The Space Between:
Characterizing the Microhabitats and Ranges of *Tamias alpinus* and *Tamias speciosus* in Yosemite National Park

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ABSTRACT

Range contraction and expansion are of particular concern for mountaintop species such as *Tamias alpinus* (Alpine Chipmunk) and *Tamias speciosus* (Lodgepole Chipmunk). Over the past century, *T. alpinus* has shown an upward range contraction and is now absent from lower elevation sites. In contrast, the *T. speciosus* expanded its range at both its upper and lower elevational limits. To understand the mechanisms and processes underlying this shift, this study is the first to quantify and pair microhabitat variables with range maps created from radio-telemetry point data. *T. alpinus* and *T. speciosus* habitat use points were significantly different in elevation, height and branching pattern of dominant tree species (ANOVA, p=0.0142, p=0.0003959, p=0.002616). Elevation and slope, height, and canopy cover of dominant tree species explained the most variation between the habitats of *T. alpinus* and *T. speciosus* (MFA). The alignment of vegetation and physical characteristics of Tamias microhabitats to telemetry range maps provides fine-scale details to a broader picture of range shifts for focal species and a foundation for future research and conservation efforts for other range-restricted species.

KEYWORDS

Range shift, niche partitioning, interspecific competition, tree structure, elevation

INTRODUCTION

Local and regional climate change has been linked to distributional changes and extinctions across a diverse biota (Parmesan 2006) and is causing severe range contraction for range-restricted species (Rubidge et al. 2006). Although current climate change research has informed the understanding of the distribution of certain species', the processes underlying contemporary range shifts remain uncertain (Beever et al. 2011). The majority of North American studies consider the responses of species over several decades, but the depth of these inferences are weakened by confounding variables such as landscape modifications, anthropologically influenced temperature variations, and limited historical sampling (Moritz et. al. 2008). To more rigorously investigate climate and biotic changes, climate change research requires a focus on the responses of species over extended time.

To consider climate change across a large scale of time, this paper considers how current microhabitat characteristics intersect with historical data from the Grinnell Resurvey Project (GRP), a survey conducted 100 years after the original Grinnell Survey Project (GSP). The original GSP surveyed five areas of California, including the Eastern and Western Sierras. Moreover, the GSP provided a foundation for the GRP to consider changes in vertebrate diversity with a breadth of sites across California and longer time span. The Resurvey not only considered vertebrate life, but also recorded a 3.7°C regional increase in average monthly temperature in over the past century in Yosemite National Park (Moritz et al. 2008). During this same band of time, a greater number of small mammal species have shown elevational range contractions, as opposed to range expansions (Moritz et al. 2008).

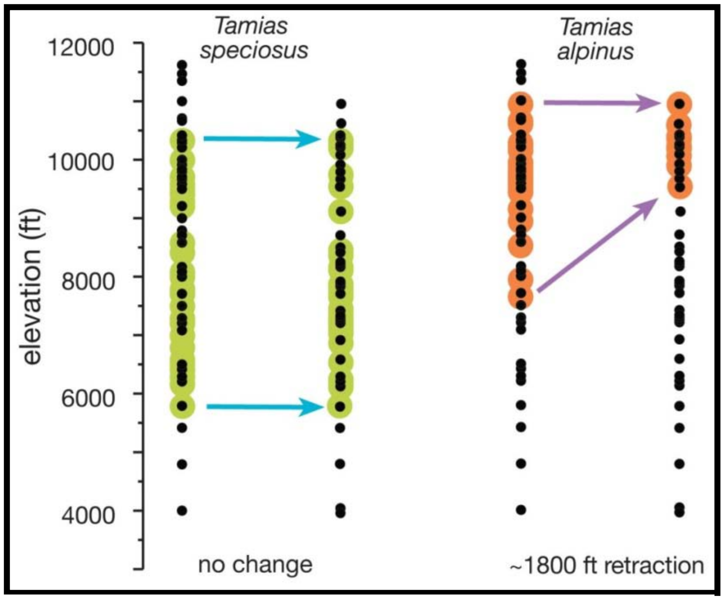


Fig. 1. **Comparison of modern and historic *T. alpinus* and *T. speciosus ranges***. Each point represents a capture point from the Grinnell Survey (left column) and the Grinnell Resurvey (right column). *T. alpinus* has exhibited a consider 1,800 ft. contraction over the past century. *Credit Jim Patton*.

Climate change is expected to force species distributions towards higher elevations and latitudes. Accordingly, over the past century, *Tamias alpinus* (Alpine Chipmunk) has shown an upward range contraction and is now absent from lower elevation sites. In contrast, *Tamias speciosus* (Lodgepole Chipmunk) expanded its range at both its upper and lower elevational limits (Fig. 1) (Moritz et al. 2008). These observations pose a concern for such mountaintop species because future habitable climate space may become too small or isolated to accommodate current geographical ranges, posing threats of extinction (Parmesan 2006, Wilson et al. 2005).

The two focal species are congeners that live in distinctly different habitats (Best et al. 1994, Harris et al. 2004) and have shown different patterns of elevational range change over time (Figure 1). Understanding their modern and historical ranges can provide insight to the biotic and abiotic processes contributing current understanding of range shifts. Particularly, in deconstructing the range of a species to vegetative and environmental variables, multiple types of microhabitats that animals may encounter can be better understood and described (Bower et al. 1994).

Here, I use capture, radio telemetry, and vegetation surveys to quantify the habitat preferences and current ranges *T. alpinus* and *T. speciosus*. Previous studies and field observations have qualitatively described the habitat differences between the two species, but this study provides the first detailed quantitative study of habitat use in *T. alpinus* in direct comparison to *T. speciosus*. My objective is to understand the relationship between microhabitat and range shifts by examining modern *T. alpinus* and *T. speciosus* habitat use points in Yosemite National Park. Evaluation of key biotic and abiotic variables will allow me to compare the microhabitats of *T. alpinus* and *T. speciosus* and ultimately understand how differences in habitat use relate to long-term patterns of elevational range change.

