). Of overall manner (dates and sites combined), population density was positively correlated to mean total length (TL), number of trout, and pH levels, and inversely correlated to total of dissolved solids. The total length of the trout was different among sample sites with the lowest and highest values in San Antonio de Murillo Creek and La Grulla Creek, respectively. Also, the total length of individuals among types of habitat units was different, with the highest values for MCP (mid-channel pool) and SRN (step run). Dates and sites pooled, the mean total length of individuals was positively correlated to population density, number of trout, habitat unit area, macrophyte cover, and inversely correlated to temperature. Low population densities (0.011–0.106/m²) combined with its small body size (38–216 mm TL) characterize this endemic trout in the southernmost part of species' geographic range.

Key words: environmental variables, habitat unit, length, native trout, *Oncorhynchus mykiss nelsoni*

Quantification of population density, biomass, and length of the individuals, as well as the relationship between these variables and habitat heterogeneity is important to compiling an inventory of salmonid habitats in rivers and streams. This data enables identification of those habitat units with a higher carrying capacity as well as their associated abiotic and biotic features, determination of their productivity, and current condition of the corresponding ecosystem (Platts and McHenry 1988).

Assesssments of the quality of the salmonid habitats in which population density is related to their habitat condition and use of habitat units, which are defined as the sections of the river or stream that can be visually delimited based on physiographical (depth, substratum, and slope, etc.) and hydrological (current and discharge) features (Bryant et al. 1992). In this sense, at least 24 types of habitat units have been identified (USDA-USFS 1990) in the mountain streams of western North America that contain trout populations and are grouped into the three major categories of pool, riffle, and run (Bryant et al. 1992; Bain and Stevenson 1999).

Despite the numerous studies that have been carried out to determine the population density of trout in the streams of western North America (cf. Platts and McHenry 1988; Budy et al. 2019), there is practically no data on the density of native trout populations in northwestern Mexico in the literature (Hendrickson et al. 2003; Hendrickson and Tomelleri 2019). The San Pedro Mártir trout, *Oncorhynchus mykiss nelson* (Evermann 1908; Fig. 1), is endemic to the western slope of the Sierra San Pedro Mártir, Baja California, Mexico (Ruiz-Campos and Pister 1995; Ruiz-Campos 2017). This southernmost subspecies of rainbow trout (Behnke 2002) inhabits small streams ranging from 560–2075 m above sea level (masl) characterized by low summer flows and hot temperatures (Ruiz-Campos 1993, 2017). This subspecies is now under special protection (Jelks et al. 2008; Semarnat 2010) to mitigate anthropogenic threats to its habitats from from irrigation, deforestation of riparian vegetation, livestock grazing, mining, and the introduction of exotic species (Ruiz-Campos 2017).

The present study evaluated the population density and individual length of *O. m. nelsoni* by type of habitat units in three stream sites (San Antonio, San Rafael, and La Grulla) at different elevations in the Sierra San Pedro Mártir, Baja California, Mexico, as well as evaluating the correlation of this data with habitat variables. The information presented here

Figure 1. The San Pedro Martir trout, *Oncorynchus mykiss nelsoni*, a rainbow trout subspecies endemic to the Sierra San Pedro Mártir, Baja California, Mexico. Photograph: Gorgonio Ruiz-Campos.

will assist in the identification of habitats with a higher abundance of this subspecies. It will also serve as a source of reference for the future monitoring and conservation of populations, as well as programs aiming to improve the habitat of this taxon.

METHODS

Study Area

The Sierra San Pedro Mártir (SSPM) is a batholithic formation (a large mass of intrusive igneous rock also called plutonic rock) extended from southern California (USA) to the southern peninsula of Baja California, Mexico (O'Connor and Chase 1989; Barajas 2018). The highest peak in this mountain system is Picacho del Diablo, standing with 3,096 masl (Barajas 2018). The headwaters of the SSPM are characterized by a series of perennial streams that drain into the Pacific Ocean and are intermittent in their middle and lower sections during the dry seasons (Tamayo and West 1964). From north to south San Rafael, San Telmo and Santo Domingo creeks are the most prominent (Fig. 2). The access to the sea by all these streams is blocked by sand bars, except during the high flows occurring after storms (Tamayo 1962). The riparian vegetation comprises mesophilic trees (plants dependent of soils moderately wet) such as *Populus fremontii*, *P. tremuloides*, *Platanus racemosa*, and *Salix lasiolepis*, shrubs such as *Baacharis salicifolia*, and herbaceous forms such as *Hydrocotyle* sp. and *Berula erecta*, which are found on the stream banks. The

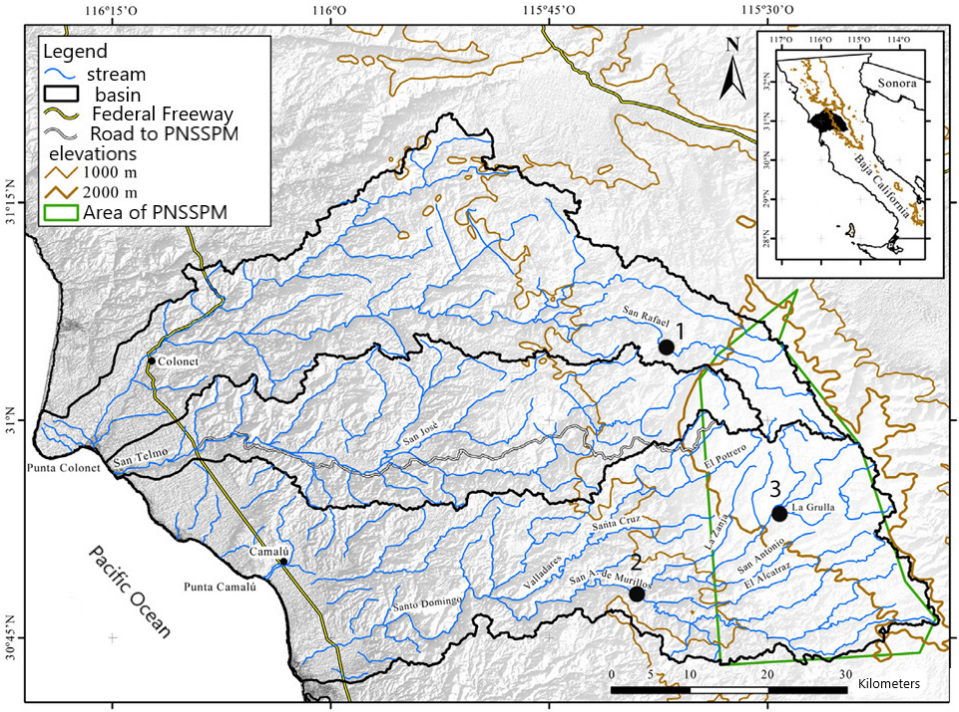


Figure 2. Study area and sampling sites for *Oncorhynchus mykiss nelsoni* in the Sierra San Pedro Mártir, Baja California, Mexico. (1) San Rafael Creek at Mike's Sky Ranch, (2) San Antonio de Murillos Creek at San Antonio Ranch, and (3) La Grulla Creek at La Grulla Meadow. PNSSPM= Parque Nacional Sierra San Pedro Mártir.

aquatic macrophytes of the region are represented by emerging *Schoenoplectus californicus* and *Typha domingensis* and submerged *Potamogeton natans*, *Nasturtium aquaticum* and *Ceratophyllum demersum* forms (Ruiz-Campos 2017).

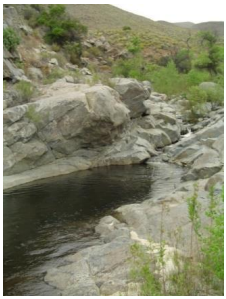
Assessment of Habitat and Population Density

We carried out nine sampling events at the three study sites between February 2014 and April 2017 (Fig. 2). These sampling sites, at all three of which the presence of the endemic trout *O. mykiss nelsoni* has been recorded, are located at different streams and elevations (San Antonio de Murillos Creek, 553–558 masl, 30º 49' 9.3'' N, 115º 37' 46.6'' W; San Rafael Creek, 1,230 masl, 31º 05' 43.0'' N, 115º 37' 18.1'' W to 1,254 m; and La Grulla Creek, 2,023–2,042 masl, 30º 53' 34.4'' N, 115º 28' 53.4'' W) encompassing this subspecies' altitudinal distribution range (Ruiz-Campos and Pister 1995; Ruiz-Campos 2017). These stream sites were selected because they contain representative habitats of the trout throughout their distribution range, and because these three sites have been repeatedly monitored for evaluation of trout abundance in different periods: 1987 to 2012 (San Rafael Creek), 1995 to 2010 (San Antonio de Murillos Creek), and 1990 to 1994 (La Grulla Creek) and (Ruiz-Campos 1989, 1993, 2017; Ruiz-Campos and Pister 1995; Ruiz-Campos et al. 1997). Due to the difficulty of accessing the subspsecies' remote sites of distribution and the logistical challenges of transporting equipment and material by mule and horse, we sampled the sites at different dates in different years. At each site, we selected stream segments of variable length for the evaluation of the habitat units and population density. The length of transect in each stream was over 160 m in all the cases (range = 169–780 m, mean = 331 m), which are representative of the different types of habitats (Ruiz-Campos 1993; Ruiz-Campos et al. 1997; Ruiz-Campos 2017).

We characterized habitats following USDA-USFS (1990), Bryant et al. (1992) and Bain and Stevenson (1999) (Fig. 3). Here, habitat units are defined as the section of the stream that can be visually delimited based on morphology (depth, substratum, and slope, etc.) and hydrological features (discharge rate and flow velocity; Bryant et al. 1992). We identified each habitat unit (see section of results for description) along the length of each transect and then characterized in terms of the following variables: morphology (length and width, average depth, slope, and dominant substratum); hydrometry (velocity of flow and discharge); water quality (temperature, dissolved oxygen, pH, conductivity, and total dissolved solids); and biological variables (average total length and number of individuals and macrophyte coverage). All the habitat variables measured in the present study were based on those described by Dolloff et al. (1993), Bain and Stevenson (1999), and Cornell et al. (2008) (Appendix 1).

The depth and current velocity for each habitat unit were measured in a cross-section of the stream at 30 cm intervals, using a pleximeter (precision 0.5 cm) and a current meter (Swoffer 2100 model, precision 0.01 m/s, Swoffer.com/products.htm), respectively. The discharge was calculated as $Q = [W * D * V] * CF$ (Hynes 1972), where Q = discharge rate (m^3/s), W = average stream width (m), D = average depth (m), V = average speed of the current (m/s), and CF = constant friction for soft (0.9) and rugous (0.8) bottoms. We recorded physicochemical variables using a Hydrolab Surveyor multiparameter water quality sonde (Hydrolab Co., Austin, TX).

We evaluated the population density in each transect, which were of variable length, one day prior to the characterization of the habitats, in order to avoid disturbing the fish.



A) Lateral Scour Pool (LSP)
D= 0.110/m^2

B) Mid-channel Pool (MCP)
D= 0.034/m^2

C) Step Pool (STP)
D= 0.067/m^2

D) Plunge Pool (PLP)
D= 0.108/m^2

E) Backwater Pool (BWP)
D= 0.0/m^2

F) Low Gradient Riffle (LGR)
D= 0.041/m^2

G) Glide (GDL)
D= 0.047/m^2

H) Step Run (SRN)
D= 0.032/m^2

I) Run (RUN)
D= 0.016/m^2

J) Dammed pool (DPL)
D= 0.016/m^2

Figure 3. Types of habitat units and mean density of *Oncorhynchus mykiss nelsoni* (individuals/m²) in streams of the Sierra de San Pedro Mártir, Baja California, Mexico, during 2014–2017. Photographs by Gorgonio Ruiz-Campos.

The length of transects for trout sampling used in this study (169–780 m) was within the range recommended by Ruiz-Campos (1993, 2017) for the population monitoring and determination of the length structure of this trout subspecies. We deployed block nets prior to sampling to eliminate emigration from the habitat unit. An electro-fishing equipment (LR-24 Smith-Root, voltage range of 200–300 V) was used to collect the trout via two sweeps conducted in each habitat unit (Dolloff et al. 1993). All individuals captured in each habitat unit were counted and kept alive in a 20-l container, with their TL (mm) measured and their sex identified, after which they were released back into their respective habitat units. We measured TL as recommended by Anderson and Neumann (1996) because this measure is more commonly used by fishery biologists than standard length and generates less stress to the fish when measuring it. The average TL ± SD of individuals captured in each habitat unit was also calculated, while the population density for each habitat unit was expressed as the number of individuals per square meter.

In order to estimate the population density of trout per kilometer of stream, as well as the population size in each stream, we measured the length of stream containing suitable habitats, based on satellital images via Google Earth and observation in field.

Statistical Analysis

Because the density and total length values of the individuals registered in this study did not show a normal distribution according to the χ^2 test of normality, we used nonparametric Kruskal-Wallis (H) and Mann-Whitney (U) tests to compare the population density and TL length values among the streams as well as among the types of habitat units. A Spearman rank correlation (r_s), with a significance level of 0.05 (Sokal and Rohlf 2012), was also applied to determine the relationships, at habitat-unit level, between each habitat variable and population density and average individual TL. We used the Statistical software 5.0 (StatSoft, Inc., Tulsa, OK) for the statistical analyses.

