University of Nevada, Reno

Geographic distribution, habitat association, and the importance of host quality for one of the rarest butterflies in North America: Thorne's hairstreak (*Mitoura thornei*)

A thesis submitted in partial fulfillment of the

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by

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ABSTRACT

Mitoura thornei, Thorne's hairstreak butterfly, is endemic to a single mountain in south-western North America. The extremely small geographic range of this species coupled with threats to its host plant, *Hesperocyparis forbesii,* motivated a study of habitat association and fine-scale mapping of both butterfly and host distributions. Often the study of habitat associations for rare or threatened species is complicated by habitat loss. In the case of *M. thornei,* the range is naturally small, which provides an opportunity to investigate small scale variation in vegetation and geographic features as they may affect larval and adult butterflies. Specifically, the following questions were posed: How much of the range of the host plant is occupied by *M. thornei* within the focal geographic area? What biotic and abiotic features predict the presence and abundance of *M. thornei*? How does tree age affect larval performance? These questions were addressed with a combination of field observations and laboratory experiments involving caterpillars. *H. forbesii* size (diameter at breast height) was found to have a significant association with the presence and absence of larval *M. thornei,* while slope, density of herbaceous plants and density of *H. forbesii* were found to be the factors most strongly associated with adult *M. thornei*. Laboratory experiments with larvae showed no effect of tree age on larval survival, but a slight reduction in adult size for individuals reared on foliage from the oldest trees. From a conservation perspective, the most important result is the widespread occurrence (greater than previously reported) of *M. thornei* throughout the study area. However, I caution that spatial factors (such as fragmentation, isolation and perimeter to

interior ratios) could be important for *M. thornei*, though these factors were not addressed directly in this study. In other words, while the presence of the host plant is essential, we do not yet understand how the spatial arrangement of this resource might affect the butterflies. In general, results illustrate the challenges of understanding habitat association for a geographically-restricted species, and the utility of studying larval and adult life history stages, both in the field and in the laboratory.

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INTRODUCTION

Fundamental to conservation biology is the need to characterize the geographic distribution and habitat associations of sensitive species. Managers need to know where species live and what features of the landscape predict occupancy and persistence of populations (Brown and Paxton 2009; New et al. 1995). Characterizing distribution and habitat can be particularly difficult for insects which have low population densities, are not easily observed or identified, or do not leave signs (such as foliage damage) that can be recorded in the absence of direct observations (New et al. 1995). Seasonality in insects presents yet another challenge, as they may be observable for only a brief period during the year. For herbivorous insects, habitat requirements necessarily include host plants and in some cases specific nectar sources (Brommer and Fred 1999; Grundel et al. 1996). However, it can never be assumed that a population or species of herbivorous insect will occupy all areas of the host plant range (Peterson 1954; Lorkovic 1958; Shapiro and Carde 1970; Singer 1971; Ehrlich et al. 1975, Wikilund 1977; Rausher 1979,) thus host distribution is a necessary but not sufficient starting point for a conservation plan.

Species with small geographic ranges present further difficulties to conservation biologists (Gaston 1999; Kunin and Gaston 1993) because field surveys may not encompass enough landscape or vegetation heterogeneity to provide adequate statistical power (Wiser et al. 1998; Hernandez et al. 2006). Here, I address the issues of distribution and habitat association for one of North America's most geographically restricted butterflies, Thorne's hairstreak, *Mitoura thornei*. As far as we know, the range of the species has been restricted historically, as opposed to recently or anthropogenically reduced, which has the advantage that I can address the challenging issue of habitat characterization within a small geographic range, while knowing that I am not excluding particular landscape features because of recent habitat destruction. In addition to addressing the issue of habitat characterization based on field observations within a limited range, I also conducted experimental rearings to ask if manipulative experiments can complement field observations in developing understanding of habitat requirements of rare species.

The focal species belongs to the genus *Mitoura*, which comprises a small radiation of butterflies in the family Lycaenidae, which specialize on host plants in the family Cupressaceae, the cypresses (Scott 1986). *Mitoura* host plants are the site of female oviposition, larval development, male lekking, and adult mating (Forister 2005, Johnson 1976, Scott 1986). Adults are found in close proximity to the host plants except when they visit nectar sources (Johnson and Borgo 1976). Populations of *Mitoura* butterflies often exhibit local adaptation to hosts, which has made them useful in studies of ecological, host-associated speciation (Downey and Nice 2011, Forister 2004, Nice and Shapiro 2001).

Thorne's hairstreak butterfly (*Mitoura thornei*) was formally recognized as a species in 1983 (Brown 1983). First collected in 1972 by Fred Thorne near Otay Lake reservoir, its range is restricted to Otay Mountain in southwestern San Diego County near the United States-Mexico border. It is a small butterfly, usually bivoltine, with the first emergence between January and March and the second emergence in mid-summer, between May and June; a third brood in early fall is possible (Winchell et al. 2008). Pupae overwinter in the duff at the base of the larval host plant, Tecate cypress

(*Hesperocyparis forbesii*, formerly *Cupressus forbesii*). Known nectar sources include California flat-topped buckwheat (*Eriogonum fasciculatum*), Ramona lilac (*Ceanothus tomentosus*), deerweed (*Lotus scoparius*) and narrowleaf milkweed (*Asclepias fascicularis*) (Winchell et al. 2008). *Mitoura thornei* is presently listed as a sensitive species by the United States Bureau of Land Management, due to its restricted range and association with a host plant that is itself a sensitive species. The range of *H. forbesii* on Otay Mountain is only slightly larger than the historically-reported range of the butterfly, and the tree grows in dense, fire-prone stands (De Gouvenain 2006).

Informal surveys for *M. thornei* conducted prior to the present study have suggested that the butterfly requires mature cypress for egg-laying and perching (Winchell et al. 2008). Host plant quality and age are tightly linked to fecundity and fertility of many herbivorous insects, and therefore, can directly affect population size (Awmack and Leather 2002). Host plant quality consists of components such as carbon, nitrogen and nutrients (Awmack and Leather 2002). Certain components, such as amount of water and nitrogen in many trees, forbs and grasses decrease with age, so Tecate cypress may become undesirable or less palatable to *M. thornei* after the tree reaches a certain age (Scriber and Slansky 1981). Also, herbivory can increase the chemical defenses in plants which may affect future oviposition and larval performance (Bowers and Stamp 1993; Hartley, S.E. 1998).

The restricted range of *M thornei*, the fire-prone nature of the host plant, and the possibility that older trees are important for population persistence led to the present study, which was designed to ask the following questions. Within the focal geographic area of Otay Mountain, how much of the range of the host plant is occupied by *M.*

thornei? What are the vegetative or landscape features that characterize *M. thornei* habitat? How does tree age affect larval performance? These questions were addressed with a combination of field observations spanning three years, and experiments involving caterpillars reared to adults in the lab on foliage of different ages. The answers to these questions add to the understanding of host and habitat-associations for specialized Lycaenid butterflies and contribute to a base of knowledge that can aid in the conservation and management of *M. thornei*.

MATERIALS AND METHODS

Study Site

The study site, Otay Mountain, is part of the San Ysidro Mountain chain. It is managed by the United States Bureau of Land Management (BLM) and includes 18,500 acres designated as Otay Mountain Wilderness. Eleven percent of Otay Mountain is included in San Diego's Multiple Species Conservation Program (MSCP). This plan aims to manage and preserve land on a large scale, therefore protecting native habitats for multiple species. Doghouse junction, Otay Mountain's highest point, is at 1087m. The range of Thorne's hairstreak's host plant, *H. forbesii*, is limited to four separate localities within chaparral communities of southern California (De Gouvenain and Ansary 2006). Otay Mountain is considered to be one of four existing localities of *H. forbesii*.