METHODS

Study site

We conducted this study from July-September 2011at two sites in Yosemite National Park: May Lake and Vogelsang (Fig. 2). We selected these two sites because *T. alpinus* and *T. speciosus* are both represented and because of the physical similarities in habitat type (May

Lake—9,280 ft., Vogelsang—10,100 ft.) At each site, we selected an area that represented an elevational transition from areas of dense vegetation to little vegetation in three distinct grids, from densely forested areas, to sparsely forested areas, to barren, rocky habitat (Fig. 2b). These three grids allowed us to focus on each habitat type separately and also as one continuous transect.

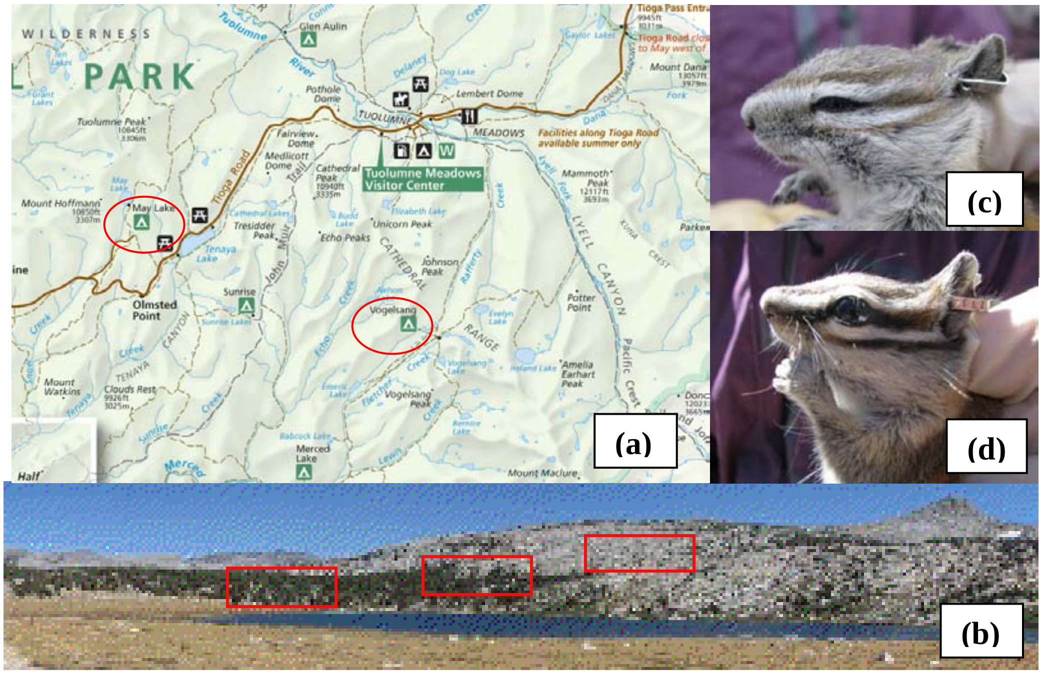


Fig. 2: Study sites, methods, and focal species. ***(a)***Study sites: May Lake and Vogelsang. ***(b)*** Idealized study area that represents a natural elevational transition from 1) densely forested, 2) sparsely forested, 3) barren, rocky substrate. The red boxes highlight the "low," "middle," and "upper" grids with respect to elevation and dominant vegetation . ***(c)*** *Tamias alpinus*. ***(d)*** *Tamias speciosus.*

Study species

The transition between three distinct areas captures key habitat transitions relevant to *T. alpinus and T. speciosus*. *T. speciosus* is generally found below tree line, where the habitat is dominated by dense pine forests. In contrast, *T. alpinus* is generally found above the tree line at higher elevations where the habitat is characterized by scattered rocks and sparsely distributed *Pinus contorta* (Lodgepole pines) (Harris 2004). Field and lab observations have documented different interspecific competition between these species. *T. alpinus* has illustrated aggressive behavior in the field, but variable amounts of aggressiveness in captivity (Harris 2011). The species are sympatric and coexist.

***T. alpinus* and *T. speciosus* capture points**

Trapping points

To consider the varying habitat types that both *Tamias* species use, I pooled points where *T. alpinus and T. speciosus* were caught with live trapping and fixed the collared individuals with radio telemetry. The elevational transition from densely forested to non forested areas was captured in three grids. We defined these three grids as “low,” “middle,” or “upper” with respect to their elevation and corresponding dominant vegetation type. Within each grid, we set approximately 25 total capture points, spaced 10m apart. Each capture point was set with two folding Sherman traps (25.5x8x8cm), usually in the shelter of shrubs, logs, between boulders, or other natural features. This added up to approximately 50 traps per grid and a total of 150 at each site. The traps were baited with oats and were open at dawn (5:30 a.m.) and closed in the late afternoon (4 or later p.m.) in five day sequences.

Radio telemetry

In addition to trapping, we also conducted radio telemetry on collared individuals. We aimed to put a radio collar on five individuals per site to track their movements. We aimed to get 2 fixes on the each individual in the morning (by 10am), at noon (by 1pm), and in the late afternoon (by 7pm), yielding a grand total of 20-25 fixes per individual. Radio telemetry was conducted for approximately 14 days at each site.