RESULTS

One-hundred-and-five habitat units pertaining to ten different habitat unit types were identified at three sites that comprised a total length of 2,980 m of the three streams sampled at three different elevations (San Antonio Creek, 553–558 m; San Rafael Creek, 1,230–1,254 m; and, La Grulla Creek, 2,023–2,042 m). We captured 410 individuals ranging from 38–216 mm TL (mean = 115.2 ± 42.7 mm) in the three streams during the study period, with average population density of 0.039/m² (range = 0.011–0.106). We calculated the mean TL by site and habitat unit in each sampling event (Table 1).

The ten types of habitat units identified (Fig. 3) corresponded to lateral scour pool (LSP, formed by flow impinging one streambank or against a partial channel obstruction), mid-channel pools (MCP, formed by mid-channel scour), dammed pools (DPL, water impounded from a complete or nearly complete channel blockage), step pools (STP, series of pools separated by short riffles or cascades), backwater pools (BWP, pool formed by log), plunge pools (PLP, pool found where stream passes over a complete or nearly complete channel obstruction and drops steeply into the streambed below, scouring out a depression), run (RUN, swiftly flowing reaches with little surface agitation and no major flow obstructions), glide (GLD, a wide uniform channel bottom with flow of low to moderate velocity), step run (SRN, a sequence of runs separated by short riffle steps), and low gradient riffle (LGR,

Table 1. Mean trout density (number/m²) and mean total length of individuals (mm) by type of habitat unit in the streams of the Sierra de San Pedro Mártir, Baja California, Mexico, from February 2014–April 2017. See abbrevations of habitat units in methods.

Date	Stream Site	Habitat Unit	Surface (m²)	Number of Trout	Mean Trout Density (m²)	Mean Total Length (mm)
3 May 2014	San Antonio	MCP	804.5	9	0.011	83.1 ± 31.5
		RUN	233.2	7	0.030	93.8 ± 40.8
		SRN	626.6	19	0.030	75.7 ± 10.7
		Total	**1664.2**	**35**	**0.021**	**82.6 ± 28.4**
13 Apr. 2015	San Antonio	RUN	1.9	8	0.019	85.3 ± 29.1
		STP	176.6	11	0.062	101 ± 22
		SRN	214.9	15	0.070	139.2 ± 18.1
		DPL	370.4	6	0.016	157.8 ± 36.2
		LGR	111.0	5	0.045	82.5 ± 14.8
		MCP	68.4	0	0.000	
		Total	**1353.3**	**45**	**0.033**	**116.9 ± 37.4**
23 Feb. 2014	San Rafael	GLD	1043.9	108	0.104	103.5 ± 33.2
		LGR	52.9	8	0.151	112.5 ± 32.5
		Total	**1096.9**	**116**	**0.106**	**108.7 ± 32.9**
21 Mar. 2015	San Rafael	GLD	939.4	5	0.005	117.6 ± 13.6
		SRN	196.6	1	0.005	114
		LGR	165.7	3	0.018	118.1 ± 19.7
		RUN	929.6	8	0.009	130.6 ± 24.2
		STP	286.3	13	0.045	117.5 ± 16.9
		Total	**2517.6**	**30**	**0.012**	**121.5± 19.0**
24 May 2015	San Rafael	PLP	16.2	2	0.124	45
		RUN	998.4	16	0.016	158.5 ± 38.2
		BWP	18.4	0	0.000	
		SRN	72.4	3	0.041	77 ± 18.4
		LSP	9.1	1	0.110	193 ± 0.0
		STP	95.2	1	0.011	218.0 ± 0.0
		LGR	38.4	0	0.000	
		Total	**1248.1**	**23**	**0.018**	**158 ± 49.5**
26 Sep. 2014	La Grulla	MCP	938.7	40	0.043	108.1 ± 46.7
		GLD	121.4	10	0.082	99.4 ± 48.1
		Total	**1060.1**	**50**	**0.047**	**106.3 ± 46.6**
9 Aug. 2015	La Grulla	GLD	573.6	32	0.056	98.6 ± 44.1
		MCP	587.8	43	0.073	129.0 ± 36.8
		Total	**1161.4**	**75**	**0.065**	**116.0 ± 42.6**

Table 1. continued.

Date	Stream Site	Habitat Unit	Surface (m²)	Number of Trout	Mean Trout Density (m²)	Mean Total Length (mm)
17 Sep. 2016	La Grulla	MCP	1118.8	17	0.015	149.5 ± 32.4
		GLD	412.7	0	0.000	
		Total	**1531.4**	**17**	**0.011**	**149.5 ± 32.4**
29 Apr. 2017	La Grulla	GLD	710.6	7	0.010	153.3 ± 24.4
		MCP	810.8	12	0.015	193.3 ± 30.6
		Total	**1521.4**	**19**	**0.013**	**169.3 ± 32.7**
Great Total				**410**	**0.039**	**115.2 ± 42.7**

shallow reaches with swiftly flowing, turbulent water with some partially exposed susbstrate). Six types of habitat units were classified for San Antonio de Murillos Creek (LGR, RUN, SRN, STP, PLP, and MCP), eight for San Rafael Creek (LGR, RUN, GLD, SRN, BWP, DPL, LSP, and STP), and two for La Grulla Creek (GLD and MCP).

By sampling event (all the types of habitat units combined), the highest average trout density (individuals/m²) was registered in San Rafael Creek (0.106) in February 2014, while the lowest average density (0.011) was obtained in September 2016 in La Grulla Creek (Table 1). For habitat units (all sampling sites and events combined), the highest mean density occurred in LSP and PLP with 0.110 and 0.108 individuals/m², respectively (Fig. 3).

Population Density

San Antonio de Murillos Creek.—The mean population density of trout in San Antonio de Murillos Creek was obtained via two sampling events with a value of 0.035 individuals/m². In the first sampling event (3 May 2014), we collected 35 individuals in a 419 m stream segment with an average width of 6.4 m and a scanned area of 1,664 m², giving a population density of 0.021/m². By habitat unit, the population densities observed for this first sampling event were: SRN (0.03/m²), RUN (0.03/m²) and MCP (0.011/ m²) (Table 1). In the second sampling event (13 April 2015), 45 individuals were collected in a 307 m stream segment with an average width of 4.5 m and an area of 1,353 m², giving a population density of 0.033/m². The population density observed for this second sampling event, by type of habitat unit, was as follows: SRN (0.070/m²), STP (0.062), LGR (0.045/ m²), RUN (0.019/m²), DPL (0.016/m²) and MCP (0.0/m²) (Table 1).

San Rafael Creek.—The mean population density in this creek during three sampling events was 0.039 individuals/m². In the first sampling event (23 February 2014), we collected 116 individuals in a 217 m segment of stream with an average width of 4.0 m and a scanned area of 1,097 m², giving a population density of 0.106 individuals/m². By type of habitat unit, the density of trout was GLD (0.104.m²) and LGR (0.151/m²) (Table 1). In the second sampling event (21 March 2015), 30 individuals were collected in a 780 m stream with an average width of 2.9 m and an area of 2,518 m², giving a population density of 0.012/ m². By type of habitat unit, the population density, in descending order was: STP (0.045/ m²), LGR (0.018 m²), RUN (0.009/m²), SRN (0.005/ m²) and GLD (0.005/m²) (Table 1).

In the third sampling event (24 May 2015), we caught 23 trout in a 439 m stream segment with an average width of 2.7 m and a surface area of 1,248 m², giving a population density of 0.018/m². By type of habitat unit, the population density, in decreasing order was: PLP (0.124/m²), LSP (0.110/m²), SRN (0.041/m²), RUN (0.016/m²), STP (0.011/ m²), BWP and LGR (0.0/m²) (Table 1).

La Grulla Creek.—The mean population density of the trout in La Grulla Creek recorded over four sampling events was 0.039 individuals/m². In the first sampling event (26 September 2014), we collected 50 individuals in a 262 m segment of stream with an average width of 4.43 m and a surface area of 1,060 m², giving a population density of 0.047. The population densities observed for the two types of habitat units sampled during this first event were 0.082/m² for GLD and 0.043/m² for MCP (Table 1). In the second sampling event (9 August 2015), 75 individuals were collected in a 169 m segment of stream with an average width of 6.8 m and a surface area of 1,161 m², giving a population density of 0.065/m². By type of habitat unit, the population density for this second sampling event was 0.073/m² for MCP and 0.056/m² for GLD (Table 1). In the third sampling event (17 September 2016), we collected 17 individuals in a 179 m segment of stream with average width of 9.8 m and a surface area of 1,531 m², giving a population density of 0.011/m². By type of habitat unit, the population density for this third sampling event was 0.015 and 0.00/m² for MCP and GLD, respectively (Table 1). In the fourth sampling event (29 April 2017), we captured 19 individuals in a 208 m segment with an average width of 6.2 m and a surface area of 1,521 m², giving a population density of 0.013 individuals/m². By type of habitat unit, GLD and MCP presented respective population densities, for this fourth sampling event of 0.010 and 0.015/m² (Table 1).

Statistical Analyses

Population density among sampling sites and habitat units.—The population density (individuals/m²) was statistically similar among sites sampled, considering in each site all sampling events and types of habitat units ($H = 1.0$, $n = 105$, $P = 0.619$). Despite that, we found the population density among types of habitat units (all sampling sites and events pooled) to be statistically similar ($H = 11.4$, $n = 105$, $P = 0.247$), LSP, PLP and STP, presented the highest densities (0.110, 0.108 and 0.067 individuals/m², respectively).

The population density at the San Rafael Creek site was statistically different among the three sampling dates ($H = 10.2$, $n = 51$, $P < 0.006$), especially for the sampling conducted in February 2014. Moreover, at the La Grulla Creek site, the population density was similar among the four sampling dates ($H = 5.4$, $n = 22$, $P = 0.146$). Finally, the population density at the San Antonio de Murillos Creek site was similar for the two sampling dates ($U = 75.5$, $P = 0.143$).

Length of individuals among sampling sites and habitat units.—The mean total length of individuals in three stream sites during the study period was 102.31 ± 46.40 mm in San Antonio de Murillo Creek, 116.47 ± 36.14 mm in San Rafael Creek, and 120.08 ± 45.79 in La Grulla Creek (Fig. 4). The comparison of the total length of individuals among these stream sites (all the sampling events and types of habitat units combined), revealed significant differences ($H = 13.1$, $n = 374$, $P = 0.002$), with the highest median for La Grulla Creek. Furthermore, considering all the streams sampled and sampling events, the total length of individuals among types of habitat unit was different ($H = 13.7$, $n = 357$, $P = 0.0335$), with the highest medians for MCP, SRN and LGR.

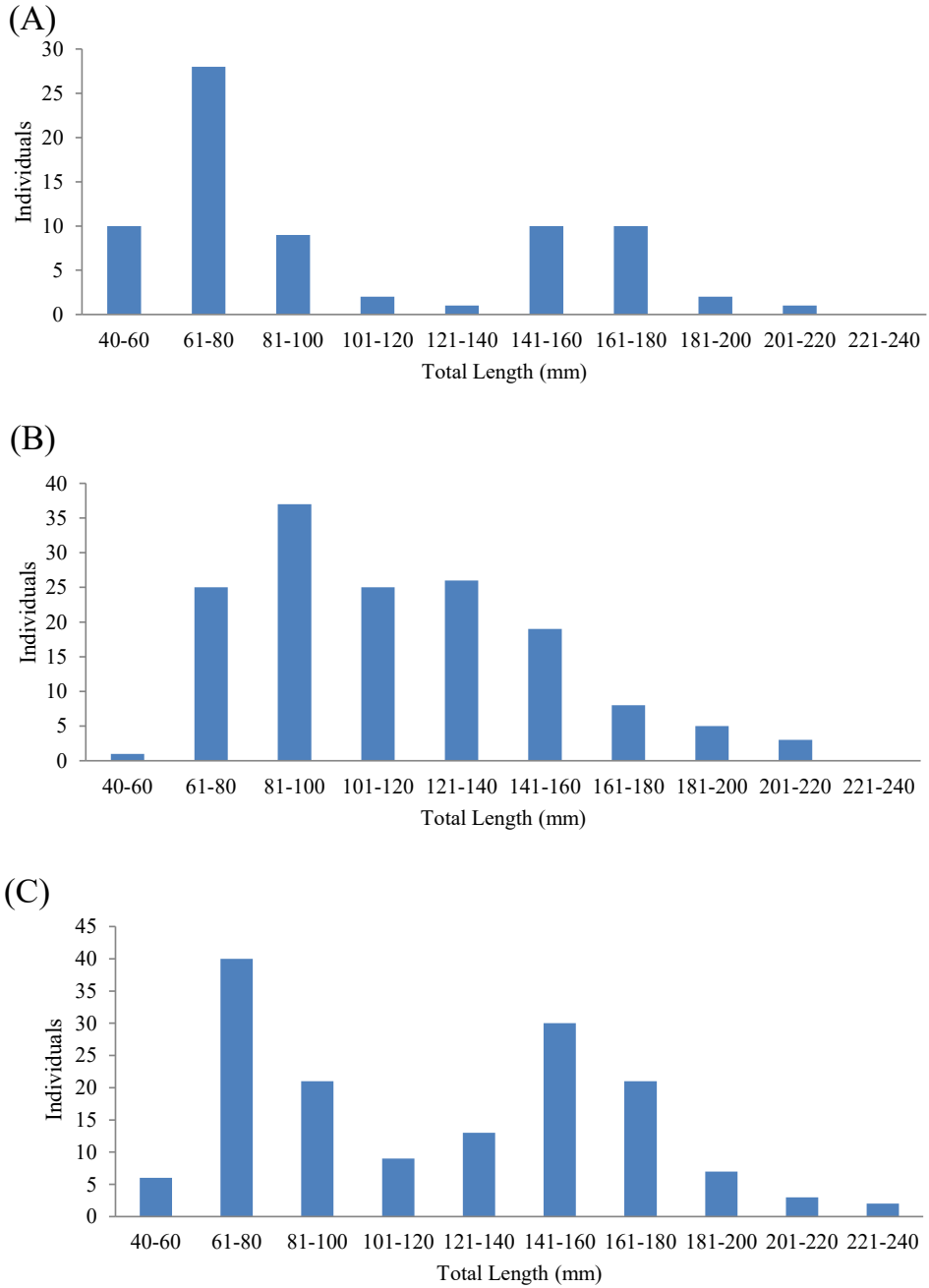


Figure 4. Frequency of total length of *Oncorhynchus mykiss nelsoni* in three streams of the Sierra San Pedro Mártir, Baja California, between February 2014 and April 2017. (A) San Antion de Murillos Creek (n = 73, $\bar{x}$ = 102.31 ± 46.40) (B) San Rafael Creek (n = 149, $\bar{x}$ = 116.47 ± 36.14) (C) La Grulla Creek (n = 152, $\bar{x}$ = 120.08 ± 45.79).