Tecate cypress mapping and survey design

To understand habitat associations of *M. thornei*, I used a survey method based on the random placement of points on a map. Points were then used as survey locations when looking for adults, larvae, and for characterizing vegetation. Before a sampling design could be implemented, a map of cypress distribution on Otay Mountain was created in 2009. A stand was characterized as containing no fewer than twenty *H. forbesii* trees that were no farther than fifteen meters apart. A tree had to be at least one meter in height to be considered one of the twenty trees. In total, 41 stands were found, ranging from 0.1 hectares to 36.5 hectares in size. Each stand was assigned a number 1 through 48. These stands were defined by walking around the stand perimeters with a handheld GPS device (Garmin).

Subsequent to the mapping of tree stands, I created 5-meter diameter, circular survey points with and around each stand. Perimeter points were assigned to be equally spaced 200 meters apart around the border of the stand. The number of perimeter points for each stand then determined the number of exterior and interior points per stand. Each individual stand was given exterior and interior survey points each equal to the number of perimeter points. The exterior points were placed, at random, at least ten meters from and no further than one hundred meters outside the perimeter border, and at least ten meters apart from each other. The exterior points were created to allow for the detection of *M. thornei* that were using areas outside of stands of *H. forbesii* for nectar sources. The interior points were placed, at random, no closer than ten meters inside from the perimeter border and at least ten meters apart from each other. In total, 624 points were created (See Appendix 1and Fig 1). A map of the area and each individual point was downloaded onto a Trimble handheld GPS unit which was used to locate points in the field for vegetation and *M. thornei* surveys.

The only exception to the placement of points described above was for stands that had essentially no width and were single lines of *H. forbesii* trees occurring in canyon bottoms and ditches. Having no interior, these stands only consisted of perimeter and exterior points, but were otherwise treated as the other stands.

Butterfly surveys

Mitoura thornei surveys were conducted in 2010 and 2011. Both stands and points within stands were assigned random numbers, and were surveyed in the order of those random numbers. When arriving at each point in the field, trees and plants were tapped to flush out any butterflies within the five m radius and within a five minute time span. If a *M. thornei* butterfly was observed, it was captured to confirm a positive identification. Temperature, wind speed and percent cloud cover were recorded at each point. *M. Thornei* surveys were only conducted in good "butterfly weather"; in other words, if temperature was above 18.3 degrees Celsius, and the wind speed was below 4.5 m/s (Winchell et al. 2008). Surveys were conducted between 1000 and 1500 hours (Winchell et al. 2008). In total, 229 points were surveyed for adult *M. thornei*; see Fig. 1 and Appendix Table 1.

Vegetation surveys

Vegetation surveys were similarly conducted at each point, subsequent to the survey for butterflies as described above. From the center of each 5-m diameter point, 4 transects were walked, each 5 meters long and each ninety degrees apart. The first transect direction was determined using a random number generator (restricted to 0 through 360). A flag was dropped at 0.5 meter increments along each of the four transects and all plant species touching the flag or above the dropped flag were recorded. The plant species at zero meters was recorded each time, giving a total of 44 transect samples per 5-meter diameter survey point. In addition to fully characterizing host plant presence in the survey points, two *H. forbesii* trees along each of the four transects were measured for height and diameter at breast height- DBH (Forestry Supplies metric fabric diameter tape), for a total of eight trees per point (or fewer when trees were not present along each of the four transects) along with any trees that the flag was below or touching in the four set transects. The locations of the *H. forbesii* trees chosen to be measured were determined by a random number between 0 and 5 m. These trees were also used to determine the average diameter at breast height (DBH) and height of the *H. forbesii* trees within each survey point. Slope and crown density were measured at the center of the point. Finally, a compass was used to determine slope and a densitometer was used to determine crown density (Forestry Suppliers Spherical Crown Densiometer). In total, 360 points were surveyed for vegetation.

Larval surveys

Given logistical and time constraints in the field, I did not survey for larvae throughout the entire season. Instead, larval surveys were conducted towards the end of each flight season, when I expected to have the greatest success in locating larvae. The purpose of the larval surveys was to maximize my ability to document the distribution of

M. thornei on Otay Mountain. In other words, I took advantage of the fact that larvae can be surveyed in this species to extend the amount of time that we were able to search for the presence of a generally cryptic species with a short adult flight window. In addition, the documentation of larval presence and absence allowed me to investigate conditions potentially associated with adult oviposition and larval development. The larval surveys started in April when the first adult flight season was coming to an end, adults had laid eggs, and the eggs had time to incubate and hatch. Larval surveys were started again in late June/early July into August, after the second flight season. Larval surveys were performed in stands and points that had not been surveyed for adults as time was limited and my primary goal (as stated above) was to document the presence of *M. thornei* (adults or larvae) on the mountain. A list of points was compiled where adults were not observed or which had not yet been visited and randomized to determine an order to conduct larva surveys. Thus the points surveyed for adults and larvae were non-overlapping, but the stands surveyed were overlapping. At each point, eight *H. forbesii* trees were chosen by using lists of random compass points and meters. A 1.5m x 1.5m beat sheet was placed underneath each tree to catch all larvae. In total, 129 points were surveyed for *M. thornei* larva.

ANALYSIS

Habitat Association

To address my primary goal regarding habitat association, we conducted permuted Mantel tests. Mantel tests allow me to address problems involved with variables that are spatially non-independent, which is the case with both of the predictor variables (putative habitat characteristics, which I refer to for simplicity as environmental variables) and response variables (adult and larval *M. thornei* data). Two different spatial levels were investigated: stand level and point level (see Table 1 for a summary of the analytical design). Stand level variables were calculated by taking the averages of each variable from all the point data associated with each particular stand (including perimeter, exterior and interior points). Stand level analyses were used to view habitat associations at a scale that is useful for future conservation and management, as in which areas of Otay Mountain are of higher priority due to greater *M. thornei* adult and larval presence or abundance. In contrast to the stand level analyses, point level analyses were used to study with finer resolution associations among *M. thornei* and biotic and abiotic factors, as a stand may be composed of areas of different concentrations of vegetation types, or *H. forbesii* densities, for example. Three different sets of *M. thornei* data were investigated as response variables: presence/absence, abundance, and the fraction of points (at the stand level) in which individuals were present.

Presence/absence data was composed of ones to indicate presence and zeroes to indicate absence of *M. thornei* adults and larvae at stand and point levels. The presence/absence analyses allowed me to ask specifically where *M. thornei* occurs on the mountain.

M. thornei abundance data consisted of the raw numbers of *M. thornei* seen at the stand and point levels. Abundance analyses allowed us to investigate variation in the density of adults and larvae and the potential associations with environmental variables, and complements the use of presence/absence data (which was focused simply on where *M. thornei* occurs). In my abundance data, I included observations that were zero, both at the point and the stand level. Given large enough datasets, locations with zero observations could be excluded from an "abundance" analysis, which would then focus strictly on density variation within occupied areas. However, I have included zeros in my"abundance" analysis for statistical power, and I recognize that the insights provided by the abundance data are not completely orthogonal to the insights associated with the presence/absence data.