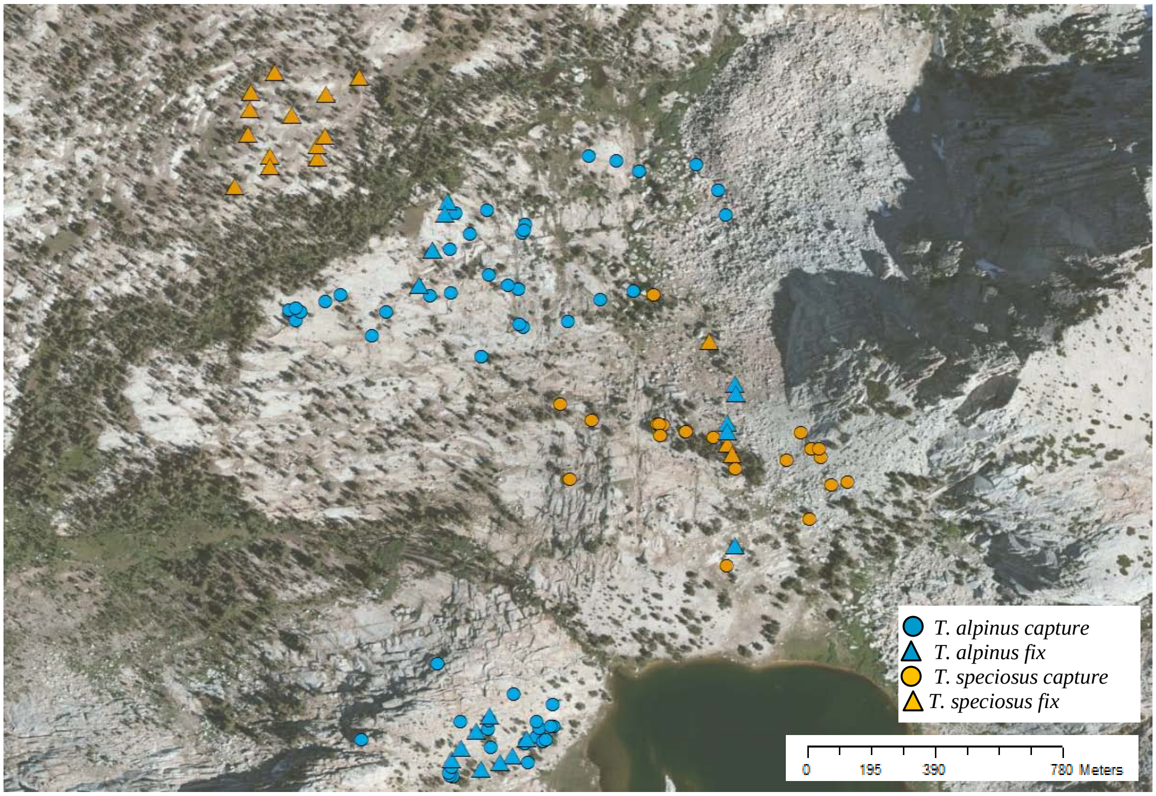


Fig. 3. Capture and radio telemetry points of *T. alpinus* and *T. speciosus* at Vogelsang. Capture and radio points are denoted as triangles and circles, respectively. *T. alpinus* points are shown in blue and *T. speciosus* points in gold. The overlap in capture and telemetry points can be noted.

Pooled capture and telemetry points

Radio telemetry points and capture points were pooled so that vegetation survey were categorized into three points: *T. alpinus*, *T. speciosus*, and randomly selected points. It was reasonable to pool capture and telemetry points because the points overlapped and occurred in similar, if not the same areas (Fig. 3). Pooling the two types of points also provided more data to compare the vegetation characteristics of their respective points. A visual inspection illustrates that when we divide the points by species, the majority of telemetry and capture points overlap.

Vegetation surveys

Each of the grids served as guidelines for setting trapping points and conducting vegetation surveys. We adapted vegetation surveys from the Natural Conservancy, the US Geological Survey, and the National Park Service to design a survey that provided a comprehensive overview of the prominent physical and biotic variables in each plot, including forest cover, ground cover, number and diameter breast height (DBH) of trees >10cm, number and DBH of down logs>10cm, and substrate type (e.g. duff, leaf litter, etc.) We conducted vegetation surveys at all points where we successfully captured and fixed a chipmunk, and five randomly selected points. To survey each point, we used a stick and four 5 m ropes to create a circular plot that was divided into four quadrants to make it easier to quantify ground cover or similar variables.

While the survey provides a clear, comprehensive view of the habitat at select vegetation points, comparing each variable is beyond the scope of the current study. For the purpose of feasibility, I concentrated on a subset of the survey: Tree species, tree structure, ground cover of trees and plants, environmental variables, and physiognomic category. I selected these five variables because they provide a comprehensive picture of each survey plot and capture the factors that I hypothesized would influence a microhabitat. Below are the details on survey methods for each of these variables (Table 1):

Table 1. **Summary of variables**. A quick reference to the variables included in the statistical analyses and the categories that they were grouped under.

Variable	Method of measurement
Tree species	Identified dominant (most common) tree species
Tree structure	
Height (Ht.)	categorized as <5 m, 5-10 m, 10-15 m, and 15 m. Ht. of dominant tree species were averaged.
Diameter at Breast Height (DBH)	measured diameter of dominant trees > 10cm in diameter with diameter tape
Branching pattern	categorized in categories: (1) no branches, (2) branches present only in the crown, (3) branches present half way down, (4) branches present all the way to the ground
Canopy Cover	classified on a scale of 5 to 100%, increasing in 5% increments.
Boulders	
Number of boulders	counted boulders at least two out of three of those dimensions were >10cm
Mean boulder volume	length, width, and height of each boulder

Environmental variables	
Slope	recorded by compass
Aspect	recorded by compass
Elevation	recorded by GPS
Habitat type	Categorized surrounding habitat type (e.g. forest, shrubland, sparse forest)

Tree species: We recorded the dominant (most common) tree species in the plot and identified the trees by using field guides (Law's Field Guide to the Sierra Nevadas, Trees and Shrubs of California) and took photos for future referencing.

