Microhabitat characteristics and management of the Trinity bristle snail in the Greater Trinity Basin of northern California

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FULL RESEARCH ARTICLE

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Abstract

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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Introduction

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 km^2 or ~17.9% of the total area encompassed by Trinity County jurisdictional boundaries (n = 8,307 km^2). 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.

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.

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 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 km^2). 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 sample location, which were considered "optimal" for terrestrial snails inhabiting mixed conifer, riparian, and hardwood forest communities (Sullivan 2022).

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

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

Component and variable
18. Relative water availability (annual, ephemeral, perennial)
19. Stream classification (1 [fish bearing], 2, 3, 4)

Statistical Analyses

All statistical analyses performed used R (R Core Team 2021) and statistical significance was set at $\alpha \leq 0.05$. 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 (χ^2) evaluated post-hoc delineations of clustered samples by PCA. Nonparametric Spearman's rank correlation (r_s; 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).

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.

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 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, 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**).

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).

Air and substrate temperature.—Air temperature averaged 11.3 ℃ (min = 4.1 ℃; max = 13.9 ℃), 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.

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 shrub, 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.

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 m^2 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 ($\bar{x}$ = 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.

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.

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 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 (**Fig. 6**). 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.

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

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 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.

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.

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%
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 (℃)	0.472	-0.022	-0.044
5. Soil (℃)	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

Component statistic	PC I	PC II	PC III
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.

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 (χ^2 = 57.0, df = 4, p < 0.001) and PC II (χ^2 = 70.0, df = 4, p < 0.001). Clustered samples A (10.2%, n = 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).

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
1. Elevation (m)	x̄ = 782.0; min = 310; max = 1,378
2. Exposure (degrees)	x̄ = 102.7; min = 1.0; max = 315.0
3. Slope (degrees)	x̄ = 54.0; min = 20.0; max = 65.0
4. Air temperature (℃)	x̄ = 11.3; min = 4.4; max = 13.9
5. Soil/substrate temperature (℃)	x̄ = 10.0; min = 4.4; max =11.7
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 (%)	x̄ = 81.5; min = 50.0; max = 98.0
8. Distance to nearest tree or shrub (m)	x̄ = 6.0; min = 0.9; max = 14.6
9. Distance to nearest large woody debris (m)	x̄ = 3.3; min = 0.1; max = 16.8
10. Percent dominant substrate	Moss-covered boulders (x̄ = 58.0%), leaf litter leaf litter (x̄ = 54.2%), bare talus (x̄ = 20.0%), gravel (x̄ = 18.3%), bare boulders (15.0%), and cliffs (x̄ = 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%.

Microhabitat component and variable	Suitable microhabitat criteria
13. Size large woody debris (cm)	x̄ = 64.3; min = 12.7; max = 137.2
14. Depth leaf litter (cm)	x̄ = 8.1; min = 2.5; max = 10.2
15. Distance to nearest rock habitat (m)	x̄ = 9.5; min = 0.3; max = 45.7
16. Size distribution of rock type (diameter cm)	x̄ =25.2; min = 7.6; max = 61.0
17. Distance to nearest stream/drainage (m)	x̄ =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.

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 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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Literature Cited

- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in B. N. Petrov and F. Csáki, editors. 2nd International Symposium on Information Theory, Tsahkadsor, Armenia, Budapest, USSR.
- Anderson, S. H., and K. J. Gutzwiller. 1996. Habitat evaluation methods. Pages 592–606 in T. A. Bookhour, editor. Research and Management Techniques for Wildlife and Habitats. 5th edition, revised. The Wildlife Society, Bethesda, MD, USA.
- Armijo, P. 1979. *Monadenia setosa* (California Northern River Snail) Interim Species Management Plan, U. S. Forest Service #2670 – Surveys, Studies, and Plans.
- Barker, G. M. 2004. Natural Enemies of Terrestrial Mollusks. CABI Publishing, Oxon, United Kingdom.
- Barrett, J. G. 1966. Climate of Trinity County. United States Department of Agriculture Soil Conservation Service, Redding, CA, USA.
- Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. The network dynamics hypothesis: how river networks structure riverine habitats. BioScience 54:413–427.
- Brown, J. H., and B. A. Maurer. 1989. Macroecology: the division of food and space among species on continents. Science 243:1145–1150.