In each site, the total length of individuals among sampling events was different for San Rafael Creek ($H = 20.2$, $n = 149$, $P < 0.001$) and La Grulla Creek ($H = 21.8$, $n = 152$, $P < 0.001$) but similar in San Antonio de Murillos Creek ($H = 1.0$, $n = 73$, $P = 0.326$).

Relationship between population density and mean individual total length and the habitat variables.—The correlation analysis conducted on the population density by habitat unit (with all sampling sites and events combined, $n = 105$) and contrasted to each habitat variable (Table 2), showed a significant positive relationship ($P < 0.05$) with mean total length ($r_s = 0.584$), number of trout ($r_s = 0.843$), velocity of current ($r_s = 0.224$), and pH ($r_s = 0.202$), and an inverse correlation ($P < 0.05$) with total of dissolved solids ($r_s = –0.203$). Number of trout showed a positive correlation to habitat unit area ($r_s = 0.371$). Similarly, mean total length was observed to positively correlate with area of habitat unit ($r_s = 0.279$), trout density ($r_s = 0.584$), number of trout ($r_s = 0.680$), and macrophyte cover ($r_s = 0.243$), although it was inversely correlated with temperature ($r_s = –0.247$).

The estimate population size of the trout for the studied streams based on occupiable habitat was as follows: La Grulla Creek with a total length of 14.5 km was 2,853 individuals (197 trout/km of stream); San Antonio Creek stream with a total length of 39.9 km was 4,398 individuals (110 trout/km of stream), and finally, the San Rafael Creek with a length of 21.8 km was 2,566 individuals (117 trout/km of stream).

Table 2. Spearman correlation values (r_s) between mean individual total length and density of trout (*Oncorhynchus mykiss nelsoni*) and each habitat variable in mountain streams of the Sierra San Pedro Mártir, Baja California, México, from February 2014 to April 2017. Values in bold are significant at 0.05 and 105 df.

Variable of Habitat	Mean Individual Total Length (mm)	Density of Trout (individuals/m²)
Type of habitat unit	0.003	0.043
Area of habitat unit	0.279	–0.048
Depth	–0.054	0.013
Velocity of current	–0.102	0.224
Flow rate	–0.051	0.074
Stream slope	–0.061	–0.088
Macrophyte cover	0.243	0.033
Temperature	–0.247	–0.129
pH	–0.004	0.202
Dissolved oxygen	0.038	0.096
Conductivity	0.004	–0.152
Total disolved solids	0.057	–0.203
Number of trout	0.680	0.843
Mean total length		0.584

DISCUSSION

The San Pedro Mártir trout is represented by a small metapopulation distributed in first and second order creeks in the western slope of the Sierra San Pedro Mártir, Baja California, Mexico (Ruiz-Campos and Pister 1995; Ruiz-Campos 2017), with local populations estimated in this study between 110 and 197 trout/km of stream. Comparatively, the present study found an average population density of 0.039 individulas/m² (min = 0.011, max = 0.106) for San Pedro Mártir rainbow trout, which is low but within the range (0.01–4.2) reported for salmonid populations in mountain streams in western North America (Platts and McHenry 1988). Comparatively, the population density of *O. m. nelsoni* is similar to that reported for other populations of rainbow trout at Colorado Plateau (0.07, Leiner 1995); Saghen Creek, California (0.01, Decker and Erman 1992), mountain streams in New Mexico (0.008–0.348, Leiner 1995), and streams in the Sierra Nevada, California (0.02–0.17; Knapp and Dudley 1990), but with a lesser density than those reported for a remote stream in the southern California (0.119–0.362; Barabe 2021).

The highest mean population density (0.106 individuals/m²) recorded in the San Rafael Creek in the sampling on 21 February 2021, is coincident with the peak of known spawning for this trout (Ruiz-Campos 2017), where the breeding adults trend to move along the stream in searching of sand-gravel beds for the building of redds especially toward glides (Ruiz-Campos 2017). This last type of habitat represented a higher proportion (95%) of the stream sampled. The low population density of trout in the streams of the SSPM is resulting from a combination of factores that characterize this southern aquatic habitat as the small size of the streams (width and depth), low biomass of prey (Ruiz-Campos 1993; Solís-Mendoza 2016), wide daily variation in temperature and dissolved oxygen, and reduced flows in the summer (Ruiz-Campos 2017; Meza-Matty et al. 2021).

Spatially, the stream sites sampled in this study that are representative of the subspecies' altitudinal distribution range (Ruiz-Campos and Pister 1995), showed similar values of average population density, being an indicative of appropriate habitat conditions (Ruiz-Campos et al. 1997; Ruiz-Campos 2017). By total length of individuals, the largest trout were captured in the La Grulla and San Rafael creeks, where there are a higher frequency and surface of habitat units as pools (MCP), which are mainly used as foraging sites by the adult individuals (Ruiz-Campos 2017).

However, at each stream site, namely the sampling date, influenced the population density at both the San Rafael and La Grulla sites, mainly in terms of such variables as macrophyte cover (especially at La Grulla Creek), temperature, and area of habitat unit, and total length of individuals. In this sense, Hynes (1972) determined that the most important abiotic factors in salmonid survival in stream habitats are temperature, flow velocity, discharge, and escape cover. Lewis (1969) and Rinne (1982) identified pool volume to be significantly correlated with trout populations in Montana and New Mexico, respectively. Discharge rate has been successfully used to explain the biomass of brook trout in Michigan (Latta 1965), Atlantic salmon in Maine (Havey and Davis 1970), and brown trout in Wisconsin (White 1975), while a number of studies have identified cover as a limiting factor for trout populations (Binns and Eiserman 1979; Hunt 1974; Wesche 1980). Other authors have discovered relationships between trout populations and depth (Stewart 1970), invertebrate biomass (Murphy 1979), and large organic debris (Sedell et al. 1982).

In the streams sampled by the present study in the SSPM, the highest population

densities occurred in types of habitat units with low frequency, which are of a small size and pertain to different types of pools, such as step pools and plunge pools. Ruiz-Campos (1993) pointed out that trout have a marked preference for inhabiting pools, as reflected in the higher population density found by the present study for this type of habitat. This was especially notable for MCP in La Grulla Creek (0.073 individuals/m²), in August 2015 (cf. Table 1), whose central erosion pools are characterized by high levels of macrophyte coverage that provides a higher quantity of prey as compared to glides and runs (Solís-Mendoza 2016).

The habitat units as lateral scour pools, step pools, or plug pools, which are known to be used as temporary thermal refuges by rainbow trout during the day in summer (Baltz et al. 1991; Roberts et al. 2013; Nusslé et al. 2015; Meza-Matty et al. 2021) because they are deeper and more thermally stable than the other habitat units in the streams. Thus, the high dissolved oxygen levels enable their resident individuals to maintain a lower level of metabolic expenditure (Jonsson et al. 1991).

The current habitat of the San Pedro Mártir rainbow trout is considered well preserved (Ruiz-Campos 2017) due to the inaccessibility and remoteness to human settlements of the species distribution, although having risk categories from medium-low to medium-high in the connectivity of their habitats based on the classification of Shepard et al. (2005) and Muhlfeld et al. (2015).

However, in recent years, the anthropogenic impact of agricultural activity has been increasing significantly in the lower parts of the basins of the coastal valleys found in the communities of Colonet, San Telmo, Camalú, and Vicente Guerrero in the region. A highwater demand is reported for these communities for the irrigation of crops via streambed wells or the channeling of flows from the upper part of the basins. This situation may lead to the eventual expansion of the use of water from those streams in which the subspecies of interest is distributed (San Antonio de Murillos Creek, Potrero Creek, La Zanja Creek, and San Rafael Creek). Therefore, it is essential that, in the short term, appropriate prevention measures are taken to ensure the conservation of the habitats of this trout and other native aquatic forms.

The present study will serve as a baseline for the future monitoring of the population density of the San Pedro Mártir rainbow trout and the quality and quantity of its habitats. The determination of the population density in each one of the streams studied by type of habitat unit will allow to identify the carrying capacity of trout in each one of them (productivity), as well as the microhabitats preferred by this endemic subspecies. The use of measurements of total length in trout for the monitoring of the population structure turns out to be more practical and less stressful than other body measurements (standard length and weight) when handling the live individuals and they must return to the capture sites.

Additionally, this study will provide an indispensable source of information to assist in elucidating the environmental and anthropogenic factors that modulate the population density of this subspecies, including the effects of the imminent global climatic change that will reduce the geographic distribution of this endemic trout (Ruiz-Campos 2017; Meza-Matty et al. 2021) and other trout species in southestern North America (Zeigler at al. 2019). These monitoring efforts will assist in establishing the abundance patterns of this trout subspecies in the short, medium, and long term, by means of habitat unit and population density inventories that should be carried out at a minimum of every three years (Hunter 1990).

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Appendix 1 Mean values and standard deviation (SD) of environmental variables (structural and physiographic) measured by sampling event for trout in three streams of the Sierra San Pedro Mártir, Baja California, Mexico. SAS= San Antonio stream, SRS= San Rafael stream, and LGS= La Grulla stream. Temp.= temperature, Diss. Oxyg= dissolved oxygen, Conduct.= conductivity, and TDS= total of dissolved solids.

Stream		Date	Depth (m)	Flow Velocity (m/s)	Discharge (m^3/s)	Stream Slope (°)	Cover by Macrophytes (%)	Temp. (°C)	pH	Diss. Oxyg. (mg/L)	Conduct. (mS/cm)	TDS (g/L)
SRS	Mean	Feb. 2014	0.13	0.38	0.16	20	1	11.5	9.4	11.2	0.30	0.13
	SD		0.04	0.08	0.02	7	0	0.7	0.6	0.3	0.09	0.00
SAS	Mean	May 2014	0.26	0.17	0.13	15	1	24.8	7.1	6.6	0.32	0.15
	SD		0.16	0.17	0.09	6	0	4.4	0.0	1.5	0.01	0.00
LGS	Mean	Sep. 2014	0.40	0.16	0.06	13	71	17.5	8.7	5.6	0.19	0.14
	SD		0.33	0.29	0.08	7	19	1.3	0.3	1.0	0.06	0.01
SRS	Mean	Mar. 2015	0.18	0.34	0.13	20	1	16.9	8.4	6.1	0.27	0.16
	SD		0.10	0.14	0.07	13	0	3.3	0.3	0.2	0.04	0.14
SAS	Mean	Apr. 2015	0.20	0.25	0.18	25	10	17.3	8.8	5.3	0.14	0.13
	SD		0.09	0.13	0.23	20	16	1.9	0.3	0.5	0.05	0.06
SRS	Mean	May 2015	0.24	0.45	0.21	33	1	15.8	9.9	6.8	0.28	0.18
	SD		0.09	0.15	0.07	15	0	0.8	0.1	0.7	0.00	0.00
LGS	Mean	Aug. 2016	0.20	0.01	0.40	12	93	19.7	7.4	4.4	0.22	0.09
	SD		0.14	0.00	0.27	5	3	0.9	0.2	0.3	0.20	0.04
LGS	Mean	Sep. 2016	0.18	0.04	0.05	15	57	15.4	8.3	6.3	0.33	0.21
	SD		0.06	0.04	0.03	3	26	1.6	0.2	0.8	0.06	0.04
LGS	Mean	Apr. 2017	0.14	0.14	0.07	15	96	16.3	6.8	7.8	0.42	0.27
	SD		0.04	0.11	0.06	2	2	0.4	0.1	0.8	0.06	0.03
Total	Mean		0.21	0.26	0.15	22	21	17.6	8.4	6.4	0.26	0.16
	SD		0.14	0.19	0.15	14	35	3.9	1.0	1.5	0.09	0.09

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FULL RESEARCH ARTICLE

Status and distribution of Arroyo Chub within its native range

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The Arroyo Chub (*Gila orcutti*) is a small cyprinid native to coastal drainages of Los Angeles, Orange, Riverside, and San Diego counties. We surveyed the seven drainages historically known to support the species in 2012-2014 and again in 2019 to determine current range and distribution. We compared our results to the most recent species account we could locate (1993). We detected Arroyo Chub in 18 of the 40 streams (45%) and within six of the seven native watersheds in our 2012-2014 surveys, while our 2019 surveys located fish in all of the seven native watersheds. This native species has retreated to the headwaters in most watersheds and the number of populations have declined since the most recent species account. Non-native species, habitat loss, urbanization, water development, flood control, and drought are thought to be the primary causes of this decline.