Finally, I investigated a third summary statistic as a response variable. At the stand level, I summarized both larval and adult presence as the fraction of points in which individuals were observed ("fractional presence"). This gave me an index of the pervasiveness of presence within stands, which preliminary analyses suggested could provide insights that were complementary to those involving abundance and presence/absence.

Analyses proceeded in two phases. First, simple pairwise Mantel tests (Mantel 1967) were used as a screening process to focus further analyses on important variables. Subsequently, multiple regression on distance matrices (multiple Mantel tests; or MRM) were then used to examine associations between our response variables and multiple predictor variables, using only those environmental variables that were found to be significant in the initial screening with pairwise tests (Lichstein 2007). The response variables were the different *M. thornei* data sets, which included presence/absence, abundance and fractional presence (Table 1). MRM allows for the consideration of multiple predictor variables, while allowing for inter-correlations among those predictors, as in a multiple regression. Geographic distance was included in all MRM models because, although it may not have always been a significant variable in pairwise Mantel tests, it was a straightforward way to assess the possibility of spatial autocorrelation.

The environmental variables analyzed were *H. forbesii* density, *H. forbesii* DBH (diameter at breast height), crown density of points and stands, woody plant richness, herbaceous richness, density of leaf litter, bare ground and rock, size of stands, slope of stands and points, and distance between either stands or points. Initially, *H. forbesii* height and crown density were included, but they were eliminated from the list of predictor variables because of their high correlation with *H. forbesii* DBH, and *H. forbesii* density, respectively (correlations were greater than 0.9)

In all cases, Mantel analyses (both pairwise and multiple) were non-parametric, rank-based tests, which is appropriate given the non-normality and heterogeneous nature of both predictor and response variables. Finally, I acknowledge the problem of multiple comparisons, which is well known with respect to multiple tests, and is particularly relevant for me at the level of pairwise Mantel tests conducted with each variable separately. Rather than take an approach of adjusting for multiple comparisons, as with the Bonferroni correction, I have instead (as described above) used the two-step process that culminates in analyses (MRMs) involving multiple predictors in single models. This approach was a compromise between the most conservative method (discarding variables following correction for multiple comparison in pairwise tests) and the most liberal (interpreting all significant variables from pairwise tests).

Both Primer v.6 and R were used for analyses. Primer was used for initial exploratory analyses and for the generation of Euclidean distance matrices (Lichstein

2007; Elmore and Richman 2000). Final pairwise and MRM analyses were executed in the *ecodist* R package.

Larval experiment

In addition to the more general goal of determining habitat association, my study was motivated by the need to address the possibility that *M. thornei* caterpillars do not perform equally well when consuming *H. forbesii* foliage of different ages. An original hypothesis, based on observations of lepidopterists, was that *M. thornei* are primarily associated with more mature trees, raising the possibility that survival was somehow compromised in stands lacking mature trees (Winchell et al. 2008). Subsequent to that observation, results presented by Congedo (2011) suggested that young foliage was not inferior for caterpillars, though these conclusions did not involve caterpillars reared to adults. I obtained 86 larvae from eight wild-caught *M. thornei* females, and reared 56 of them to adults on foliage of three different ages. Plant material was kept in a refrigerator and larvae were fed fresh cuttings at least every five days. Larvae were reared individually in 150 mm diameter Petri dishes. All dishes were kept under ambient room-temperature (20 to 23 degrees Celsius) on lab benches with overhead lights set on a twelve hour light-dark cycle. Each time the plant material was changed, deaths of individual larva were recorded. At approximately 3 weeks after the start of pupation, individual pupae were weighed to the nearest 0.01 mg on a Mettler Toledo XP26 microbalance. Rearing was done at the University of Nevada, Reno, generally following protocols used previously for *Mitoura* caterpillars (Forister 2004).

Foliage for experiments was collected from a single spot on Otay Mountain chosen because it had a diversity of Tecate cypress age classes in immediate proximity. The three different ages of trees were represented by three size classes: trees less than 2 m in height, between 2 and 3 m, and greater than 3 m. From each size (age) class, foliage was selected, and different trees, a total of six from each size class, were sampled on repeat visits. Foliage was shipped to the University of Nevada, Reno by wrapping the freshly cut stems in wet paper towels in a cooler with freezable ice packs and shipped using overnight delivery.

Results from rearing experiments were analyzed in R, using Pearson's chi-squared test for the number of larvae that survived or died on foliage of the different ages, and a simple analysis of variance (ANOVA) on the adult body masses of butterflies reared on the three different types of foliage.

RESULTS

Habitat Association

In total, 358 points were surveyed for vegetation and 229 points were surveyed for *M. thornei* (larval and adult) presence and abundance in association with 41 stands of *H. forbesii* (Appendix 1). Seventy-five *M. thornei* adults were observed in 22 stands spread throughout the Otay Mountain study area, for an average of 4.4 *M. thornei* adults per stand. Thirty-eight *M. thornei* larvae were found in 26 points, representing 17 separate stands. *M. thornei* adults or larvae were found in a total of 31 of the 41 *H. forbesii* stands. Both *M. thornei* larvae and adults were found in eight of the stands. Six percent of adult *M. thornei* observations were at exterior points, 48% at perimeter points, and 46% at interior points. 45% of the larvae observed were at interior survey points, and 55% were at perimeter points. In addition, 43 adult *M. thornei* were observed in 26 random, unassigned points. These butterflies were found when walking around Otay Mountain going to and from assigned points. The unassigned points were treated like the assigned points in that vegetation surveys were conducted. The unassigned points were given a number, 1-38, and were included in the point-level analyses but not in the stand level analyses. See Fig. 1 for a map of points and stands surveyed, and Fig. 2 for a map of all *M. thornei* occurrences; Fig. 3 shows the distribution of density of the host plant within the study area.

The analyses were multi-faceted, and results are described here first at the point level, starting with larvae then adults; then I move to the stand level, covering larvae and adults (Table 1). In all cases, I describe environmental variables that were found to be significant in pairwise tests and then I describe results from the multiple Mantel tests. Because my conclusions ultimately rest on the multiple Mantel tests, the results from pairwise tests are given in appendices and results from multiple Mantel tests are given in Tables 2 and 3.

At the point level, a number of predictor variables had significant associations with the presence and absence of larvae, as follows: crown density, *H. forbesii* DBH, *H. forbesii* height (all significant at $P < 0.01$), and geographic distance among points ($P = 0.038$); significance for *H. forbesii* density was $P = 0.05$, which is not less than 0.05, but we carried the variable through to the next level of analyses (multiple Mantel tests) nonetheless (Appendix 2). Correlation coefficients for all of these variables were positive, with the exception of geographic distance which had a slight negative correlation coefficient (-0.063). For the multiple Mantel analysis (MRM) of larval presence/absence at the point level, only one of the predictors emerges as significant: *H. forbesii* DBH (Table 2). The whole model was significant (P = 0.021) though the overall amount of variation explained was very low (R^2 = 0.026). In contrast to the results associated with the presence and absence of larvae, pairwise analyses of abundance did not detect any significant associations with environmental variables (Appendix 2), thus a multiple Mantel test for larval abundance at the point level was not performed.

For adult *M. thornei* at the point level, density of *H. forbesii, H. forbesii* DBH, slope, density of herbaceous plants, and geographic distance among points were all found have a statistically significant association with presence and absence of butterflies in pairwise Mantel tests (Appendix 2). These relationships are all positive associations, with the exception of herbaceous density and geographic distance, which are slight negative associations. In the multiple Mantel analysis of these variables, *H. forbesii* DBH importance was lost, while the other variables were retained as significant (Table 2); however, the overall R^2 was again quite low (0.017). As with larvae, no environmental variables were found to predict adult abundance, thus I did not perform a multiple Mantel test on the adult abundance data at the point level. See Fig 4. for graphs showing larval and adult presence and absence and the three variables with which they are most strongly associated.