Tree structure: We measured the height, diameter at breast height (DBH), branching pattern, and canopy cover. The height categories included <5 m, 5-10 m, 10-15 m, and 15 m. DBH was recorded to estimate basal area live trees and were counted separately from fallen dead trees. We recorded data on branching pattern by placing each tree in one of four categories: no branches, branches present only in the crown, branches present half way down, branches present all the way to the ground. While branching pattern was categorized, the recorded observations were ordinal and discrete and overall acceptable in the framework of our statistical analysis. For the dominant tree species in the plot, we classified canopy cover on a scale of 5 to 100%, increasing in 5% increments.

Boulders: Boulder cover included the number of boulders and the mean volume of boulders. We recorded the approximate volume of all boulders at each point by measuring length, width, and height of each boulder for which at least two out of three of those dimensions were greater than 10 cm. For each boulder, we noted if there were any rock overhangs that chipmunks might be able to slip under.

Environmental variables: Environmental variables were represented by slope, aspect, and elevation of the surveyed plot. Slope and aspect were recorded by compass and elevation was taken by Global Positioning System (GPS) units.

Habitat type: To further record the type of vegetation captured by the plot, we recorded dominant habitat type in the larger area surrounding our 5 m-radius plot. Categories included forest, shrubland, sparse forest, etc.

Data analysis

MFA

Since we began with measuring a breadth of physical and biotic variables, I was interested in identifying which of these factors distinguished the habitats of *T. alpinus* and *T. speciosus*. This breadth allowed me to examine many different individual variables and combinations of variables simultaneously. I chose to use a Multiple Factor Analysis (MFA), which is similar to a Principal Component Analysis (PCA), but allowed me to group several variables that represented a similar function into a single group. This also provided more flexibility and ensured that multiple variables describing one feature of the habitat did not weigh more heavily in the outcome. Moreover, this analysis allowed me to incorporate both categorical and continuous variables. For all statistical tests, I used the statistical program R.

ANOVA

To examine the significance of the variables explaining variance identified by the MFA, I ran an ANOVA comparing *T. alpinus* habitat use points, *T. speciosus* habitat use points, and randomly selected vegetation survey points and the quantitative variables. I performed Tukey-Kramer post-hoc tests on the results from the ANOVA to determine which pairwise differences were significant.

Range maps

Using the GPS coordinates of the points where we successfully trapped or fixed a chipmunk, I created maps illustrating the distribution of the two types of habitat use points. I used Quantum GIS (QGIS) to convert the KMZ files to KML files. This provided vector layers of telemetry and capture points for *T. alpinus* and *T. speciosus* at ML and VO, respectively. I then indepdently exported the layers as shapefiles. I imported the shapefiles into ArcMap to plot the points and used the 'Minimum Convex Polygons' feature to connect the points and create polygons to represent the ranges of the two species.

RESULTS

T. alpinus and *T. speciosus* habitat use points were significantly different in elevation, height and branching pattern of dominant tree species (ANOVA). The variance between habitats of the two species can be further explained by the interactions of elevation, slope, and branching pattern of the dominant tree species (MFA). These noted variables illustrated varying amounts of explanatory power. Variance in axis 1 is largely attributed to elevation, whereas the variance in axis 2 is mostly explained by the interplay of the slope of the sampled point and branching pattern. Connecting these small scale features to a broader picture, range maps created with the capture and telemetry points provide a visual representation of the two species' habitats (Fig. 5).

ANOVA

An analysis of variance (ANOVA) for the quantitative variables yielded significant differences in elevation (p=0.01420), height of dominant tree species (p=0.0003959), and branching pattern of dominant tree species (p=0.00262) between *T. alpinus* and *T. speciosus* use points (Table 2). A Tukey-Kramer post-hoc test showed that the difference in elevation was explained most by the difference in *T. alpinus* and *T. speciosus* points (p=0.0104). The difference in height of dominant tree species was also attributed to *T. alpinus* and *T. speciosus* group (p=0.000611). Unlike elevation and tree height, the difference in branching pattern was greatest between *T. alpinus* and randomly sampled vegetation points. Slope, DBH of the dominant species, canopy cover of dominant species, mean boulder volume, and boulder count were not significant.

Table 2. **Summary of statistics**. A one-way ANOVA showed that elevation (ft), height of dominant tree species (m), and branching pattern were significant at the 0.05, 0.001, and 0.01 level, respectively. Difference in elevation and branching pattern was greatest between *T. alpinus* and *T. speciosus*. The significant pairs from the Tukey-Kramer test are denoted with the letter "a."

	T. alpinus		***T. speciosus***		**Control**	
	x ± SE		*x ± SE*		*x ± SE*	
Elevation (ft) *	10047.39 ± 411.43	(a)	9875.45 ± 474.89	(a)	9695.030 ± 454.00	(b)
Slope (degrees)	23.46 ± 11.34		18.69 ± 8.70		18.96 ± 11.29	
Height of dominant tree species (m) ***	1.73 ± 3.14	(a)	5.45 ± 4.34	(a)	6.04 ± 4.96	(b)
DBH of dominant tree species (cm)	30.48 ± 72.68		79.18 ± 195.65		40.92 ± 52.01	
Canopy cover of dominant tree species	3.37 ± 1.86		3.27 ± 2.00		3 ± 2.00	
Branching pattern of dominant tree species**	2.96 ± 1.46	(a)	1.85 ± 1.21	(b)	2.03 ± 1.26	(a)
Mean boulder volume (cm^3)	89674.08 ± 95810.6		136295.11 ± 290517.7		120000.48 ± 184411.1	
Number of boulders	23.23 ± 11.24		18.83333 ± 15.15		30.58824 ± 45.07	

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

MFA

The MFA condenses the variance in the fifteen variables into 2 axes (Fig. 1a: axis 1=8.38%, axis 2=7.11%). The variation in the two axes can be explained by a combination of continuous variables. Each variable is represented by a vector; and the proximity of the arrow to a dashed axis and the length of the vector explain which axes it is correlated to and the magnitude of the association, respectively. Axis 1 is strongly associated with elevation and slightly with boulder volume and DBH and negatively correlated the number of boulders. Axis 2 has a strong positive correlation with slope, branching pattern, and canopy cover and has a strong negative association with height of the dominated species. Elevation most strongly influences the variance in the axis 1, whereas slope and branching pattern most strongly influence the variance in the axis 2.