Key words: Arroyo Chub, *Gila orcutti*, status update

The Arroyo Chub (*Gila orcutti*) is a small cyprinid (Fig. 1) native to coastal drainages of Los Angeles, Orange, Riverside, and San Diego counties in California. This species has a relatively deep body and caudal peduncle, large eyes (for a cyprinid), a short rounded snout, and a subterminal mouth (Moyle 2002). Average adult lengths are 70–100 mm, and fish are silver or gray to olive green dorsally, white ventrally, and connected with a dull gray lateral band (Moyle 2002). Considered true omnivores, Arroyo Chub eat algae, insects, and small crustaceans (Moyle et al. 2015). Spawning generally occurs in June and July, but the eggs of females ripen in small batches (Tres 1992), allowing spawning to occur anywhere from February through August.

Typically, Arroyo Chub are found in slow-moving sections of cool to warm (10–26°C) streams dominated by sand and silt substrates (Wells and Diana 1975; Saiki et al. 2007; O'Brien et al. 2011), but Feeney and Swift (2008) found fish in pools with gravel, cobble, and boulder substrates, illustrating the diversity of habitat used by this species. These fish are adapted to survive the fluctuating conditions present in southern California streams, including warm, hypoxic conditions in summer (Castleberry and Cech 1986), and high flows and turbidity levels in winter.

Figure 1. Arroyo Chub captured in San Juan Creek, Orange County, California.

The decline of California's native fishes has been well documented (Moyle 1976; Moyle et al. 1989; Moyle et al. 1995; Moyle et al. 2011; Moyle et al. 2015), and Arroyo Chub are no exception. Reasons for the decline are numerous and include habitat loss, urbanization, water development, flood control, and the introduction of invasive species. These factors have led to a reduction in the preferred habitat of Arroyo Chub within the coastal plain of southern California. Unfortunately, it is impossible to accurately quantify the magnitude of this decline, because comprehensive, range-wide studies of Arroyo Chub prior to these anthropogenic impacts are absent. Swift et al. (1993) published the only range-wide assessment, while other reports have only described the species distribution within specific drainages (Haglund and Baskin 1995; Warburton et al. 2000; O'Brien et al. 2011; Packard 2012).

METHODS

We designed the present range-wide assessment of Arroyo Chub to determine: (1) which of the native streams still support Arroyo Chub populations and quantify the area occupied within each, and (2) identify potential locations where restoration and translocation could occur.

We conducted surveys throughout the seven watersheds to which Arroyo Chub are native. From north to south these are: Malibu Creek, Los Angeles River, San Gabriel River, Santa Ana River, San Juan Creek, Santa Margarita River, and the San Luis Rey River. Historic locations of the species were obtained from Swift et al. (1993), unpublished field reports, consultation with local fisheries experts, and records within the California Natural Diversity Database. We selected most survey locations based on historic records or sites within the historic native range that contained suitable habitat. However, the Walnut Creek sample location met neither of these conditions and was sampled based on information from a local resident.

The sampling occurred annually at some sites from 2012 through 2021, with a wide-

spread effort from 2012–2014. Before sampling a selected location, we performed visual surveys and sometimes covered several miles of stream to locate water, suitable habitat, and fish. After the widespread effort from 2012–2014, we focused our efforts thereafter on locations where positive detections occurred. We sampled each site with a 1.2 × 1.8 m seine with a mesh size of 3 mm or dip nets with a mesh size of 3 mm. Most sites were in small streams rarely more than 5 m wide or deeper than 1 m. Since Arroyo Chub are most commonly found in shallow, slow-moving streams with pools that contain aquatic vegetation, such areas were preferentially sampled. Every effort was made to sample a minimum of 100 m at each sampling location, but intermittent streams often prevented this. We used dip nets in areas that could not be effectively seined such as undercut banks or complex structure such as boulders and woody debris.

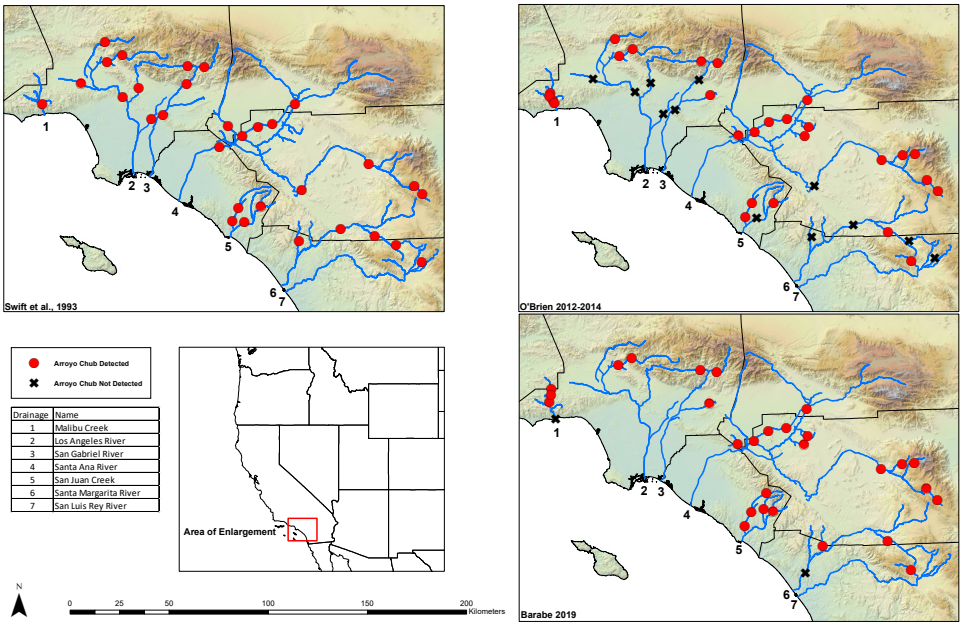

Figure 2. Arroyo Chub presence/absence within each of the seven native watersheds by survey year.

RESULTS

Between April 2012 and June 2014, we surveyed a total of 95 sites within 40 streams across the seven watersheds of which Arroyo Chub are native (Table 1). Fish were detected in 18 of the 40 streams (45%) and within six of the seven native watersheds. Of the 18 streams where Arroyo Chub were still present, nine streams (50%) also contained non-native aquatic fauna. We conducted range-wide surveys again in 2019 and report the survey results chronologically from north to south below.

Malibu Creek— Historic survey data (Swift et al. 1993) reported Arroyo Chub at one location in Malibu Creek (mainstem). Our surveys conducted in 2012–2014 found fish at four locations within the watershed (Upper and Lower Malibu Creek, Liberty Canyon, and Lower Las Virgenes Creek). The Liberty Canyon fish were only in the lower section near the confluence with Malibu Creek. Our 2019 surveys found fish at three locations (Upper

and Lower Las Virgenes Creek, and Liberty Canyon) (Fig. 2). No documentation of the species occurring in Las Virgenes Creek and Liberty Canyon could be found and the Las Virgenes population began immediately above a 2 m barrier to upstream migration. It is likely this barrier has prevented invasive species from colonizing the upper section and any project attempting to remove this barrier should carefully consider potential impacts to Arroyo Chub. All locations we sampled in the mainstem contained non-native gamefish (Table 2) including Largemouth Bass (*Micropterus salmoides*), Common Carp (*Cyprinus carpio*), and Black Bullhead (*Ameiurus melas*).

Los Angeles River— Swift et al. (1993) reported Arroyo Chub at seven locations within the watershed (Rio Hondo, Arroyo Seco, two in the mainstem, two in Big Tujunga Wash, and Pacoima Creek). Our 2012–2014 surveys found fish at two locations (Big Tujunga Wash and Pacoima Creek), and our 2019 surveys found fish at one location (Big Tujunga Wash) (Fig. 2). Pareti and Morales (2019) reported Arroyo Chub in Haines Creek, a tributary of Big Tujunga Creek. Non-native gamefish were found in Pacoima Creek (2019) and Big Tujunga Wash (Table 2).

San Gabriel River— Historic accounts of Arroyo Chub (Swift et al. 1993) reported fish at four locations within the San Gabriel Watershed (two in the mainstem, East Fork San Gabriel River, and West Fork San Gabriel River). Surveys conducted in 2005 observed large numbers of Arroyo Chub in Cogswell Reservoir and Upper West Fork (J. O'Brien, California Department of Fish and Wildlife, unpublished data). Our surveys conducted in 2012–2014 found fish at four sites (West Fork San Gabriel River, Bear Creek (tributary to the West Fork), East Fork San Gabriel River, and Walnut Creek). Walnut Creek is not reported as a historic location for this species. Additional surveys in 2017 confirmed continued Arroyo Chub presence in Upper West Fork, and our 2019 surveys found fish at five locations (East and West Forks of the San Gabriel River, Bear Creek (tributary to West Fork), Cattle Canyon (tributary to East Fork), and Walnut Creek) (Fig. 2). Non-native fishes were noted (Table 2) at two sites, including the first documented occurrence of the Oriental Weather Loach (*Misgurnus anguillicaudatus*) in Walnut Creek. In October 2020, the Bobcat Fire burned 46,861 ha (115,796 acres) of the Angeles National Forest (Inciweb 2020), including 93% of the West Fork Watershed (USFS 2020). Follow up surveys in 2021 have indicated significant debris flows occurred resulting in major habitat modifications. This likely impacted Arroyo Chub in the short-term, but no surveys have been conducted as of the writing of this manuscript.

Santa Ana River— Swift et al. (1993) reported Arroyo Chub at ten locations within the Santa Ana Watershed (five in the mainstem, Aliso Creek, Temescal Wash, two in San Jacinto Creek, and Indian Creek). Our 2012–2014 surveys found fish in two locations (Aliso Creek and the mainstem Santa Ana River). We found dry reaches in several streams including the formally occupied site within Temescal Wash, and non-native fishes were encountered at most sites. Data provided by Riverside Corona Resource Conservation District (RCRCD) from 2015–2021 reported Arroyo Chub at nine locations within the watershed (two in the mainstem, Sycamore Canyon Creek, Goldenstar Creek, Indian Creek, South Fork San Jacinto River, North Fork San Jacinto River, Aliso Creek, and Hemet Lake (B. Mills, Riverside Corona Resource Conservation District, personal communication)(Fig. 2). Annual invasive species removal efforts (Table 2) in the mainstem typically result in Arroyo Chub as bycatch, but RCRCD has noted a sharp decline in the number of this species captured in the last few years. We sampled the Aliso Creek population in 2020 and had difficulty locating Arroyo Chub within the stream, but easily captured Fathead Minnows (*Pimephales promelas*).

Table 1. Sites surveyed to assess presence/absence of Arroyo Chub in southern California from 2012–2014.