At the stand level, the response variables were abundance (as with the point level), but also the fraction of points occupied within stands (Table 1). At this spatial scale of analyses, I found a number of environmental variables that were significant in pairwise analyses, though none of these variables retained individual significance in multiple Mantel tests. This is most likely because predictor variables are at least partly correlated with each other, and this becomes more of an issue at the stand level, where replication is less than at the point level. The significant variables at the stand level in pairwise analyses can be found in Appendix 3; while whole-model multiple Mantel tests are reported in Table 3.

For larvae at the stand level in pairwise analyses, density of the combination of leaf litter, rock and bare ground was significantly associated with larval abundance. This was a negative association (correlation coefficient = -0.20), which can be understood as the negative association between resources for larvae (i.e. host plants) and the presence of bare ground. *H. forbesii* DBH was significantly associated with larval fraction seen (Fig 5a), but no other variable was shown to be significant, so a multiple Mantel test was not performed. For adult abundance at the stand level, the size of stands and woody richness (all woody plants excluding *H. forbesii*) were found to be predictors in pairwise analyses (Appendix 3). The former (size of stands) has a positive association with adult abundance, while woody richness is a negative association. *H. forbesii* density was strongly associated with adult fraction seen (Fig 5b), but no other environmental variable for fraction seen was found, so a multiple Mantel test was not performed. As stated above, multiple Mantel tests at the stand level did not reveal any significant associations with environmental variables for adults or larvae (Table 3).

Larval experiments

Eighty-six larvae were provided with Tecate cypress foliage collected from *H. forbesii* trees that were either young, of medium age, or relatively old. I did not detect a difference in survival on the three types of foliage ($\chi^2 = 0.18$, $P = 0.92$). However, I did detect a highly significant effect of foliage age on pupal biomass: individuals reared on the older foliage eclosed as smaller pupae ($F_{2,53} = 9.35$, $P = 0.00033$). Although the absolute effect was small, we can expect that variation in pupal size is correlated with adult fecundity, as has been observed in other butterflies and other lycaenids in particular (Roff 1980; Leimar 1996). I do not, of course, know if any effect on adult fecundity would translate to meaningful differences in population growth in the field. However, I can at least confirm that older foliage is not a superior larval resource for *M. thornei*: if anything, it is slightly inferior (Fig 6).

DISCUSSION

My most important finding for the conservation and management of *M. thornei* is the widespread presence of larvae and adults across Otay Mountain. *M. thornei* adults were found in 22 of the 41 stands, or 54% of the stands. *M. thornei* larvae were found in 17 stands, representing 41% of the total stands. Together, *M. thornei* adults or larvae were found in 31 of the 41 stands, or 76% of the stands surveyed (Fig. 7). The occupied stands are spread throughout the mountain, and include both small and large stands. Prior to my study, *M. thornei* was known from only a fraction of those stands, and primarily restricted to roadside locations.

The ubiquity of *M. thornei* throughout the study area posed a distinct challenge for our study of habitat associations. Nevertheless, certain habitat variables emerged as significant predictors of response variables, at least at the spatial scale of individual survey points where statistical power was greatest. In particular, the size and density of the host plants were important for larvae and adults, respectively (Table 1). In addition, for adults I found a positive association of response variables with slope, as well as a negative association with herbaceous density. The association with slope may be explained by the tendency for *H. forbesii* to occur and cluster in drainage areas on Otay Mountain (Lucas, pers. observation). The negative association with herbaceous density could be explained simply by the reduced presence of *H. forbesii* associated with areas of very high herbaceous plant density, despite the fact that some of the latter serve as nectar sources for *M. thornei*. Although these variables all showed an association with *M. thornei*, it is important to note the very low R^2 values, which indicate that very little of the variation in *M. thornei* presence or abundance was explained. This could be the result of other key environmental variables that were unknown and not measured, or that variation in *M. thornei* presence and abundance is essentially stochastic within the geographic limits circumscribed by the host plant. Although the environmental variables studied explained little variation, these results should not be taken to mean that the host plant is the only requirement for *M. thornei* persistence (this interpretation is discussed further below).

Larvae and adults were surveyed in non-overlapping sets of points. This was done as a result of logistical constraints, as discussed above, but mainly to maximize my ability to search for *M. thornei* presence in our study area. While the sets of points (for larvae and adults) were non-overlapping, they were both random samples of the study area, and I kept the analyses of the two types of data (larval and adult) separate with the possibility of learning something about different habitat associations for the different life history stages. The variables associated with larval and adult response variables were not identical (Table 1), and they were only found together in eight of the 41 stands. However, it is important to remember for all of my habitat-association analyses that the multiple Mantel tests explained a very small portion of the variance in the presence, absence or abundance of *M. thornei* (Tables 1 and 2). Thus I leave open the possibility that adults and larvae can be found more reliably in habitats with different characteristics as an interesting possibility for future study.

Because of the inherently rare and elusive nature of our focal species, I used laboratory-rearing experiments to gain further insight into *M. thornei* host associations. Larvae were reared on fresh foliage collected from trees of three different age classes, using size as a proxy for age.

Larval experiments showed that individuals that were reared on foliage from older trees matured into adults that were smaller than larvae that were reared on foliage from young and medium aged *H. forbesii* trees. The result that the oldest foliage might be relatively inferior for developing larvae is interesting in the light of the fact that neither *M. thornei* larvae nor adults were found in Little Cedar Canyon, the stand which appeared to be the oldest in age on Otay Mountain. *H. forbesii* in Little Cedar Canyon had the largest DBH and the second tallest trees of any stand on Otay Mountain. Thus the oldest *H. forbesii* trees might not provide optimum habitat for either larvae or adults. This is consistent with work by Congedo (2011) who found that *M. thornei* preferentially used young trees for oviposition. My findings are contrary to the suggestions made from previous observations that proposed that *M. thornei* used only mature trees for oviposition (Winchell 2008). Because adult weight is correlated with fecundity, it may be that oviposition by *M. thornei* females on less than optimum foliage could affect butterfly abundance. This has been shown with *Zerynthia rumina*, the Spanish Festoon butterfly which is less abundant in areas where *Z. rumina* larvae fed on host plants that had lower nutritional quality (Jordano and Gomariz 1994).

As discussed above, my most important discovery for the conservation of *M. thornei* is that the butterfly is found throughout the protected area of Otay Mtn. Within that area, the butterfly is widespread but never locally common, and my best habitat models were only slightly successful at predicting facets of butterfly occurrence. Put simply, I find that *M. thornei* is coextensive with *H. forbesii* in the focal area. *H. forbesii* is an obligate seeder, meaning its seed bank germinates and grows rapidly following a fire (Little 1975; Zedler 1977, 1981, 1995; Dunn 1986; Vogl et al. 1988). While it is not listed as threatened or endangered by the federal government, it is classified as seriously endangered by the California Native Plant Society (California Native Plant Society, 2012; De Gouvenain and Ansary 2006). Wildfires in the region of the study area have occurred with increased frequency in the last twenty years. Fires consumed 22,700 acres in 1996 and 2,900 acres in 1994 in the Otay Mountain area. Most recently, the Mine fire in 2003 burned 45,000 acres and the Harris fire of 2007 burned over 90,000 acres. The short time intervals between fires pose a threat to the reproduction of *H. forbesii* if the trees are not able to build sufficient seed banks (De Gouvenain and Ansary 2006).