In addition to examining how the quantitative variables, the variance for categorical variables also lend weight to understanding the differences in habitat use. As with the variance explained by the continuous variables, the variation in the two axes can be explained by a combination of categorical variables (Fig. 1b). Site type and environmental variables have high predictive power on axis 1. Aspect had a high predictive power on both axes. Tree structure and ground cover have low predictive power on both axes.

The variance in habitats explained by the ANOVA results, continuous and categorical data can be further described and conceptualized visually (Fig. 1c). It is expected that randomly selected points where we conducted vegetation surveys should show no clear association with either axis. However, it is clear that points where *T. alpinus* was caught or fixed are positively correlated axis 2 and is weakly correlated to axis 1. This is also visually apparent by the black points clustered around the positive region of axis 2. Conversely, *T. speciosus* points are not clearly correlated with one axis and appear more scattered in distribution.

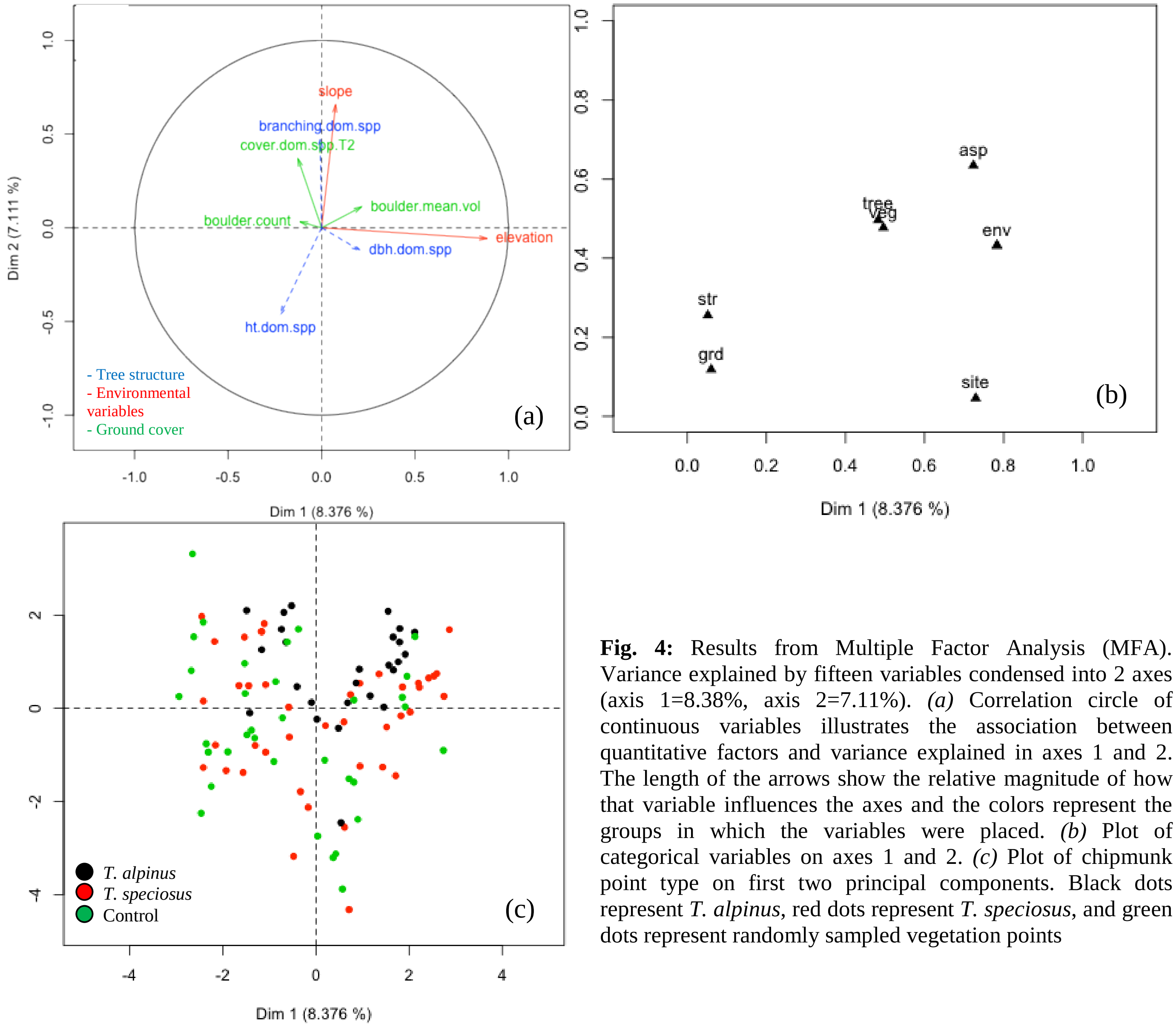
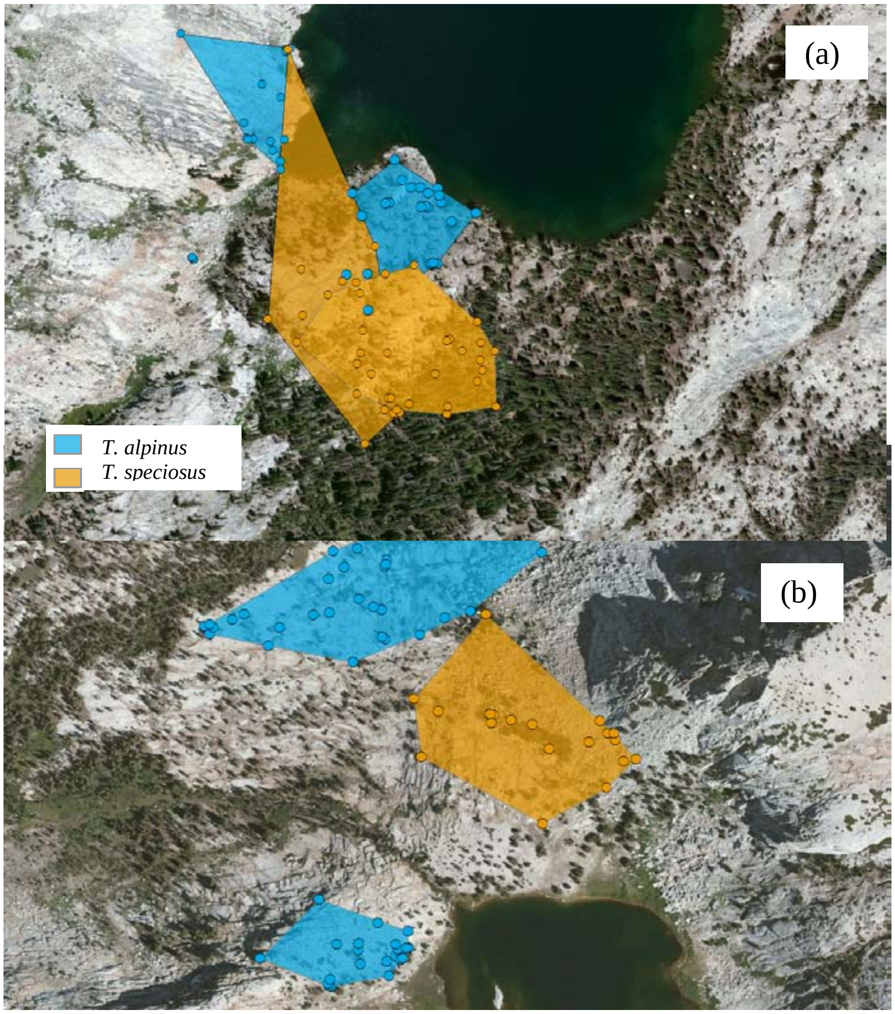