Watershed	Stream/Site	Arroyo Chub Found	# Sites surveyed	Latitude	Longitude	Historical Information	Abundance	Invasive Species Present
Malibu Creek	Cold Creek	N	1	34.07911	-118.69906	None	None	N
	Lower Malibu Creek	Y	2	34.04997	-118.69037	CNDDB	Common	Y
	Upper Malibu Creek	Y	1	34.16443	-117.89645	CNDDB	Common	Y
	Liberty Canyon Creek	Y	1	34.10989	-118.71529	None	Common	N
	Medea Canyon Creek	N	2	34.11693	-118.75555	None	None	Y
	Triunfo Canyon Creek	N	2	34.12674	-118.79599	None	None	Y
	Lower Las Virgenes Creek	Y	1	34.09694	-118.72017	Survey report	Common	Y
	Upper Las Virgenes Creek	N	1	34.144	-118.70131	None	None	Y
Los Angeles River	Lower Big Tujunga Creek	Y	3	34.30241	-118.25996	CNDDB	Rare	Y
	Upper Big Tujunga Creek	N	1	34.28667	-118.22869	Survey report	None	N
	Haines Creek	N	1	34.26673	-118.34906	CNDDB	None	Y
	Los Angeles River	N	2	34.17773	-118.4962	CNDDB	None	Y
	Bull Creek	N	1	34.17964	-118.49784	None	None	Y
	Little Tujunga Creek	N	1	34.28227	-118.3705	CNDDB	None	N
	Pacoima Creek	Y	2	34.34469	-118.36119	Survey report	Rare	N
San Gabriel River	North Fork San Gabriel River	N	3	34.24928	-117.86193	CNDDB	None	N
	West Fork San Gabriel River	Y	3	34.24928	-117.87653	CNDDB	Common	Y
	East Fork San Gabriel River	Y	3	34.23335	-117.79562	CNDDB	Rare	Y
	Cattle Canyon Creek	N	1	34.22797	-117.76517	CNDDB	None	N
	Bear Creek	Y	1	34.24513	-117.88713	CNDDB	Rare	N

Watershed	Stream/Site	Arroyo Chub Found	# Sites surveyed	Latitude	Longitude	Historical Information	Abundance	Invasive Species Present
	Big Mermaids Canyon Creek	N	1	34.2447	-117.90062	CNDDB	None	N
	Walnut Creek	Y	2	34.09139	-117.82872	Survey report	Rare	Y
	San Gabriel River	N	1	34.16443	-117.89645	CNDDB	None	Y
Santa Ana River	Upper Santa Ana River	Y	1	34.03765	-117.3567	CNDDB	Common	Y
	Upper Santa Ana River	N	1	34.99435	-117.3905	CNDDB	None	Y
	Middle Santa Ana River	N	1	34.97113	-117.42235	CNDDB	None	Y
	Middle Santa Ana River	N	1	34.92499	-117.59613	CNDDB	None	Y
	Sunnyslope Creek	N	1	34.97142	-117.43099	CNDDB	None	Y
	Aliso Canyon Creek	Y	3	33.89435	-117.69127	Survey report	Rare	N
	Arroyo Tequisquite Creek	N	1	34.96761	-117.43175	CNDDB	None	Y
	San Jacinto River	N	1	33.73975	-116.83772	CNDDB	None	N
	Temescal Creek	N	3	33.89933	-117.59142	CNDDB	None	Y
San Juan Creek	Lower San Juan Creek	N	1	33.47724	-117.6784	CNDDB	None	Y
	OSO Creek	N	1	33.52059	-117.67479	CNDDB	None	Y
	Upper San Juan Creek	Y	3	33.58618	-117.52002	CNDDB	Rare	Y
	Middle San Juan Creek	N	3	33.50559	-117.6443	CNDDB	None	Y
	Bell Creek	Y	2	33.63047	-117.55424	CNDDB	Rare	N
	Hot Springs Creek	Y	2	33.5986	-117.51233	CNDDB	Rare	N
	Upper Trabuco Creek	N	3	33.67421	-117.53709	CNDDB	None	N
	Middle Trabuco Creek	Y	1	33.58087	-117.6388	CNDDB	Rare	Y
	Lower Trabuco Ck	N	1	33.58384	-117.63751	CNDDB	None	Y

Watershed	Stream/Site	Arroyo Chub Found	# Sites surveyed	Latitude	Longitude	Historical Information	Abundance	Invasive Species Present
Santa Margarita River	Tijeras Creek	Y	1	33.59278	-117.63131	Survey report	Rare	N
	Santa Margarita River	N	4	33.43125	-117.19633	CNDDB	None	Y
	Temecula Creek	Y	3	33.43071	-116.85472	CNDDB	Rare	Y
	Rainbow Creek	N	2	33.41033	-117.20885	CNDDB	None	Y
	De Luz Creek	N	3	33.44308	-11732076	CNDDB	None	N
	Sandia Creek	N	2	33.42998	-117.24756	CNDDB	None	N
San Luis Rey River	Murrietta Creek	N	3	33.56082	-117.23654	None	None	Y
	Upper San Luis Rey River	N	1	33.30852	-116.69429	CNDDB	None	Y
	Agua Caliente Creek	N	1	33.28832	-116.65341	CNDDB	None	N
	Lower San Luis Rey River	N	8	33.2204	-117.35718	None	None	Y
	Middle San Luis Rey River	N	2	33.35456	-117.03879	None	None	Y

We were only able to capture the target species in one short section of intermittent stream. The Blue Ridge Fire burned the entirety of the Aliso Creek Watershed in October 2020 and will likely impact this isolated population.

San Juan Creek— Historic survey data (Swift et al. 1993) reported Arroyo Chub in four locations within the San Juan Watershed (two in the San Juan Creek mainstem, and two in Arroyo Trabuco). Arroyo Chub were absent from the lower mainstem site in our 2012–2014 surveys but were found in the upper mainstem site and in tributaries such as Hot Springs Creek, Bell Creek, and Tijeras Creek. One section of Upper Arroyo Trabuco and middle San Juan Creek mainstem was dry. Non-native minnows and Western Mosquitofish (*Gambusia affinis*) (Table 2) were common at most of the sampling locations, but were not observed in Tijeras Creek, Upper San Juan Creek, and Upper Arroyo Trabuco. We found an additional population of the target species in the headwaters of Arroyo Trabuco in 2016 (R. Barabe, California Department of Fish and Wildlife, unpublished data). Our 2019 surveys found fish in three locations (Lower Arroyo Trabuco, Tijeras Creek, and San Juan Creek) (Fig. 2). Although the populations in Bell Creek and Upper Arroyo Trabuco could not be located in 2018 and 2019, both were relocated in 2021. Dam removal in San Juan Creek (conducted by the US Forest Service) led to an expansion of the occupied habitat approximately 0.24 km upstream.

Santa Margarita River— Swift et al. (1993) found Arroyo Chub at four locations within the Santa Margarita Watershed (De Luz Creek, and three locations in Temecula Creek). Our 2012–2014 surveys only found fish in one location (the headwaters of Temecula Creek), which has a series of perennial pools with no invasive species. Most of our survey sites had sufficient flow and instream habitat for the target species but contained non-native predatory fishes (Table 2). Our follow up surveys in 2019 detected fish in the same single location in Temecula Creek (Fig. 2). Surveys conducted in summer of 2021 show this area drying quickly. An additional population of Arroyo Chub was known to persist in the mainstem Santa Margarita River on Marine Corps Base Camp Pendleton, but no fish have been seen since a high flow event in 2017 (D. Cie, USMC Camp Pendleton Base Biologist, personal communication). An additional population of the target species was discovered in Sandia Creek (Fig. 2) (June 2021). A few invasive Redeye Bass (*Micropterus coosae*) were seen in Sandia Creek.

San Luis Rey River—Swift et al. 1993 reported Arroyo Chub in one location (Agua Caliente Creek), a small, headwater tributary. Our 2012–2014 surveys were unable to locate fish within this watershed, although multiple locations were sampled (Table 1). In addition to the sites listed, several other sites were visually surveyed but not sampled due to a lack of water or suitable habitat. Large sections of the San Luis Rey River mainstem were dry, channelized, or contained non-native fish species (Table 2). We found Arroyo Chub in the West Fork San Luis Rey River in 2017 (Fig. 2). The fish were found in a short section of intermittent stream where a series of seven perennial pools persist. We have revisited this site annually to monitor this population and conduct invasive species removal.

DISCUSSION

When comparing the survey data from Swift et al. (1993) to the data collected in 2012–2014, and from 2016–2021, significant declines in the number of Arroyo Chub populations were noted in the Los Angeles, San Gabriel, and Santa Margarita rivers. In the Los Angeles River Watershed, four populations were apparently extirpated from 1993 to

Table 2. Invasive species observed within each watershed sampled for Arroyo Chub in 2012-2014 and 2019.

Site	Non-native species found
Malibu Creek	Largemouth Bass *Micropterus salmoides* Black Bullhead *Ameiurus melas* Common Carp *Cyprinus carpio* Crayfish *Procambarus clarkia*
Los Angeles River	Largemouth Bass *Micropterus salmoides* Black Bullhead *Ameiurus melas* Green Sunfish *Lepomis cyanellus* Red Shiner *Cyprinella lutrensis* Western Mosquitofish *Gambusia affinis* Crayfish *Procambarus clarkia*
San Gabriel River	Largemouth Bass *Micropterus salmoides* Weather Loach *Misgurnus anguillicaudatus* Common Carp *Cyprinus carpio*
Santa Ana River	Largemouth Bass *Micropterus salmoides* Channel Catfish *Ictalurus punctatus* Black Bullhead *Ameiurus melas* Green Sunfish *Lepomis cyanellus* Black Crappie *Pomoxis nigromaculatus* Fathead Minnow *Pimephales promelas* Red Shiner *Cyprinella lutrensis* Golden Shiner *Notemigonus crysoleucas* Western Mosquitofish *Gambusia affinis* Crayfish *Procambarus clarkia* Bluegill *Lepomis macrochirus*
San Juan Creek	Golden Shiner *Notemigonus crysoleucas* Red Shiner *Cyprinella lutrensis*
Santa Margarita River	Largemouth Bass *Micropterus salmoides* Black Bullhead *Ameiurus melas* Green Sunfish *Lepomis cyanellus* Redeye Bass *Micropterus coosae* Western Mosquitofish *Gambusia affinis* Crayfish *Procambarus clarkia*
San Luis Rey River	Largemouth Bass *Micropterus salmoides* Common Carp *Cyprinus carpio* Black Bullhead *Ameiurus melas* Green Sunfish *Lepomis cyanellus* Western Mosquitofish *Gambusia affinis*

2012, and an additional one was lost from 2012 to 2021. Two populations were lost in the San Gabriel River Watershed from 1993 to 2012, and the Santa Margarita River Watershed lost four populations from 1993 to 2012. A range contraction occurred in the Malibu Creek Watershed, where fish were not found in the mainstem, and no fish were seen in Agua Caliente Creek (San Luis Rey River Watershed).

Moyle et al. (2015) reported Arroyo Chub as vulnerable to extinction in its native range within the next 100 years but considers the species more stable when non-native populations are included. In his overview of the species, Swift et al. (1993) listed fish as common in only four streams within its native range: Santa Margarita River (including De Luz Creek), Arroyo Trabuco, San Juan Creek, and Malibu Creek. Within these four streams, the 2012–2014 surveys found Arroyo Chub abundant only in Malibu Creek (note that sampling did not occur in lower Santa Margarita River where they were reported to be still extant), and small, but stable populations, in Las Virgenes Creek (Malibu Watershed), Bell Creek (San Juan Watershed), Walnut Creek (San Gabriel Watershed) and in the upper Santa Ana River. A robust and dispersed population was found in the West Fork San Gabriel River Big Tujunga Creek (Los Angeles Watershed) between Hansen and Big Tujunga dams. Surveys conducted in 2019 found fish abundant in San Juan Creek, Arroyo Trabuco, Tijeras Creek (San Juan Watershed), West Fork San Gabriel River (San Gabriel Watershed), Big Tujunga Creek (Los Angeles Watershed), and Las Virgenes Creek (Malibu Watershed).

Considering the preferred habitat of Arroyo Chub is slow-moving or backwater sections of streams with muddy or sandy bottoms (Moyle 2002), it is likely the species occupied much of the low elevation channels of all seven native streams, meaning an even larger range-wide contraction occurred after European settlers began colonizing this area. The current distribution (Fig. 3) shows how this species has been relegated to upstream, headwater sections of streams. Most of the streams where the species still occur are on U.S. Forest Service land, which are generally mid to high gradient mountain stream systems.

There are a number of factors implicated in the observed decline of Arroyo Chub, including urbanization (habitat loss, habitat fragmentation, non-native species introductions, channelization, water extraction/addition, and agriculture) climate change and drought. For example, five of the seven native streams have large segments that are not suitable for Arroyo Chub due to channelization, which reduces or eliminates access to floodplain habitat with side channels and back-water pool habitat while increasing flow velocity.

Each of the seven native watersheds have extensive urbanization. Urban and commercial development near streams can lead to an increase in non-native species introductions (Copp et al. 2005) and the loss of freshwater fishes (Marchetti et al. 2006). Additionally, Brown et al. (2005) found alien species dominant at urban sites in southern California. Non-native aquatic species were present within each of the seven native watersheds, usually in areas no longer occupied by Arroyo Chub. In Malibu Creek, lower Arroyo Trabuco, Santa Margarita and San Luis Rey rivers, relatively good habitat was present in certain sections, but Arroyo Chub were not detected. This is likely due to abundant populations of non-native fishes such as Largemouth and Redeye Bass, Green Sunfish (*Lepomis cyanellus*), Black Bullhead, Western Mosquitofish, and minnow species. Schrank et al. (2001) found extirpation of the endangered Topeka Shiner (*Notropis topeka*) in Kansas was linked to the abundance of introduced Largemouth Bass, and Western Mosquitofish have been implicated in eliminating small fish species in many locations through predation and competitive interactions (Myers 1965; Meffe and Snelson 1989; Moyle 2002). Each of these non-native species were

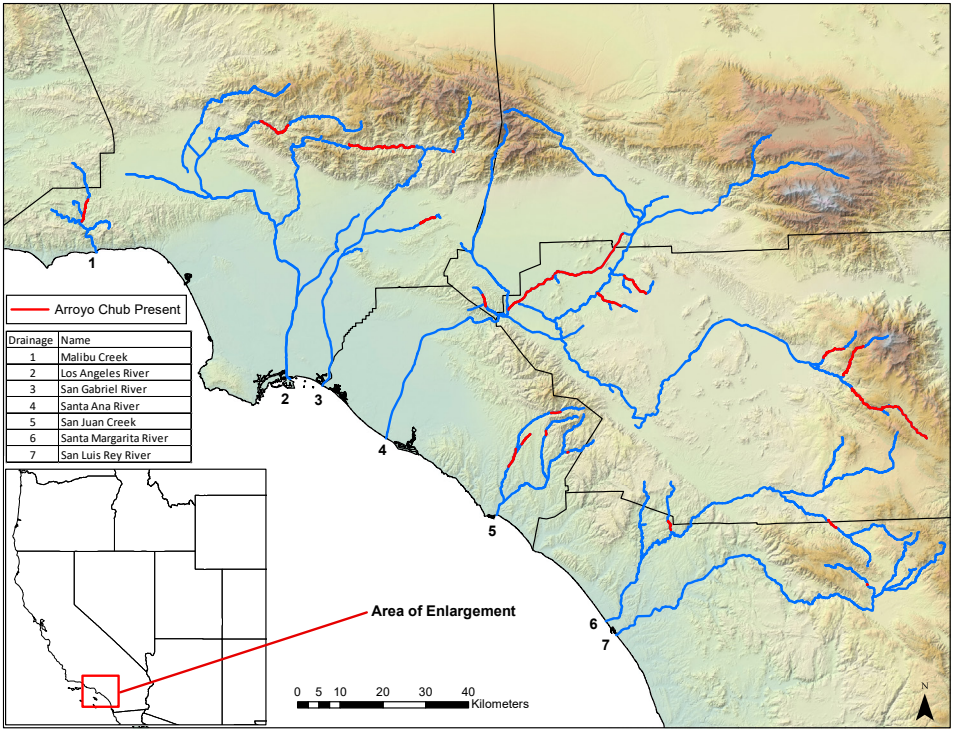

Figure 3. The approximate upstream and downstream extent of each Arroyo Chub population (in red).

observed across the survey range and were often far more abundant and widespread than Arroyo Chub. Additionally, the Red Swamp Crayfish, (*Procambarus clarkia*), is known to predate on fish eggs and larvae (Mueller et al. 2006) and was ubiquitous throughout the low elevation flood plains of all seven native watersheds. Crayfish were especially abundant in Malibu, San Juan, and Walnut creek watersheds.