Although management of *H. forbesii* is not simple, I can conclude that the management and conservation of *M. thornei* is somewhat simplified by the results that I have presented. It appears that management can focus on the preservation and protection of the host plant, rather than on a suite of more complex habitat variables that are often associated with rare or localized butterflies (Singer 1972, Schultz 1998, Konvicka et al.

2008). This finding should not be interpreted as suggesting that the best management of *H. forbesii* should encourage or allow a monoculture on Otay Mountain. As stated above, perimeter survey sites accounted for 55% of all larval occurrences and 48% of adult occurrences. This raises the possibility that *M. thornei* utilizes edges or perimeters of stands of its host plant for some behaviors, for example possibly scouting for nectar sources or searching for mates or even looking for optimal oviposition sites which could be more difficult to find in the center of dense stands. Thus I conclude my study by raising the suggestion that further studies of *M. thornei* could profitably target spatial issues: specifically, which arrangements of host plant patches (in terms of isolation, perimeter to interior ratio, etc.) are most beneficial to population persistence?

Of course, the world is changing rapidly and in ways that are not easy to foresee. Butterfly ranges are shifting in association with a shifting global climate (Parmesan 2006, Forister et al. 2010), and habitat and host associations are even shifting in some species (Oliver et al. 2009). Widespread presence of *M. thornei* in the study area now should not be taken as a prediction of its future occupancy throughout the mountain, and one of the rarest butterflies in North America should be monitored into the future.

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Table 1. Summary of response variables used in analyses for different spatial scales (columns) and life history stages (rows). See main text for description of the three different types of response variables (presence/absence, abundance and fractional presence). For all response variables associated with different spatial scales and life history stages, both pairwise and multiple Mantel tests were performed

	Point	Stand
Larvae	Presence/Absence	Fractional presence
	Abundance	Abundance
Adults	Presence/Absence	Fractional presence
	Abundance	Abundance

Table 2. Multiple Mantel test results at the point level with two response variables: larval and adult presence/absence (“P/A”).

		F	Coefficient	P	R^2
Larvae P/A	Whole model	72.54		0.021	0.026
				P	
	TC DBH		3.45 e-02	**0.018**	
	% Tecate		1.81 e-02	0.89	
	Distance		-1.24 e-05	0.14	
Adults P/A	Whole model	114.17		0.0030	0.017
				P	
	Slope		3.77 e-03	**0.017**	
	Density of herbaceous plants		-2.02 e-01	**0.044**	
	Density of Tecate cypress		1.43 e-01	**0.049**	
	Average Tecate cypress DBH (diameter at breast height)		1.28 e-02	0.249	
	Distance between stands		-7.91 e-06	0.100	

Table 3. Multiple Mantel test results at the stand level with two response variables and two life stages

		F	Coefficient	P	R^2
Larva Abundance	Whole model	11.91		0.11	0.030
	LLRBG		-2.19	0.077	
	Distance		-3.49 e-05	0.431	
Adult Abundance	Whole model	23.83		0.067	0.058
	Stand size		7.38 e-02	0.056	
	Distance		-5.83 e-05	0.530	

Figure Legends

Figure 1. Numbered stands and survey points on Otay Mountain. Each point is a survey point (625 total); stands are numbered 1-48.

Figure 2. Map illustrating locations where *M. thornei* was seen. Each dot represents an occurrence. Occurrence is either *M. thornei* adult or larva. Stands are numbered as in Fig. 1.

Figure 3. *H. forbesii* density at points that were surveyed for *M. thornei* adults. Size of circles represents the different categories of density as indicated in legend.

Fig. 4. Box plots, 3 above plots illustrating *M. thornei* larvae presence/absence (x- axes) and the three most significant environmental variables from pairwise Mantel tests (y- axes). Bottom 3 plots illustrate *M. thornei* adults presence/absence (x- axes) and the three most significant variables from the pairwise Mantel tests (y- axes). Crown density, cypress density, and slope scale units 0-100%. DBH units in centimeters. Cypress height units in meters. See Appendix 2 for a complete list of pairwise Mantel response variables and correlations with environmental variables.

Fig. 5. (a) Scatterplot illustrating adult *M. thornei* fractional presence (y- axis) as a function of H. forbesii density (x- axis) at the stand level. (b) Scatterplot illustrating larval *M. thornei* fractional presence as a function of *H. forbesii* DBH (x- axis) at the stand level.

Fig.6. Summary of results from *M. thornei* larval rearing experiment. Top panel shows survival of caterpillars reared on foliage from trees in three different age classes (no significant differences in survival). Bottom panel shows weights (means and standard errors) of pupae reared from caterpillars on the same three types of foliage. Lower case letters indicate significant differences at P = 0.05.

Fig. 7. Graph illustrating the percent of stands (y- axis) that *M. thornei* adults, larvae, adults and larvae, and adults or larvae were seen in (top panel) and percent of points *M. thornei* adults and larva were seen (lower panel).

Fig. 1

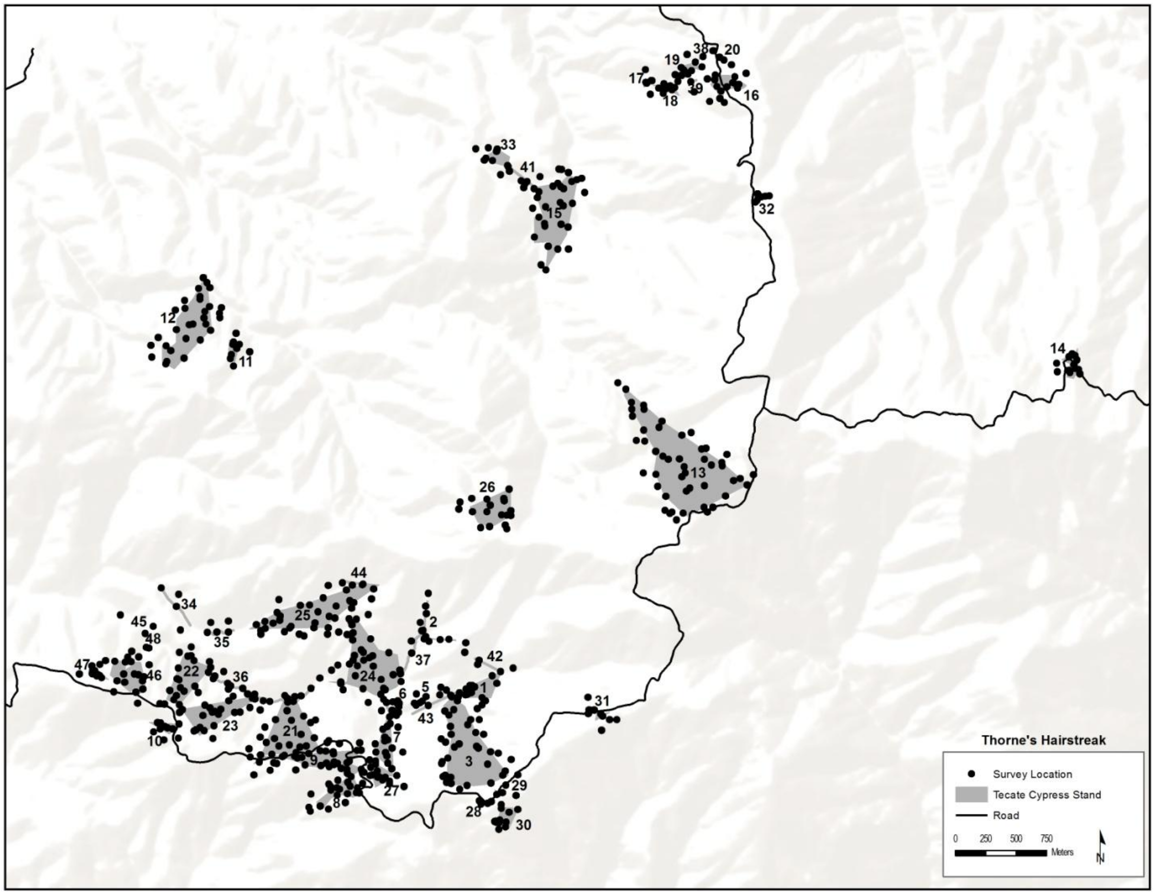
Thorne's Hairstreak
Survey Location
Tecate Cypress Stand
Road
0 250 500 750
Meters
N