Fig. 4: Results from Multiple Factor Analysis (MFA). Variance explained by fifteen variables condensed into 2 axes (axis 1=8.38%, axis 2=7.11%). *(a)* Correlation circle of continuous variables illustrates the association between quantitative factors and variance explained in axes 1 and 2. The length of the arrows show the relative magnitude of how that variable influences the axes and the colors represent the groups in which the variables were placed. *(b)* Plot of categorical variables on axes 1 and 2. *(c)* Plot of chipmunk point type on first two principal components. Black dots represent *T. alpinus*, red dots represent *T. speciosus*, and green dots represent randomly sampled vegetation points

Range maps

A visual inspection of the ML map shows the range of *T. alpinus* (blue) is limited to xeric areas, characterized by little to no vegetation. The ranges of the *T. speciosus* individuals overlap in areas of heterogeneous terrain and vegetation. While VO does not illustrate an identical pattern, the three collared individuals show distinct ranges with no overlap. The two collared *T. alpinus* individuals show ranges with different elevation and capture different microhabitats (vegetated and non vegetated). The range of *T. speciosus* individual is situated between the two *T. alpinus* individuals and captures diverse habitat types similar to the collared individuals from ML.

Fig. 5*:* Ranges of *T. alpinus* and *T. speciosus* from radio-telemetry point data (a) May Lake (ML) and (b) Vogelsang (VO). Ranges and points where *T. alpinus* individuals were fixed are shown in blue. Ranges and points where *T. speciosus* were fixed are shown in gold.



DISCUSSION

Summary

The results are organized in two parts that examine the (1) biotic effects and (2) abiotic effects on habitat preference by incorporating quantitative microhabitat variables and ranges of the two focal species constructed with radio-telemetry tracking. The influence of tree structure (height, branching) demonstrates a differences in habitat use and suggests a connection to interspecific interactions (p=0.0003959, p=0.002616). Elevation and slope further describe the variance between Tamias habitat use and confirm the elevational separations between the two species (MFA, Fig. 4). The interplay of these biotic and abiotic factors corresponds to the locations where a chipmunk was trapped or fixed. *T. alpinus* habitat use points are distributed more across axis 2 than axis 1, suggesting that variation in slope and branching patterns are important factors describing *T. alpinus* habitat (Fig. 4c). By explaining vegetation and physical characteristics of Tamias microhabitats and aligning these quantitative measures to range maps, we can gain fine-scale details on a broader picture.

Biotic effects on habitat

Tree Structure

Height of dominant tree species. The interaction variables indicate a relationship between the forms of the landscape and the function it serves. Height of the dominant tree species offers another dimension of habitat utilization. While many of our measurements emphasized variables along horizontal space (e.g. ground cover, boulders, etc.), the significance of tree height describes the possibility of utilizing vertical space (p=0.0003959). Structural aspects of vegetation (e.g. branch angle, branch diameter, etc.) and temporal segregation have explained differences in habitat use among Cricetid rodents in Californian scrubland (Meserve 1976, 1977). Similarly, vertical spaces created by these structural elements provide another element of niche partitioning. For many small mammal assemblages, segregation of food and habitat facilitate the coexistence of species (Albanese et al. 2011, Meserve 1976)

Habitat segregation on a vertical dimension can reduce competition in the horizontal plane among small mammals (Albanese et al. 2011). Vertical space may reinforce the segregation of species that overlap in the niche dimensions of habitat and food, particularly among Sciurids (Schoener 1974). *T. speciosus* is omnivorous and has been described as a generalist, favoring seeds of grasses, forbs, and trees, specifically white fir, red fir, sugar pine, Jeffrey pine (Best et al. 1994). The life history of this chipmunk suggests that it may be utilizing this third dimension of its niche for foraging.