From 2012 through 2016, California experienced one of the most severe droughts in over a century (Griffin and Anchukaitis 2014; Swain et al., 2014). Persistent drought conditions reduced streamflow and some historically occupied sites such as Agua Caliente (San Luis Rey Watershed) and substantial sections of De Luz Creek (Santa Margarita Watershed), San Juan, and Pacoima (Los Angeles Watershed) creeks were dry when sampling occurred. The 2013–2014 water year had some of the lowest precipitation totals observed for southern California (Griffin and Anchukaitis 2014). In many cases, follow-up sampling the ensuing year was also not productive as stream flows were even lower due to the ongoing drought. Surveys conducted in 2019 failed to locate Arroyo Chub in Pacoima Creek, and extirpation of this population is believed to have occurred as a result of this drought.

Arroyo Chub exhibit a high temperature tolerance and are physiologically adapted to hypoxic conditions and wide temperature fluctuations present in southern California streams (Moyle 2002). Both authors have observed fish in standing pools where water temperature exceeded 30° C. These traits, coupled with the ability to persist in small streams with widely fluctuating flows, have led Moyle et al. (2013) and others (Castleberry and Cech 1986), to the conclusion that Arroyo Chub are less vulnerable to climate change when compared to species with narrower environmental tolerances.

Most of the stable Arroyo Chub populations are small and isolated in headwaters (Fig. 3), leaving them vulnerable to extirpation through the combined effects of stochastic events and the loss of genetic diversity (Benjamin et al. 2016). Stream fragmentation has been reported to increase the risk of extinction by reducing connectivity, habitat area, and complexity (Rieman and McIntyre 1993, 1995, 1996; Reeves et al. 1995; Schlosser and Angermeier 1995; Dunham et al. 1997).

Recent genetic analysis of the remaining Arroyo Chub populations reported a high level of population differentiation both within and between drainages, likely stemming from barriers to gene flow such as dams, and current watershed boundaries (Benjamin et al. 2016). Furthermore, Benjamin et al. (2016) found eight distinct populations from the six native watersheds sampled (no fish were captured in the San Luis Rey River). Fish from Pacoima Creek and Big Tujunga Wash (both in the Los Angeles Watershed) and the West Fork San Gabriel River and Walnut Creek (both in the San Gabriel Watershed) were reported as distinct populations, illustrating how quickly the effects of barriers to downstream migration can lead to changes in population structure. Urbanization has also been linked to reductions in genetic variation and impacts to gene flow have been reported (Bessert and Orti 2008).

Arroyo Chub were once considered a nuisance species in Crystal Lake (Vestal 1942) and populations may continue to persist in other lentic waters such as Big Bear Lake. Future research is recommended to determine if these populations persist. Additionally, there are populations outside of their native range in the Santa Clara, Ventura, and Santa Maria river basins, where habitat modifications are less severe. Future research is also recommended to determine the genetic origins of these non-native populations as they could be useful in maintaining the genetic diversity of the native populations and serve as a backup in case of loss due to a stochastic event.

Climate change, urbanization, development, and invasive species impacts could lead us to a grim outlook for Arroyo Chub, but the current population in Tijeras Creek provides a bright spot. This population is present and thriving in water currently proposed for 303(d) listing as impaired for benthic macroinvertebrates and phosphorous. The key here is likely the absence of non-native competitors and predators. Leveraging Arroyo Chub tolerance to poor water quality could prove to be an advantage in conservation of the species. In those streams where we did not detect the target species, yet a historical account of the species exists, over half (54%) contained non-native aquatic fauna. Conducting invasive species removals in small natural bottom creeks throughout the native range could provide additional habitat, and coupled with translocation, could help us prevent this species from becoming threatened or endangered.

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FULL RESEARCH ARTICLE

Machine learning to understand patterns of burn severity from the SCU Lightning Complex Fires of August 2020

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The SCU Lightning Complex Fire started on 16 August 2020 and burned more than 395,000 acres of woodlands and grasslands in six California counties. Satellite images of pre-fire green vegetation biomass from both 2020 springtime (moist) and summertime (drier) periods, along with slope and aspect were used as predictors of burn severity patterns on the SCU Complex landscape using machine learning algorithms. The main finding from this analysis was that the overall burn severity patterns of the SCU Complex fires could be predicted from pre-fire vegetation biomass, slope, and aspect model input variables with high accuracies of between 50% and 80% using Random Forest machine learning techniques. The August and April biomass cover variables had the highest feature importance values. It can be concluded that the amount of dry biomass present at a given location was essential to predict how severely and completely the 2020 fires burned the vegetation cover and surface soils across this landscape.

Key words: burn severity, machine leaning, NDVI, random forest, wildfire

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The SCU Lightning Complex Fires started on 16 August 2020 as a result of hundreds of lightning strikes in the Diablo Range of northern California, and burned within six counties: Alameda, Contra Costa, Santa Clara, San Joaquín, Stanislaus, and Merced (CALFIRE 2020). A total of 222 structures were destroyed in these fires. The SCU Complex Fires were declared nearly 100% contained on 10 September 2020, after burning over an estimated 160,498 ha (396,600 acres; WERT 2020) and becoming the third-largest wildfire recorded in California's modern history.

In the wake of a disaster of this magnitude, resource managers require timely information about burn severity patterns, for purposes ranging from addressing immediate hazards such as landslides and tree falls, to monitoring runoff of chemicals in waterways, and managing long-term post-fire recovery of watersheds and woodland stands (WERT 2020). The use of multispectral (remotely sensed) burn severity metrics has become common across

North American forests (French et al. 2008). The normalized burn ratio (NBR; Key and Benson 2006) from satellite imagery was developed expressly to assess post-fire changes in reflectance of healthy vegetation, soils, and soil moisture (Potter 2016).

There have been several noteworthy modeling studies to predict burn severity levels from wildfires. For instance, Whitman et al. (2018) found that pre-fire stand structure and composition, topography, and fire weather at time of burning were the best predictors of burn severity from boreal forest fires. Wetlands burned less severely than uplands, and open stands with high basal areas showed lower burn severity than in upland vegetation stands. Burn severity has been shown to be a product of pre-fire vegetation conditions and fuel loads (Boucher et al. 2016; Lydersen et al. 2017) and topography (Krawchuk et al. 2016).

Topographic aspect can influence the amount of solar radiation and moisture availability on a hillslope, which in turn can directly influence fire behavior, as well as indirectly through the control over differences in vegetation composition and biomass fuel density (Estes et al. 2017). Steeper slopes may also lead to greater preheating of fuels and increased rate of spread when fire is moving upslope (Estes et al. 2017). Localized weather conditions related to topography, such as wind speeds and surface temperatures during the periods of intense burning, can strongly influence fire behavior and combustion rates (FCFDG 1992; Krawchuk et al. 2016). Along these lines, Potter (2017) reported that seasonal climate conditions (maximum air temperatures and low moisture) at the time of ignitions of large wildfires on the central and southern California coasts were significant controllers of the total area burned at high severity and the edge complexity of high severity burn patches on the fire landscape.

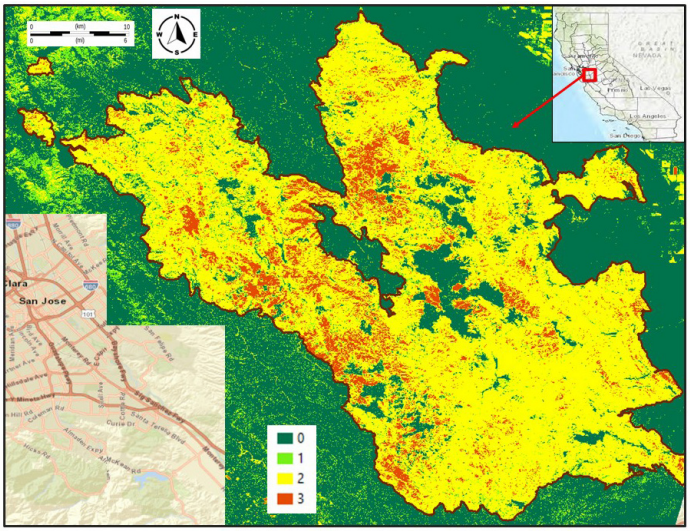


Figure 1. Map of Landsat dNBR burn severity classes resulting from the 2020 SCU Complex fires. Color legend of burn severity class labels is as follows: 0 = no burn, 1 = low burn, 2 = moderate burn severity, and 3 = high burn severity. Inset map of major highways in the Santa Clara Valley shows actual proximity of the fire boundary outline to San Jose urban areas.

The purpose of this study was to describe and explain the geographic variability in burn severity classes resulting from the 2020 SCU Complex Fires. Plant communities that burned in the SCU Complex wildfires included coast live oak (*Quercus agrifolia*), blue oak (*Q. douglasii*), valley oak (*Q. lobata*), and black oak (*Q. kelloggii*) woodlands, plus chamise (*Adenostoma fasciculatum*) shrublands, Diablan sage scrub, non-native annual grassland of brome grass, and native perennial grassland (White 1966; Fry 2008; Stahle et al. 2013). The main objective of this study was to characterize the relative importance of spatially

mapped landcover attributes, namely topography and vegetation cover density, as controls on burn severity in this extreme fire event. Satellite images of pre-fire green vegetation density in terms of relative biomass from both 2020 springtime (moist) and summertime (drier) periods, along with slope and aspect were used as predictors of August–September 2020 burn severity classes in a machine learning approach. For mapping of fire fuel in terms of vegetation biomass amounts prior to the 2020 fires in California, we have analyzed the Landsat normalized difference vegetation index (NDVI) as a surrogate for burnable biomass, as has been done in similar studies of wildfire mapping (Radočaj et al. 2021).

METHODS

Satellite Image Data

We calculated the SCU Complex NBR index from satellite image dates, both pre- and post-August of 2020, from the near infrared (NIR; 0.85–0.88 μm) and shortwave infrared (SWIR; 1.57–1.65 μm) bands of the Landsat 8 sensor Collection 2 images at 30-m pixel size, according to the equation:

$$NBR = (NIR - SWIR)/(NIR + SWIR)$$

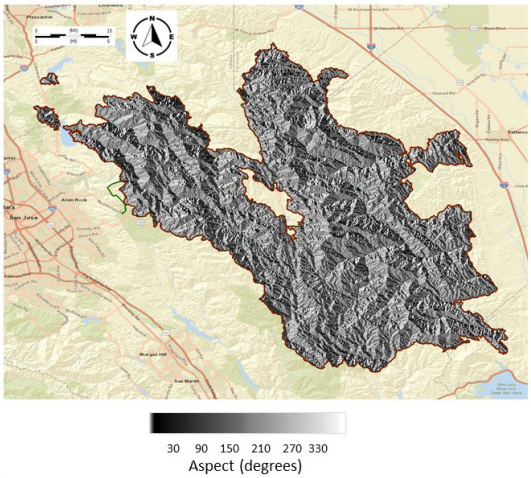
We differenced pre-fire (24 July 2020) and post-fire (26 September 2020) NBR images to generate a dNBR map product for the SCU Complex Fires. Burn severity classes of low, moderate, and high levels can cover a dNBR value range of –500 to 12,000 over burned land surfaces. Positive dNBR values represent a decrease in vegetation cover and a higher burn severity class, while negative values represent an increase in live vegetation cover following the fire event.

We defined four classes of burn severity for this study as no burn (0-NB) at dNBR < 500, low burn severity (1-LBS) at dNBR > 500 and <= 1000, moderate burn severity (2-MBS) at dNBR > 1000 and <= 5000, and high burn severity (3-HBS) at dNBR > 5000 (Potter 2016). These classification levels generally followed the burn severity thresholds determined by Miller and Thode (2007) based on a composite burn index (CBI) for California forests. The CBI was developed to assess on-the-ground fire effects on plants and soils (i.e. burn severity) by sampling over strata of the vegetation remaining post-fire: litter, low shrubs, small trees, tall shrubs and sapling trees, intermediate trees, and tall trees.