- Burke, T. E., J. S. Applegarth, and T. R. Weasma. 1999. Management recommendations for survey and manage terrestrial mollusks. United States Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR, USA.
- Coppolino, M. L. 2008. Land snail collection strategies. Pages 12–14 in K. E. Perez and J. Ray, editors. A Guide for Terrestrial Gastropod Identification. American Malacological Society, Carbondale, IL, USA.
- Corder, G. W., and D. I. Foreman. 2014. Nonparametric Statistics: A Step-by-step Approach. John Wiley and Sons, Inc., Hoboken, NJ, USA.
- Cucherat, X., and S. Demuynck. 2008. Sampling strategies and collecting techniques for land and freshwater molluscs. MalaCo 5:244–253.
- Diankha, O., and M. Thiaw. 2016. Studying the ten years variability of Octopus vulgaris in Senegalese waters using generalized additive model (GAM). International Journal of Fisheries and Aquatic Studies 2016:61–67.
- Duncan, N., T. E. Burke, Dowlan, and P. Hohenlohe. 2003. Survey protocol for survey and manage of terrestrial mollusks species from the Northwest Forest Plan. Version 3.0. Available from: http://www.or.blm.gov/surveyandmanage/sp.htm
- Dunk, J. R., W. J. Zielinski, and H. K. Preisler. 2004. Predicting the occurrence of rare mollusks in Northern California forests. Ecological Applications 14:713–729.
- Early, D., K. Hamm, and D. Lampher. 2012. Green Diamond Resource Company. Final monitoring report, Incidental Take Permits #2081-2008-016-01 and #2081-2009-026-01 for Timber Harvest Plans 1-07-0676HUM, 1-07-195HUM, 1-08-071HUM, 2-07-166TRI, and 2-029-021TRI.
- Everitt, B. S., and T. Hothorn. 2011. An Introduction to Applied Multivariate Analysis with R. Springer, New York, NY, USA.
- Fontaine, B., O. Gargominy, and E. Neubert. 2007. Priority sites for conservation of land snails in Gabon: testing the umbrella species concept. Diversity and Distributions 13:725–734.
- Foster, A. D., and J. Ziegltrum. 2013. Riparian-associated gastropods in western Washington: community composition and the effects of forest management. Northwest Science 87:243–256.
- Furnish, J., T. Burke T, T. Weasma, J. Applegarth, N. Duncan, R. Monthey, and D. Gowan. 1997. Survey protocol for terrestrial mollusk species from the northwest forest plan, draft version 2.0. U.S. Department of Agriculture, U.S. Forest Service, and Bureau of Land Management.
- Gotmark, F., T. Von Proschwitz, and N. Franc. 2008. Are small sedentary species affected by habitat fragmentation? Local vs. landscape factors predicting species richness and composition of land mollusks in Swedish conservation forests. Journal of Biogeography 35:1062–76.
- Graveland, J., R. van der Wal, J. H. van Balen, and A. J. van Noordwijk. 1994. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. Nature 368:446–448.
- Hastie, T., and R. J. Tibshirani. 1990. Generalized Additive Models. Chapman and Hall, London, UK.
- Kelley, R., S. Dowlan, N. Duncan, and T. E. Burke. 1999. Field guide to survey and manage terrestrial mollusk species from the northwest forest plan. Bureau of Land Management, Oregon State Office, Salem, OR, USA.
- Madsen, H., and P. Thyregod. 2011 Introduction to General and Generalized Linear Models. Chapman and Hall/CRC, Boca Raton, FL, USA.
- Marozzi, M. 2013. Nonparametric simultaneous tests for location and scale testing: a comparison of several methods. Communications in Statistics – Simulation and Computation 42:1298–1317.
- Miller, J. R., and R. J. Hobbs. 2007. Habitat restoration—do we know what we're doing? Restoration Ecology 15:382–390.
- Morris, D. W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia 136:1–13.
- Morrison, M. L. 2001. A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. Journal of Wildlife Management 65:613–623.
- Mote, P., and E. Salathe. 2010. Future climate in the Pacific Northwest. Climatic Change 102:29–50.