The vertical dimension offers an interesting relationship between interspecific interactions of the two species. Ability or inclination to use overstory has been observed between congeners, T. amoenus and *T. speciosus*; as well as documented by field observation describing the tendency for *T. speciosus* to skirt up trees when released from the trap (Sharples 1983). Partitioning of resources is usually viewed as a mechanism by which competition is reduced and stable coexistence of similar species is established (Sharples 1983). Since the fundamental niche of *T. alpinus* includes the habitat of *T. speciosus*, the presence of *T. speciosus* may reduce its success in this habitat (Heller 1971). The height of the dominant tree species may not only explain differences in habitat use, but be a part of the product of niche partitioning and competition.

Branching pattern of dominant tree species. While the height of the tree offers a vertical dimension to a species' niche, understanding the branching may be the gateway to understanding this dimension of habitat utilization. Branches are a physical segregation of vertical space. Moreover, branch diameter, angle, and height affect the climbing ability of rodents (Albanese et al. 2011). Studies on vertical space and microhabitats have been primarily focused in deserts (Albanese et al. 2011), but mountaintops can be interpreted to be analogous "islands" with limited by heterogeneity and area space for organisms to inhabit.

Previous studies on the interaction with other Tamias species (*T. amoenus* and *T. speciosus*) have observed that the overlapping occurrence of these species within a single altitudinal zone is possible because of the existence of different vegetational types (Sharples 1983). Vertical space may present a significant role as refuge from competition (p=0.002616). Branching may present minimizing antagonistic species interactions, as well as a maximizing of possible habitat space and promoting coexistence (niche partitioning).

Abiotic effects on habitat

Elevation

Elevation proves to play a significant bottom-up role in determining the differences in habitat preference between the two species (p=0.01420). Elevation indicates that *T. alpinus* and *T. speciosus* capture and telemetry points recorded in this study support GRP records, that *T. alpinus* and *T. speciosus* are utilizing spaces at different elevations and vegetation types (MFA, Fig. 4a,b). The majority of the variance on axis 1 is explained by elevation, a basis to understanding the type and kind of vegetation that can exist. Since elevation affects both biotic and abiotic interactions, elevation is an inherent control on the ecosystem structure and hence the vegetation available for utilization. Lodgepole Pine, Mountain Hemlock, Red Fir, Whitebark, and Western White Pine, dominant species in the sites, are highly influenced by availability of sunlight, water, and other abiotic factors and exist above 9,000 ft (Parker 1988, Stuart et al. 2001). Naturally, the most dominant features of a microhabitat—the trees—have an elevational gradient that influences the elevational and home ranges of the two focal species.

Slope

The significance of elevation, height, and branching pattern of the dominant tree species from the ANOVA matched the significant results of the MFA, but suggests the interactions between the variables are explaining different dimensions of variance. Shorter trees with low branching were associated with habitats of steeper slope, whereas taller trees with high branching corresponded to habitats of a lower slope (Fig. 4a, see axis 2). Trees at higher elevations are expected to be smaller and shorter (Fig. 4a). Abiotic factors are influenced by slope, such that steeper slopes have more sun exposure, less soil moisture and nutrients than shallower slopes.

In considering the continuous variables in the MFA, the association between slope, branching pattern, and canopy cover is explaining the majority of variance in axis 2. The interaction between slope and branching pattern is a simplified example of an abiotic and biotic exchange. Ecosystem, hydrologic, and geomorphological processes highly influence the slope of a microhabitat. Moreover, these physical processes are circular: they influence the species of tree that may grow and hence the branching pattern and canopy cover, but also are influenced by the existing vegetation conditions (Cañón et al. 2011). Slope then not only influences the substrate or structure that *T. alpinus* or *T. specisosus* may use, but can significantly modify the microclimate that an individual may experience, such as solar radiation and ambient temperature (Bennie et al. 2008).

Non-significant results

Boulders

Qualitatively, personal and published field observations support the hypothesis that habitat differences could be explained by boulders (Clawson et al.1994). Higher elevation survey sites that are situated above treeline are dominated by boulder fields, which suggest that boulders would explain habitat differences. However, results from the ANOVA and MFA both do not support this, suggesting that ground cover may not have the most predictive power. Moreover, the insignificance of boulders may also be attributed to the large variance in mean boulder volume ($x \pm SE_{alpinus}=89674.08 \pm 95810.6$ cm^3, $x \pm SE_{speciosu}=136295.11 \pm 290517.7$ cm^3, $x \pm SE_{control}=120000.48 \pm 184411.1$ cm^3) and mean number of boulders ($x \pm SE_{alpinus}=23.23 \pm 11.24$, $x \pm SE_{speciosu}=18.83333 \pm 15.15$, $x \pm SE_{control}=30.58824 \pm 45.07$). We measured only the length, width, and height of each boulder and the total number within each plot; and it is possible that these measurements did not capture significant parameters that describe boulders. The shape and size of the boulders or the percent of the plot area covered by rock may have been captured more of the variance between *T. alpinus* and *T. speciosus* habitat use.

Connecting microhabitat to ‘Ecological Niche’

Microhabitats often are described in terms of small-scale, physical, and biological discontinuities that are thought to affect, directly or indirectly, reproductive performance. The selection or avoidance of particular microhabitats by small mammals has been tied to a number of factors: exposure to elements; predatory risk; inter- and intra-specific interactions; differential resource availability (Bower et al. 1994) Microhabitats, for that matter, are essentially reflections of the specializations of an organism. Specialization can be defined as the use of a relatively restricted subset of resources or habitats in the field by focal species compared with other species (Colle 2009). Largely, specialization depends on species-specific characteristics and is contingent on environmental constraints, such as diet, competition, or temperature (Devictor et al. 2009). To understand these factors that influence specialization and build the ecological niche of a species, integration of microhabitat and environmental factors is required. The process in examining fine-scaled details of this study is not to exhaustively describe the system, but to be able to connect quantitative methods and qualitative observations.