The Landsat 8 Collection 2 normalized difference vegetation index (NDVI) provides consistent spatial and temporal profiles of relative vegetation canopy biomass (Verbesselt et al. 2010) according to the equation:

$$NDVI = (NIR - Red)/(NIR + Red)$$

resulting in values between –1.0 and 1.0 NDVI units. We multiplied NDVI values by 10,000 to preserve decimal places in integer file storage. Low values of NDVI (near 0.1) indicate barren land cover whereas high values of NDVI (above 0.8) indicate dense canopy cover. NDVI has been proven as an accurate index of herbaceous green cover in grasslands of California and can be converted into seasonal herbaceous biomass (g carbon/m^2) each year (Potter 2014a). We obtained Landsat 8 images from both 3 April 3 and 9 August 2020 for cool season (April) and warm season (August) pre-fire NDVI map layers.



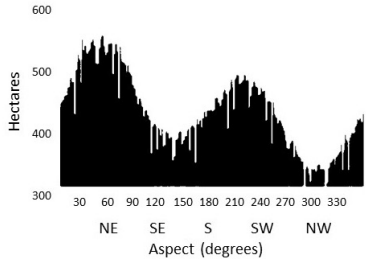


Figure 2. (a) Map of the aspect of the hillslopes and (b) Distribution of land area by hillslope aspect across the SCU Complex burned area.

Slope and Aspect Layers

Digital layers for slope and aspect for the SCU Complex burned area were determined at 30-m spatial resolution from the United States Geological Survey (USGS) National Elevation Dataset (NED) using the ArcGIS Spatial Analyst Toolbox (ESRI, 2021). This tool uses a 3 by 3 cell moving window to process the digital elevation data into continuous gridded slope and aspect values.

Machine Learning and Statistical Analysis

To predict dNBR burn severity classes for the SCU Complex fire area from NDVI, slope, and aspect spatial layers, we used the Scikit-learn machine learning library for the Python programming language (Pedregosa et al. 2011). Scikit-learn features various classification and regression algorithms including decision trees, support vector machines, Random Forest, and k-means nearest neighbor, all operating with the Python libraries NumPy and SciPy.

Among all the Scikit-learn machine learning methods, we selected the Random Forest method from Breiman (2001) for this analysis, because it has the ability to perform both classification and regression prediction. Random forests are an improved extension on classification and regression trees (CART) (Liaw and Weiner 2018). Moreover, Random Forest methods have the following advantages: handles categorical predictors naturally, computationally simple to fit, has no formal distributional assumptions, and performs automatic variable selection.

The Random Forest model operated as follows: first, the algorithms computationally "grow" a forest of ntree trees. For each tree from 1 to ntree, a sample of size N is taken from the dataset with replacement (bootstrap) to grow the tree. A selection of m variables, independently for each node tree, is made, and the tree is split at each node by determining which variable will create the highest proportion of homogenous classification using Gini impurity. Trees are grown until the nodes can no longer be split, unless otherwise specified

with a max_depth variable to prevent overfitting of the data. For classification, majority voting is used to generate aggregated predictions of the ntree trees. For model training, 70% of the data points are selected while the remaining 30% of data points are split to create the "testing" data, used to unbiasedly evaluate the model's fit on the training dataset. The error rate of all the OOB predictions is the OOB error rate of the random forest result.

Random forest can also compute the importance of variables in two different ways. For this study and related classification problems, Gini criterion impurity can be used to measure variable importance (Pedregosa et al. 2011). For a given tree, the Gini variable importance for a particular variable of interest is the weighted average of the decrease in the Gini criteria impurity of the splits based on this variable. This is averaged over the ntree trees in the forest to get the Gini importance for the forest. The other variable importance calculation is called permutation importance, which is based on predictive accuracy. The testing error rate is computed from both a data set obtained from permuting the values of a particular variable of interest in the testing data and the original testing data. The difference between these two testing error rates gives the permutation variable importance.

Output statistics from the Random Forest model were generated as a classification matrix report including class prediction accuracies (as seen in Fig. 5), and as the F1 score for each predicted class, which can be interpreted as a weighted average of the precision and recall, where an F1 score reaches its highest possible value at 1, indicating perfect precision and recall, and has a lowest value at 0 (Pedregosa et al. 2011). The relative contribution of precision and recall to the F1 score are equal. The F1 score is also known as the Sørensen–Dice coefficient. The feature importance of each predictor variable in the model is also captured to understand the weight of each variable in predicting the overall burn severity classes.

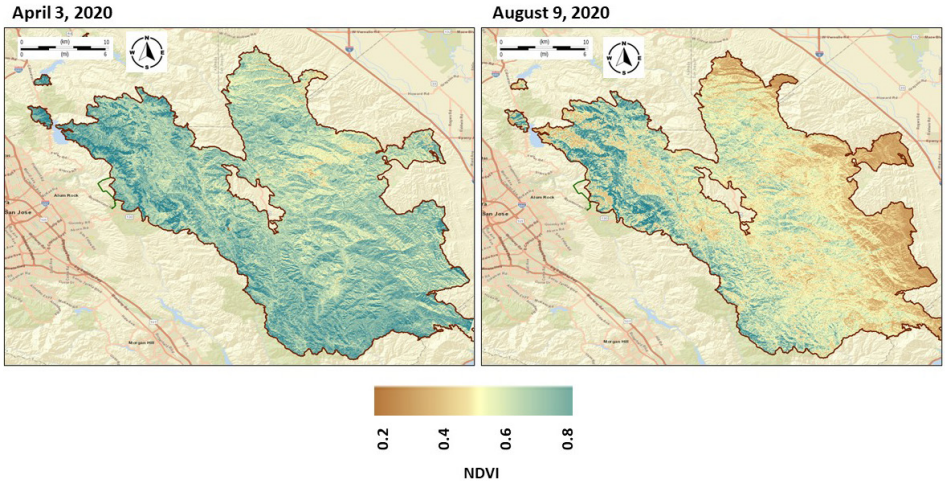


Figure 3. Pre-fire maps of NDVI in April and August of 2020 across the SCU Complex burned area.

As a large image data set with multiple variables, the entire SCU Complex burned area proved to be too large (at 1.7 million row entries) to run all at one in Scikit-learn. Therefore, we first tested a random sampling approach into smaller image subsets, about one-third the size of the entire burned area, which would still allow one to make strong statistical inferences about the entire dataset. Several down-sampling methods were tested to compare their performance to the random subsets sampling approach. Subsequently,

we tested down-sampling methods, including Near Miss and Edited Nearest Neighbor, to compare their performance to the random subsets sampling approach.

In cases such the SCU Complex fires with a skewed burn severity distribution among classes, data sampling methods can used to compensate for a large class imbalance. Random down-sampling (over or under) methods generally show improved overall results in machine learning applications (Leevy et al. 2018). As a result of this type of down-sampling, the majority burn severity class should not take over the other classes during the training process, and all classes will be well-represented by the decision function.

The Near Miss undersampling method selects all data from the minority class and then focuses on sampling from the larger class(es). The algorithm computes the distance between all data in the majority class to the data in the minority class then selects pixel datapoints of the majority class with the smallest distance to the minority class(es). In this case, the burn severity class with the smallest number of pixels in the SCU Complex area, low burn severity (LBS 1), was used to set the maximum number of pixels for sampling of all the other burn severity classes for new Random Forest runs. Therefore, all data for class 1 is selected and burn severity classes 0, 2, and 3 are sampled equally using the Near Miss method.

Edited Nearest Neighbors (ENN) was also tested as an undersampling method. This technique focuses on removing noisy and ambiguous data on the class boundaries to address the class imbalance and also make the distinction between classes clearer. The data in the majority class that are misclassified as the minority class are removed and those correctly classified are selected. In addition, the data in the minority class that are misclassified have their nearest neighbors from the majority class deleted to reduce classification ambiguity. This method, unlike the Near Miss undersampling method, does not create an equal amount of pixel data across each class, but rather attempts to select the least ambiguous dataset to increase prediction accuracy.

RESULTS

Landsat Burned Severity Patterns

The SCU Complex burned severity classes mapped using 2020 Landsat NBR images (Fig. 1) were bounded to the north by the Livermore Valley, to the east by the San Joaquin Valley, to the south by the Pacheco-Pass Highway, and to the west by the Santa Clara Valley and the City of San Jose. A total of 1,454 km² (359,220 acres) was estimated by the Landsat dNBR to have burned in low to high severity classes during this lightning complex fire. The distribution of land area among burned severity classes was low severity 5%, moderate severity 83%, and high severity 12%. Taken as a whole, the dNBR data set for SCU Complex burned area classes can be described as highly imbalanced, because the four burn severity classes were unequally represented across the study landscape.

Most of the SCU Complex burned area was mapped on steep terrain with an average slope gradient of over 35% (WERT 2020). The burned area exhibited 1242 m (4,076 ft) of vertical relief, ranging from about 90 m (300 ft) above mean sea level (amsl) in deep, lower elevation canyons, up into the mountainous eastern sections of the burned area at 1334 m (4,376 feet) elevation. Aspect of the hillslopes across SCU Complex burned area was skewed slightly to more northeastern-facing slopes than to southeastern- and southwestern-facing slopes (Fig. 2).

Maps of pre-fire NDVI in 2020 across the SCU Complex burned area showed the

patterns in the density of green plant cover during the relatively cool season (April) and again during the warmer season (August), including areas where evergreen oak woodland and shrubland cover predominated (Fig. 3). These oak woodland and shrub-covered watersheds were most extensive in the northwestern portions of the SCU Complex burned area. Locations where annual grassland plant cover predominated are identified by high NDVI (> 0.4) in April and lower NDVI (< 0.4) in August. These herbaceous plant-covered watersheds were most extensive in the eastern margins of the SCU Complex burned area. Judging from the cool-to-warm season transition in NDVI shown in Fig. 3, the majority of vegetation cover that burned in late August of 2020 had dried out and turned from green to brown at the time of ignition.

Correlation Matrix

The correlation matrix results for the four predictor variables and the predicted burn severity classes (Fig. 4) showed that the only significant (linear) correlation detected was between NDVI in April and in August. This NDVI correlation at R = 0.57 was not unexpected, because areas with evergreen woodland and shrub cover do not change in live canopy cover as much as grass-covered areas and in grazed rangelands of the study landscape. However, slope, aspect, and NDVI (in either April or August) were not strongly correlated across the 2020 burned area in any other one-to-one comparison of these predictor variables.

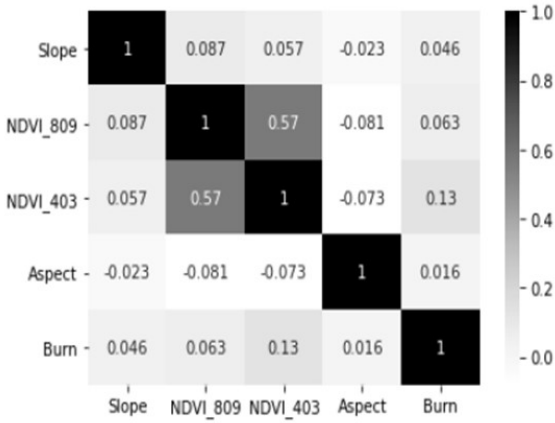


Figure 4. Correlation matrix for predictor (model input) layers and predicted burn severity classes in the SCU Complex fires.

Machine Learning Results

Running Random Forest on the randomly sampled (one-third) subsets of the dataset resulted in a 75% prediction accuracy overall. However, as seen in its normalized confusion matrix (Fig. 5a), this model mainly resulted in correctly classifying the most unbalanced (majority) class, namely the moderate burn severity (MBS 2), at a 95% prediction accuracy, while the high burn severity class (HBS 3) result had only a 23% prediction accuracy. For the purposes of this study, better prediction accuracies across all the burn classes are necessary and would be preferred over a high accuracy dominated by the majority burn class area. While the majority class, in this case MBS 2, makes up most of the burned area dataset, any of the minority burn classes may be considered to be of at least as great of interest.

A usefully predictive model should be able to generalize its learnings for new datasets. Generalization in part can be achieved by not overfitting the model to the training data. In the case of this study, because of the class-imbalance for MBS class 2, the model began to overfit this class. We alleviated this imbalance to reduce overfitting by performing undersampling of the training data to have an equally distributed amount of data in each class.

Applying the Near Miss undersampling method, with the smallest burn class to set the sampling level being the low burn severity (LBS 1; N = 79,269 pixels) class, Random Forest results produced a significant overall prediction accuracy of 54% for the four burn severity classes. The normalized confusion matrix (Fig. 5b) showed that this sampling method resulted in the moderate burn severity (MBS 2) with a 61% prediction accuracy, while the high burn severity class (HBS 3) had a 71% prediction accuracy, and the low burn severity (LBS 1) had a 49% prediction accuracy. The overall accuracy of the model was most strongly impacted by the difficulty in prediction of the unburned areas (class 0), whose prediction accuracy was 35% using the Near Miss undersampling method. For this model run, the F1 score results followed the prediction accuracy ranking, with scores of 0.39, 0.53, 0.58, and 0.62 for burn classes 0 to 3, respectively. The feature importance values for the four input variables from Random Forest modeling with Near Miss undersampling were output as follows: 0.31, 0.26, 0.22, and 0.22 for NDVI in August 2020, NDVI in April 2020, slope, and aspect, respectively.