Fig.2

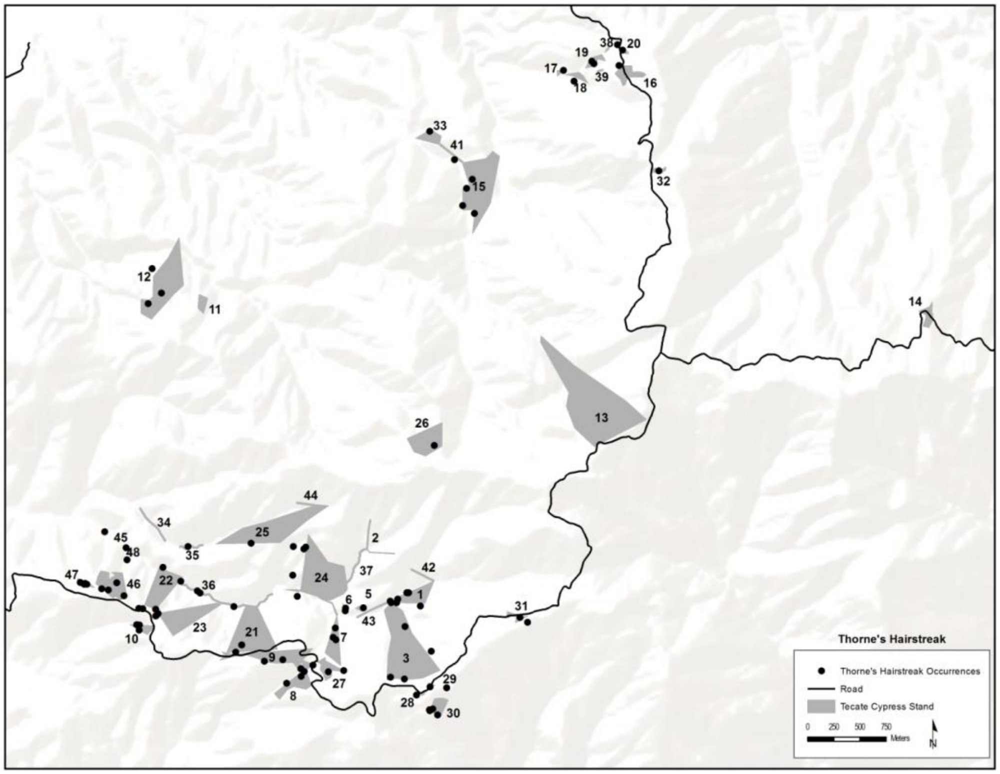
Thorne's Hairstreak
Thorne's Hairstreak Occurrences
Road
Tecate Cypress Stand
0 250 500 750
Meters
N
1
2
3
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
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Fig. 3

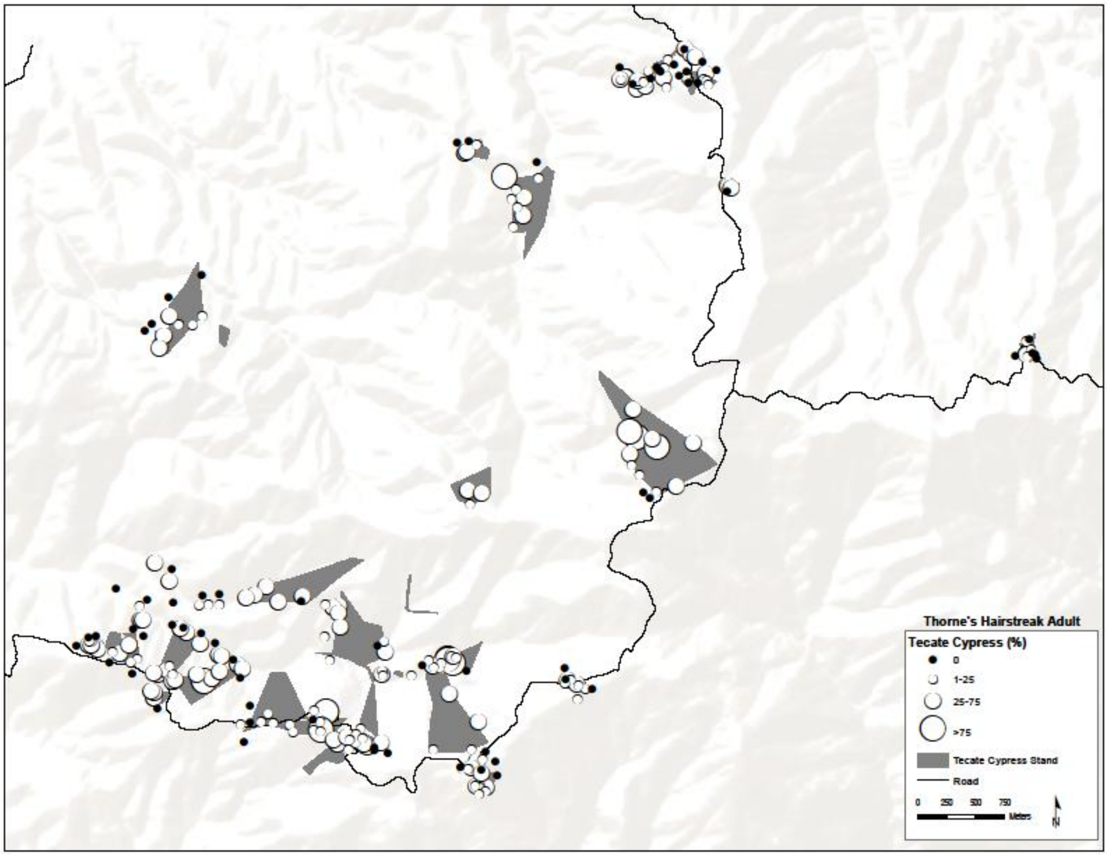

Thorne's Hairstreak Adult
Tecate Cypress (%)
0
1-25
25-75
>75
Tecate Cypress Stand
Road
0 250 500 750
Meters
N