Qualitative description of range: radio-telemetry maps

The spread of *T. alpinus* and *T. speciosus* trapping and telemetry points was different within and between sites (Fig. 4a, b). Telemetry data shows that *T. alpinus* was generally found at higher elevation and in dry, rocky areas. In contrast, *T. speciosus* was found in areas of denser vegetation below the treeline. These radio-telemetry data support field observations conducted in the 1970s (Heller 1976). *T. speciosus* habitat has been qualitatively characterized by mixed conifer and fir forests; and specificially in the western Sierras, by forests consisting of mostly Lodgepole Pines (Bower et al. 1994).

May Lake (ML)

Higher elevation sites are much more arid and dominated by boulders, whereas lower elevation sites are forested and have a number of conifers that may provide shelter for the chipmunks. Lower elevation sites may provide more heterogeneity, perhaps increasing the possibility for different pockets of resources, and hence the number of ecological niches. The occurrence of *T. alpinus* at higher elevation sites suggests that individuals in this species are using a subset of the habitat that is available (Fig. 5a). Furthermore, the significance of tree height, branching pattern, and canopy cover (MFA, fig. 2) lends validation to qualitative observations of *T. speciosus* habitat preference. Qualitative and quantitative information suggests that *T. specisosus* may be more of a generalist and that *T. alpinus* may be limited by certain physical resources or resources or physiological requirements.

Vogelsang (VO)

T. alpinus and *T. speciosus* are sympatric and have been observed to utilize overlapping fundamental niches (Best 2004). In comparison to ML, trapping and radio telemetry in VO were conducted in terrain where the slope increases quicker. The map illustrates distinct space between the two species, showing no overlap. The ranges drawn are partially a product of the small sample size (n_{VO}=3), but also highlight the large-scale differences between the habitat types and home ranges of the two species. Visually, *T. alpinus* is using dry landscape features, areas driven by the processes of elevation and slope. The overlap of fundamental and realized niches suggests patterns of interspecific aggression between the two study species. *T. alpinus* has been recorded to limit the realized niche of *T. speciosus* through aggressive behavior for limited food resources (Heller et al. 1971). This behavior may be seasonal, but can also provide an explanation of absence of *T. speciosus* in more arid habitats (Fig. 5a)

Sources of variability

Data - Pooled telemetry and capture points

Survey data was pooled for capture and telemetry points because of the similarity in habitat type between capture and telemetry points (Fig. 2). Separation of two categories may have yielded different results, and perhaps more fine-scaled details about habitat use. However, conducting surveys at telemetry points and capture points independently would have resulted in prohibitively small of sampling sizes. Pooling the data provided a larger sample size and hence increase the statistical power of my vegetation dataset.

Variance explained

While there are clear patterns distinguishing *T. alpinus* and *T. speciosus* habitats, the variance explained is low (axis 1=8.38, axis 2=7.11). We measured a breadth of variables and aimed to capture the most important factors influencing a microhabitat, but low variance suggests that the differences in habitat may be attributed to unmeasured variables. Additionally, we were limited by the nature of measuring a microhabitat and the number of categorical variables that follow suit. My decision to use the MFA was based on the goal to examine the interplay of the categorical and continuous variables and to gain a holistic understanding of habitat differentiation between the two species. However, I would have liked to include other measured variables (e.g. percentages of ground cover, DBH and number of down logs, and relative abundance of shrubs), but was limited by categorical variables, equal parameters across groups and sites, and problems with collinearity. The results presented provide a foundation to further explore variables that may better explain what variance in habitat preference may exist.

Future directions

Range maps provide qualitative information that can be meaningfully paired with quantitative information from physical and vegetative measurements to create a picture with both fine-scale resolution and scale. Also, while measured abiotic and biotic variables describe differences between Tamias habitats, there are still many unmeasured considerations. Many studies on microhabitat also acknowledge the importance of the physiology and life history of the study species (Chappell et al. 1978, Zimmerman et al. 2009). In the same chord, competition, interspecific interactions, and dispersal ability cannot be ignored (Brown 1971). Gaining more insight on the physiology and biotic interactions would provide a more comprehensive picture of the differences between *T. alpinus* and *T. speciosus* and how their organismal processes may be contributing to understanding their habitat preference and spatial utilization.

CONCLUSIONS

Species extinctions vary in scale and cause and have arisen as a concern for species who have experienced a shift in range. Recorded extinctions of mammals in western North American national parks are local extinctions, likely caused by a combination of deterministic events (e.g. habitat loss, modification and predator control, and random events both within and outside of the parks (Newmark 1995). Extinction risk is interconnected to a multitude of biotic and abiotic interactions,that when in play, determine the abundance, distribution, and ranges of organisms (Williams et al. 2009).

Beyond the current focus on climate change, niche theory has a variety of applications in conservation and restoration biology (Wake et al. 2009). It is becoming increasing evident that in the face of environmental changes, understanding the different mechanisms of habitat and resource utilization is the first step to understanding range shifts and secondly the direction of conservation efforts to protect such species (Root et al. 2003). The microhabitats and ranges constructed here were generated from individuals, but do not neglect efforts towards understanding the community and population as a whole. Quantitative habitat information can be paired with diet, physiology, and interspecific interactions to better grasp the mechanisms and processes underlying the observed historical range shifts in *T. alpinus* and *T. speciosus* and provide groundwork for examining changes in range of species with similar habitat and physiological constraints.

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