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

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FULL RESEARCH ARTICLE

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Abstract

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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Introduction

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 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.

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

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 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).

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.

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 Method

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. 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 suitability 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.

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.

Predictor variable	**Description**
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 (*O. 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.
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.

Predictor variable	Description
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).
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

Predictor variable	Description
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**

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-ha 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-ha 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.

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.

Table 2a. Regional dominance cover-type (CALVEG REGIONAL DOMINANCE COVER-TYPE)

Plant community/species	CWHR Code	Trinity County ha	% of Trinity County	Snail sample sites (n)	% of snail sample sites
Douglas fir-white fir	DW	37,526	9.4%	179	53.8%
Douglas fir	DF	154,283	38.6%	87	26.1%
Mixed conifer-pine	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 live oak	QG	19,548	4.9%	2	0.6%
Tanoak-Pacific madrone	QT	2,601	0.7%	4	1.2%
White fir	WF	27,352	6.8%	4	1.2%

Table 2b. Western forest cover-type (CALBEG SAF COVER-TYPE)

Plant community/species	CWHR Code	Trinity County hectares	% of Trinity County	Snail sample sites (n)	% of snail sample sites
Douglas fir	DF (229)	191,810	46.9%	269	80.8%
Sierra Nevada mixed conifer	SNMC (243)/td>	86,414	21.1%	38	11.4%
Ponderosa pine-Douglas fir	PPDF (244)	57,583	14.1%	15	4.5%

Plant community/species	CWHR Code	Trinity County hectares	% of Trinity County	Snail sample sites (n)	% of snail sample sites
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%

Table 2c. Vegetation cover form above (CALVEG COVER FROM ABOVE [CFA])

Plant community/species	CWHR Code	Trinity County hectares	% of Trinity County	Snail sample sites (n)	% of snail sample sites
Conifer	CON	304,091	65.0%	276	82.9%
Mixed conifer-hardwood	MIX	119,294	25.5%	49	14.7%
Hardwood	HWD	44,131	9.4%	8	2.4%

Table 2d. California Wildlife Habitat Relationship Standards for Life-form (CWHR LIFE FORM)

Plant community/species	CWHR Code	Trinity County hectares	% of Trinity County	Snail sample sites (n)	% of snail sample sites
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%

Table 2e. Wildlife habitat relationship vegetation type (CWHR TYPE)

Plant community/species	CWHR Code	Trinity County hectares	% of Trinity County	Snail sample sites (n)	% of snail sample sites
Sierra mixed conifer	SMC	172,036	41.0%	223	67.0%

Plant community/species	CWHR Code	Trinity County hectares	% of Trinity County	Snail sample sites (n)	% of snail sample sites
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%

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, 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.

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.

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%
Douglas-white fir forest (72%)	DFWF	55.0%	—	82.9%	—	—
Douglas-white fir forest (72%)	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%
Mixed conifer hardwood (2%)	MHC	—	—	2.4%	3.9%	2.4%
Mixed conifer hardwood (2%)	MHW	—	—	—	3.0%	—
Oak woodland (1%)	TOK	1.3%	—	—	—	—

Cover-type classifications	Plant species code	RDC	SAF	VGC	COV	LIF
Oak woodland (1%)	OBOP	1.0%	0.9%	—	—	—
Oak woodland (1%)	CLO	0.0%	0.6%	—	—	—
Oak woodland (1%)	CBO	—	1.2%	—	0.3%	—
Non-forest (1%)	BAR	—	—	—	2.4%	—

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).

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.

Table 4a. Percent Aggregation Type (AGGREGATION-TYPE)

Variable (CWHR code)	Trinity County (ha)	% Trinity County	Snail sample sites (n)	% snail sample sites
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	—

Table 4b. Percent over-story cover (crown) from above (CON-CFA)

Variable (CWHR code)	Trinity County (ha)	% Trinity County	Snail sample sites (n)	% snail sample sites
10–19.9%(15)	21,934.0	5.4%	14	5.0%
20–29.9%(25)	39,023.1	9.6%	7	2.0%

Variable (CWHR code)	Trinity County (ha)	% Trinity County	Snail sample sites (n)	% snail sample sites
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%(95)	6,062.2	1.5%	3	1.0%
Total	407,606.1	—	333	—

Table 4c. Percent Hardwood tree cover from above (HDW-CFA)

Variable (CWHR code)	Trinity County (ha)	% Trinity County	Snail sample sites (n)	% snail sample sites
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	—

Table 4d. Percent diameter (DBH) of over-story trees (OS-TREE-DIAMETER-CLASS)

Variable (CWHR code)	Trinity County (ha)	% Trinity County	Snail sample sites (n)	% snail sample sites

Variable (CWHR code)	Trinity County (ha)	% Trinity County	Snail sample sites (n)	% snail sample sites
Conifers Sapling 2.5 – 12.5 cm QMD (2)	17,750.8	3.9%	7	2.1%
Conifers Pole 12.7 – 25.2 cm QMD (7)	95,200.8	21.0%	22	6.6%
Conifers Small size tree 25.4 – 50.6 cm QMD (15)	160,411.2	35.4%	249	74.8%
Conifers Medium size tree 50.8 – 76.0 cm QMD (25)	162,065.5	35.7%	48	14.4%
Conifers Large size tree > 76.2 cm QMD (40)	17,995.6	4.0%	7	2.1%
Conifers Total	453,423.9	—	333	—
Hardwoods None (NA)	413,090.0	80.1%	286	86.3%
Hardwoods Pole 12.7 – 25.2 cm QMD (7)	80,073.7	15.5%	39	11.5%
Hardwoods Small tree 25.4 – 50.6 cm QMD (15)	22,825.9	4.4%	8	2.2%
Hardwoods Total	515,989.6	—	333	—

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 where 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.

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.

Seasonal Climatic Attributes

Temperature.—At sites where snails were sampled seasonal variation in the annual minimum temperature fluctuated between –3.3℃ in January ($\bar{x}$ = –0.8°C) and 12.8℃ 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℃ 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 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 I (0.974 and 0.992, respectively).

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**.

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 31,437 km^2. Of this 21.5% (309.5 km^2) consisted of medium to critically suitable macrohabitat, or ~22% 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**).

Habitat suitability score	Hectares	Percent	Average	Minimum	Maximum
Low	81,598	56.8%	27,199.5	20,199.5	35,812.8
Low-medium	31,176	21.7%	15,587.9	13,479.0	17,696.8
Medium	18,413	12.8%	9,206.2	8,037.4	10,375.0
Medium-high	8,982	6.2%	4,490.9	2,879.6	6,102.2
High	3,159	2.2%	1,053.0	588.6	1,422.9
Critical	398	0.3%	132.7	67.7	237.1

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.

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.

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**; **Fig. 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 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 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 conditions 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. 2018).

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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