Fig. 4

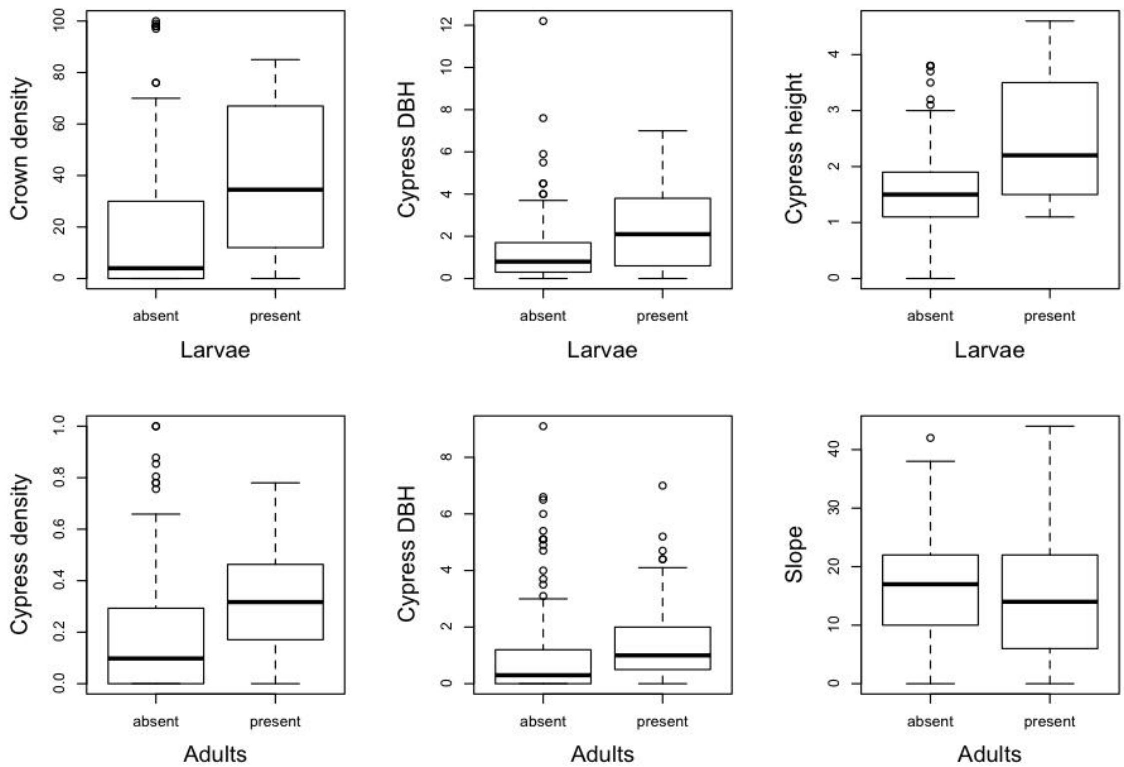
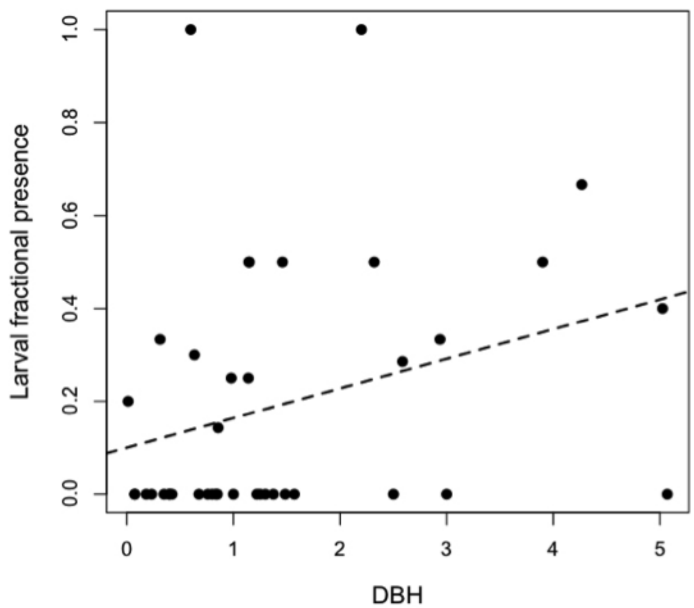

Crown density
Larvae
Cypress DBH
Larvae
Cypress height
Larvae
Cypress density
Adults
Cypress DBH
Adults
Slope
Adults
absent
present

Fig. 5

(a)


Larval fractional presence
0.0
0.2
0.4
0.6
0.8
1.0
0
1
2
3
4
5
DBH

(b)

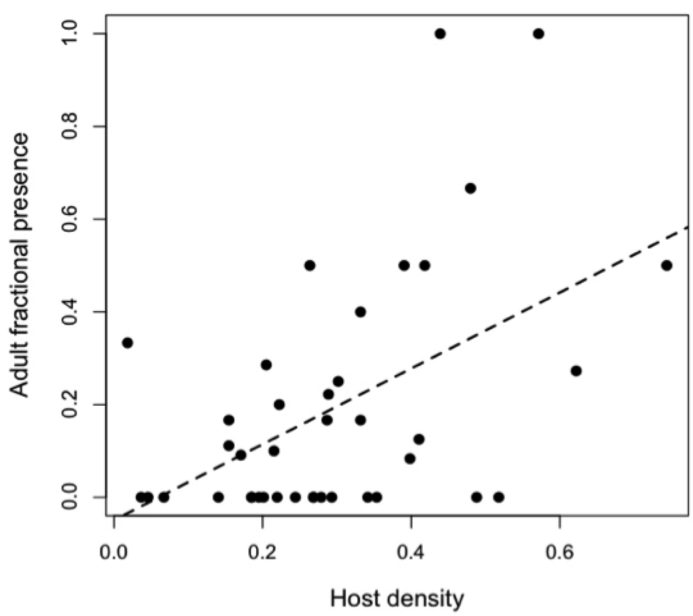
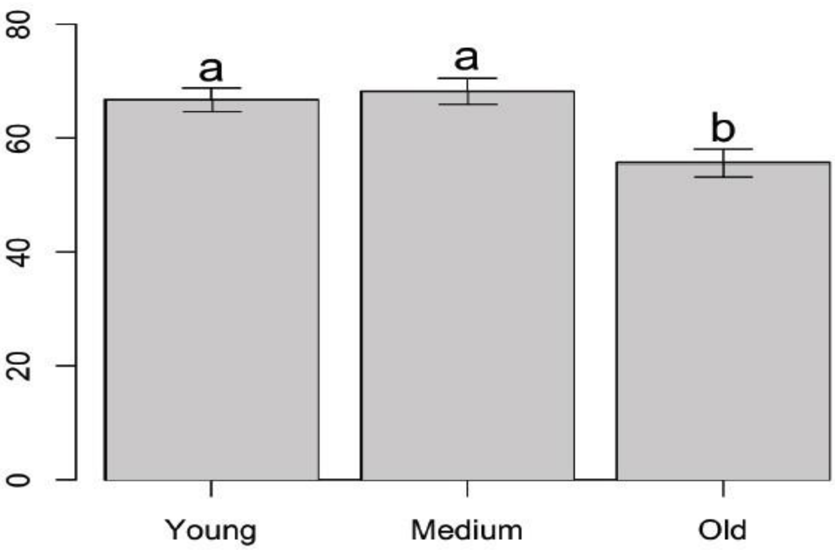

Adult fractional presence
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
Host density