Random Forest modeling using the ENN undersampling method resulted in the highest accuracy for any of the models tested, with a 90% overall prediction accuracy. Although this method still retains a high amount of pixels values in class MBS 2, its data selection technique results in higher accuracy among all four classes, compared to even the subsetted random sampling method. Using the ENN undersampling method resulted in the moderate burn severity (MBS 2) with a 99% prediction accuracy, while the high burn severity class (HBS 3) had a 58% prediction accuracy, and the low burn severity (LBS 1) had a 21% prediction accuracy. The overall accuracy of the model was also impacted by the difficulty in prediction of the unburned areas (class 0), whose prediction accuracy was 34%. Similar to Near Miss undersampling results, the feature importance outputs from the ENN random forest run showed the significance of pre-fire NDVI data in relation to predicting fire burn severity classification. In this model result, the August and April NDVI variables had even higher feature importance, with a combined value of around 0.60, and both slope and aspect showing importance outputs of 0.20 each.

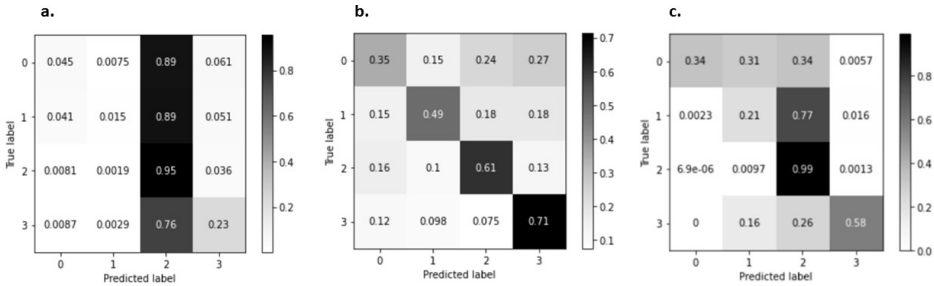


Figure 5. Classification accuracy (normalized confusion matrix) results for the Random Forest model on the (a) randomly sampled (one-third) subsets, and (b) Near Miss undersampling method for predicted burn severity classes in the SCU Complex fires. (c) ENN undersampling method for predicted burn severity classes in the SCU Complex fires. Near Miss and ENN show vastly improved performance for correct burn class predictions, seen along the main diagonal, compared to random sampling where class 2 is significantly overpredicted (column 3).

DISCUSSION

The principal finding from this study was that the overall burn severity patterns of the 2020 SCU Complex could be predicted from pre-fire vegetation green biomass, slope, and aspect variables with high accuracies of between 50% and 80% using Random Forest machine learning techniques. The August and April NDVI variables had the highest feature importance values, implying that the relative amount of dry biomass present at a given location was essential to predict how severely and completely the 2020 fires burned the vegetation cover and surface soils across this landscape. Since it was determined that pre-fire variables were predictive of fire severity, the results can be used to inform future fire mitigation activities. Specifically, the analysis of NDVI from Landsat in the months of April to June of any given year can be used to anticipate where the highest severity burning would occur in a central California woodland landscape where fire ignitions are frequent during the hottest days of the year. These machine learning methods have therefore advanced our understanding of the landscape attributes that influenced burn severity from a lightning fire complex in California mixed woodlands and grasslands.

The Near Miss undersampling technique selected for an equal number of pixels for each burn class was the most balanced and arguably most relevant machine leaning result generated from the analysis of controls on the 2020 SCU Complex burn severity patterns. Because this undersampling technique was designed to select pixel datapoints from the majority class (MBS 2) with the smallest distance to the minority class(es), it generated a representation of the SCU Complex fire that would appear to be slightly less fragmented than the actual burned area landscape. This undersampling technique resulted in the best and most balanced combined prediction accuracy for burn classes 1–3, all with individual class accuracies between 49% and 71%.

On the other hand, while the ENN undersampling technique did not select for an equal number of pixels for each burn class, it predicted the MBS 2 class at a 99% accuracy level. Nonetheless, these strong results came at the expense of a much lower prediction accuracy for low burn severity (LBS 1) class at 21% accuracy. The ENN undersampling technique would have generated a representation of the SCU Complex fire that would appear to be smoother along edges and less ambiguous in terms of variations in burned area samples along the actual class boundaries. It would have sampled each burn class area from locations separated by a longer distance from any other burn severity class area to make the distinction between classes cleaner. While this was not the actual pattern of burn severity classes that resulted from the 2020 SCU Complex fires, the results demonstrated the change in accurately that such a "smoothed along edges" burn pattern can have, compared to other more complex burn patterns.

Examining more closely the influence of the unburned class (0) in the equally-distributed (Near Miss undersampling) model run illustrated the overall difficulty of predicting areas of that did not burn during the 2020 SCU Complex fires. If patches of unburned pixels that were scattered throughout the entire SCU fire-affected area were ignored, and the model strictly focused on predicting burn severity classes 1 to 3, this adjustment would increase the Random Forest model's overall performance by up to 35%, from approximately 54% to nearly 80% prediction accuracy. Nonetheless, nearly 15,000 ha (or 9% of the entire SCU Complex coverage area) were unburned within the 2020 fire perimeter. Many of the larger patches of unburned area shown in Fig. 1 were located along creek bottom lands that were evidently spared from the rapid spread of the fire. These (relatively) lower elevation and

presumably slightly wetter creek-side locations proved to be among the most difficult for the machine learning model to determine as either burned or unburned. In addition, the location of unburned areas could largely be a consequence of the random strike points of lightning that occurred on 16 August 2020, completely unrelated to vegetation cover, slope, or aspect.

To begin to put the results from this study of the burn patterns from the 2020 SCU Complex fires into a broader regional perspective, it is worth noting that Estes et al. (2017) reported that shrub vegetation was more likely to burn at higher severity than mixed hardwood/conifer or hardwood vegetation in northern California wildfires. Likewise, we found that the pre-fire cover density of evergreen vegetation was the most important variable to predict burn severity classes within the SCU Complex. Estes et al. (2017) also reported that upper- and mid-slopes tended to burn at higher fire severity than lower-slopes in the Klamath Mountains of northern California. East- and southeast-facing aspects tended to burn at higher severity than other aspects in this region.

Compared to analysis results of several other large wildfires in central California over the past decade, the 160,498 ha SCU Complex fires had a substantially higher MBS fraction (of 83%) than did the 104,131 ha Rim Fire, which burned through the in the Stanislaus National Forest of the central Sierra Nevada in 2013. The MBS fraction was 22% within the Rim Fire burned perimeter, while its HBS fraction was estimated at 34% (Potter 2014c), which was much higher than the 12% cover of HBS area estimated for the SCU Complex fires. It was also reported by Potter (2014b) that most of the HBS areas in the Rim Fire were located in areas where high levels of pre-fire fuels were quantified by 2013 Landsat NDVI imagery.

The Diablo Range landscape lends itself to more moderate burn severity impacts than other more heavily wooded forests of the Sierra Nevada. The trees in these oak savannah and mixed woodland-grasslands are more sparsely distributed in than were dense stands of conifers that burned in the Rim Fire. Moreover, Fry (2008) reported that oak mortality was low following prescribed burning in the northern Diablo Range of Santa Clara County.

In an analysis of the 20 largest wildfires that burned near the California central coast since 1984, Potter (2017) reported that the fraction of HBS area to total area burned ranged from a minimum of 0 to a maximum of 73%, with an average of 21%. Again, this typical HBS fraction from this collection of recent Pacific coast wildfires was much higher than the 12% cover of HBS area estimated for the SCU Complex fires. The acreage of HBS patches was found to increase exponentially and significantly ($p < 0.01$) with total area burned in each of these 20 coastal fires, but since the 2020 SCU Complex fire area was larger than any of these coastal fires before it, the SCU Complex does not fit the pattern cited by Potter (2017) that wildfires in central California experience their most rapid rate of increase in acreage of HBS area when the total fire size exceeds 48,500 ha (120,000 acres). It is plausible that the SCU Complex burned mainly at MBS from start to finish of the 2020 fire period and did not expand in the fraction of HBS coverage as it progressed.

Potter (2016) recounted that the Soberanes Fire that burned in 2016 in Monterey County on the California central coast resulted in a HBS fraction of 22% of the total area impacted, whereas final moderate burn severity (MBS) area comprised about 10% of the total area burned of approximately 53,470 ha (132,130 acres). Therefore, the Soberanes Fire was typical of most wildfires on California central coast in terms of MBS and HBS fractions, and contrasts again with the SCU Complex fire that had a much lower fraction of HBS coverage.

Conclusions

Although the SCU Complex fires burned mostly at a moderate burn severity level during August and September of 2020, which was out-of-the-ordinary for a large wildfire in central California woodlands, the amount of dry biomass present, as detected from Landsat satellite data, was the most important input variable used to predict how severely these fires burned the vegetation cover and surface soils across the steep watersheds of the southern Diablo Range. The input variables used in thus study to predict burn severity levels and locations are readily available for any fire-prone region around the globe. Our study results suggest that Random Forest machine learning can be applied with confidence to predict and map potential medium and high burn severity areas accurately in advance of future fires for partially wooded landscapes in central California. While burn severity patterns can be measured post-fire, the factors that contributed to variations in burn severity levels cannot be assessed post-fire if those factors have been severely altered by the fire event, as is the case of vegetation cover. Knowing where the greatest risk for high burn severity is present on the landscape in terms of vegetation biomass can be valuable piece of information for local resource managers.

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In Memoriam: Nina Jo Kogut (1969–2021)

Fisheries scientists lost one of their strongest supporters on 17 July 2021 with the passing of Nina Jo Kogut. For over 20 years, Nina devoted her strong scientific skills to the California Department of Fish and Wildlife (CDFW), and served in a variety of capacities associated with fisheries monitoring and management.

Nina grew up in the Santa Cruz Mountains, graduating from Los Gatos High School, before serving in the United States Navy. She worked during, and funded her own advanced education, earning her B.S. in Biological Sciences at San Jose State University and her M.S. in Conservation Ecology at California State University, Sacramento.

During her early natural resources career, Nina worked as a Natural History Interpreter and seasonal employee with state and federal parks, and with several non-profit organizations before working at a local water utility district. From 1995 to 1999, she conducted a variety of field surveys for freshwater fishes (resident and diadromous species) as well as mammals, birds, reptiles, amphibians, and plants in floodplain and riparian habitats. Nina was an Environmental Scientist with CDFW from 1999 to late 2020. She began this portion of her career at the Bay Delta Office in Stockton, where she worked with Dave Kohlhorst performing research on Green and White Sturgeon, Striped Bass, and resident fish populations in the Sacramento-San Joaquin Delta. While working with her beloved survey crew aboard the Striper II, Nina brightened everybody's day with her smile, laughter, and unwavering positivity. She was the perfect blend of grit and kindness.

Nina's strong scientific curiosity, energy, and initiative displayed their importance, while she worked on CDFW's sturgeon tagging project. She observed that no matter how clean she kept the holding water, there would inevitably be clams at the tank bottom. Her proposed study to explain the phenomenon did not gain traction internally, so she confidently pursued it on her own time. Working with captured sturgeon at a local university she revealed that introduced clams, which comprised a substantial proportion of the White

Sturgeon diet, provided little nutrition and were generally passed undigested and alive. The resulting paper published in 2008 as "Overbite clams, *Corbula amurensis*, defecated alive by white sturgeon, *Acipenser transmontanus*," embodied important implications for future sturgeon management and conservation.

In 2010, Nina transitioned to the Monterey Regional Office to work with Konstantin Karpov on the use of remote operated vehicles (ROVs) for ground fish surveys and on the Marine Protected Areas program, during which she and her collaborators authored numerous outreach and education resources. In addition, she was an author of 5 peer-reviewed research papers that appeared in professional journals. While working on these projects, Nina accepted an appointment as Associate Editor for the Department's journal, *California Fish and Game*, and served in that capacity for 10 years, through publication of volume 105 in 2019. During her first year as Associate Editor, Nina revised and published the Instructions for Contributors to *California Fish and Game*; three consecutive Editors-in-Chief depended on those guidelines for nearly a decade. She also was the Copy Editor for each of the papers included in the Special Marine Issue of *California Fish and Game*, which included 11 papers assembled specifically to celebrate the centennial anniversary of California's longest-running, continuously published scientific journal and, specifically, its contributions to the science of marine biology.

After fighting a long and courageous battle with cancer, Nina retired from the Department in 2020. She was a ray of sunshine, a wonderful supporter of her co-workers, and a great friend of many. She will be sorely missed.

—FRIENDS AND COLLEAGUES OF NINA KOGUT

INFORMATION FOR AUTHORS

The California Fish and Wildlife Journal (CFWJ) is a peer-reviewed, scientific journal focused on the biology, ecology, and conservation of the flora and fauna of California and surrounding areas, and the northeastern Pacific Ocean.

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Front. Tule elk, Photo credit: K. Schneider. (CC BY-NC 2.0)

Back. Arroyo Chub (left) and Santa Anna Sucker (right) in Santa Ana River, USFWS Pacific Southwest Region

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