- Nicolai, A., and A. Ansart. 2017. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. Conservation Physiology 5:1–17.
- Noss, R. F., M. A. O'Connell, and D. D. Murphy. 1997. The Science of Conservation Planning: Habitat Conservation under the Endangered Species Act. Island Press, Washington, D.C., USA.
- Nychka, D. 1988. Bayesian confidence intervals for smoothing splines. Journal of the American Statistical Association 83:1134–143.
- Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. The American Naturalist 137:29–49.
- R Core Team. 2021. R: A language and environment for statistical computing. Available from: **https://www.R-project.org**
- Raheem, D. C., F. Naggs, R. C. Preece, Y. Mapatuna, L. Kariyawasam, and P. Eggleton. 2008. Structure and conservation of Sri Lankan land-snail assemblages in fragmented lowland rainforest and village home gardens. Journal of Applied Ecology 45:1019–1028.
- Regoli, F., S. Gorbi, D. Fattorini, S. Tedesco, A. Notti, N. Machella, R. Bocchetti, M. Benedetti, and F. Piva. 2006. Use of the land snail *Helix aspersa* as sentinel organism for monitoring ecotoxicologic effects of urban pollution: an integrated approach. Environmental Health Perspective 114:63–69.
- Roth, B. 1978. Biology and distribution of *Monadenia setosa* Talmadge. Report to U.S. Forest Service, Shasta-Trinity National Forest, Redding, CA, USA.
- Roth, B., and L. L. Eng. 1980. Distribution, ecology, and reproductive anatomy of a rare land snail. *Monadenia setosa*, Talmage. California Fish and Game 66:4–16.
- Roth, B. 1982. Life history studies and distribution of *Monadenia setosa*. Report submitted to USDA Forest Service, Shasta-Trinity National Forest, Redding, CA, USA.
- Roth, B., and P. H. Pressley. 1986. Observations on the range and natural history of *Monadenia setosa* (Gastropoda: Pulmonate) in the Klamath Mountains, California, and the taxonomy of some related species. The Veliger 29:169–182.
- Sanderson, E. W., K. H., Redford, A. Vedder, P. B. Coppolillo, and S. E. Ward. 2002. A conceptual model for conservation planning based on landscape species requirement. Landscape and Urban Planning 58:41–56.
- Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution 42:849–861.
- Shimek, B. 1930. Land snails as indicators of ecological conditions. Ecology 11:673–686.
- Smartt, R. A, and R. M. Sullivan. 1990. Distribution and ecology of *Pecosorbis kansasensis* in eastern New Mexico. Journal of Arid Environments 19:181–187.
- Sullivan, R. M., and R. A. Smartt. 1995. Genetics, ecology, and conservation of woodland snails (genus *Ashmunella*) on White Sands Missile Range, New Mexico. Department of Defense, U.S. Army, White Sands Missile Range, NM, USA.
- Sullivan, R. M. 1996. Ecology, microhabitat assessment, and endangered species management of federal species of concern terrestrial gastropods in southern New Mexico. New Mexico Department of Game and Fish, Endangered Species Program, Santa Fe, NM, USA.
- Sullivan, R. M. 1997. Conservation status assessment and population monitoring of federal candidate land snails of southern New Mexico. T and E, Inc., Las Cruces NM, USA.
- Sullivan, R. M. 2021. Phylogenetic relationships among subclades within the Trinity bristle snail species complex, riverine barriers, and re-classification. California Fish and Wildlife Journal CESA Special Issue:107–145.
- Sullivan, R. M. 2022. Macrohabitat suitability models for the Trinity bristle snail (*Monadenia setosa*) in the Greater Trinity Basin of Northern California. California Fish and Wildlife Journal, this issue.
- Talmadge, R. R. 1952. A bristled *Monadenia* from California. The Nautilus 66:47–50.
- United States Forest Service (USFS). 2005. Upper Trinity River Watershed Analysis including watershed

analysis for: Main Trinity River Watershed Coffee Creek Watershed East Fork Trinity River Watershed Stuart Fork Watershed Trinity Reservoir Watershed. Shasta-Trinity National Forest, Redding, CA. Available from: **https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm9_008541.pdf**

- United States Fish and Wildlife (USFWS). 2011. A 90-day finding on a petition to list 29 mollusk species and subspecies as threatened or endangered, under the Endangered Species Act of 1973. Docket No. FWSR8-ES-2011-0076; MO-92210-0-0008; Department of Interior, U.S. Fish and Wildlife Service, Washington D.C., USA.
- van der Laan, K. L. 1971. The population ecology of the terrestrial snail, *Helminthoglypta arrosa* (Pulmonata: Helicida). Dissertation, University of California, Berkeley, USA.
- Walton, M. L. 1963. Length of life in west American land snails. The Nautilus 76:127–131.
- Wood, S. N. 2017. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC Press, Boca Raton, FL, USA.
- Wood, S. N., N. Pya, and B. Saefken. 2016. Smoothing parameter and model selection for general smooth models. Journal of the American Statistical Association 111:1548–1575.