Fig. 6


80
60
40
20
0
a
a
b
Young
Medium
Old

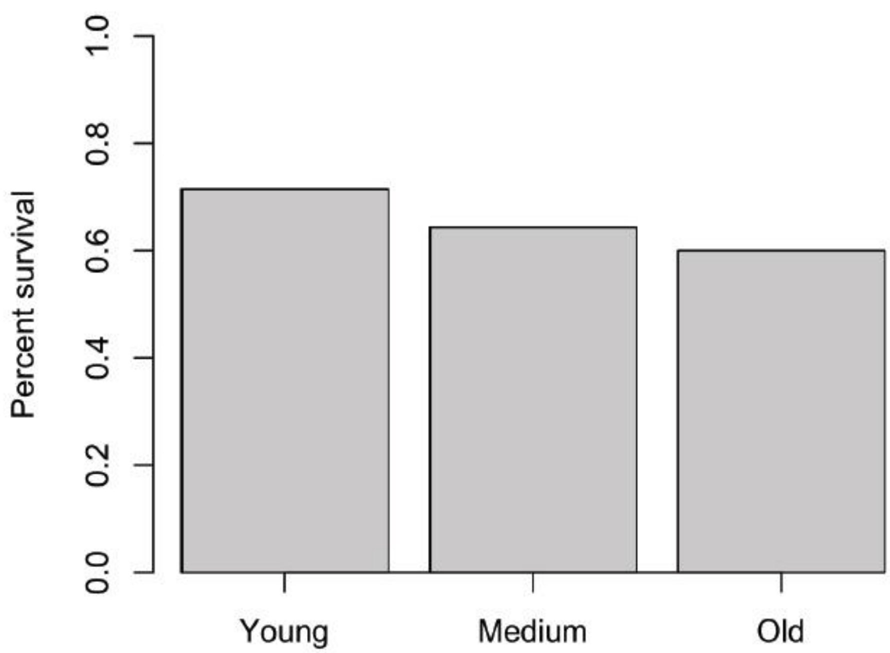
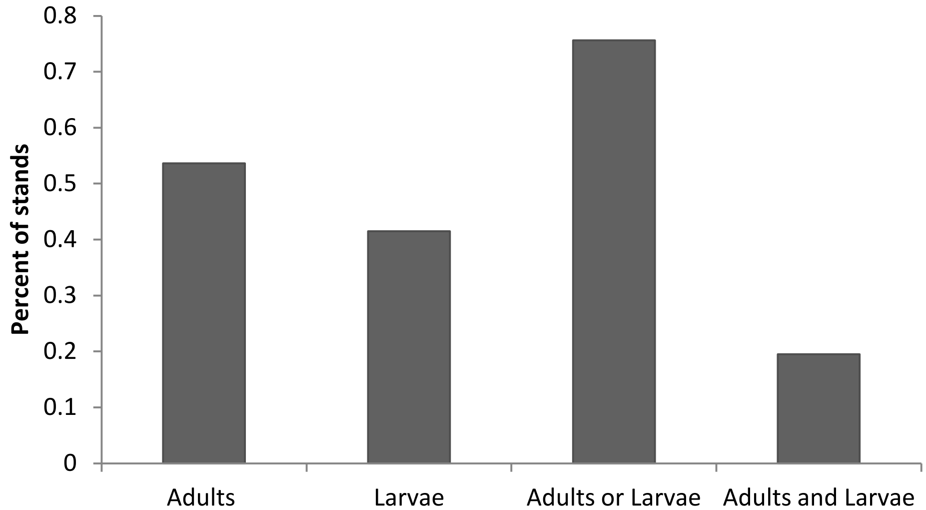
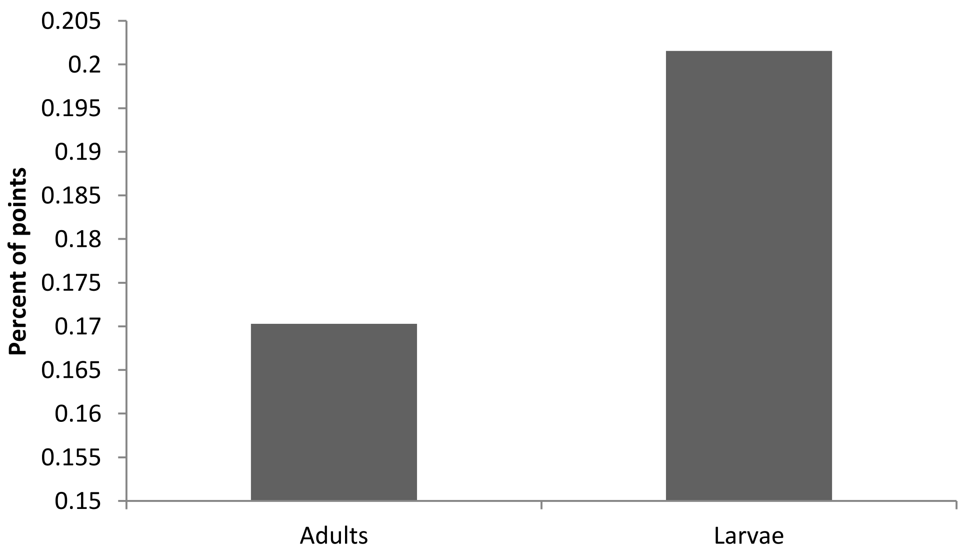

Percent survival
1.0
0.8
0.6
0.4
0.2
0.0
Young
Medium
Old

Fig. 7


0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Percent of stands
Adults
Larvae
Adults or Larvae
Adults and Larvae


0.205
0.2
0.195
0.19
0.185
0.18
0.175
0.17
0.165
0.16
0.155
0.15
Percent of points
Adults
Larvae

Appendix 1: Summary

Stand #	UTM coordinates (N,E)	Acres	Total plots mapped	Plots surveyed for vegetation	Percent surveyed for vegetation	Plots surveyed for *M. thornei*	Total adult *M. thornei* observed
1	512297.8, 3604681.3	10	18	11	61.11	10	5
3	512442.6, 3604294.8	51.4	27	17	62.96	2	9
5	511926.7, 3604594.8	0.2	6	2	33.33	0	0
6	511798.9, 3604567.7	8.7	6	6	100	4	2
7	511683.9, 3604314.1	8.7	18	9	50	1	0
8	511449.1, 3603856.8	10.2	21	13	61.9	3	5
9	511266.1, 3604109.2	16	33	33	100	12	3
10	509891.9, 3604392.0	2.6	9	3	33.33	3	0
12	510158.4, 3607926.9	33.2	30	15	50	11	3

13	514561.7, 3606428.4	90.3	48	12	25	13	0
14	517380.9, 3607354.0	3.8	12	12	100	9	0
15	513130.7, 3608721.5	37.5	33	24	72.72	10	9
16	514581.7, 3609694.6	6.2	15	11	73.33	10	0
17	513843.8, 3609704.1	0.4	6	6	100	6	1
18	514040.2, 3609683.2	1.7	9	9	100	7	0
19	514172.3, 3609790.4	2.5	9	9	100	6	2
20	514482.5, 3609896.6	0.3	3	2	66.66	3	0
21	510809.7, 3604241.6	31.2	24	8	33.33	4	3
22	509942.5, 3604623.5	17.1	18	8	44.44	6	1
23	510310.1, 3604500.7	19.1	24	11	45.83	8	1
24	511507.3, 3605013.8	41.2	39	8	20.51	7	2

25	510819.3, 3605315.0	36.6	36	10	27.77	7	0
26	512648.9, 3606147.5	16.1	18	12	66.66	3	0
27	511621.0, 3604035.7	5.1	15	15	100	11	2
28	512531.6 3603769.2	0.2	3	3	100	3	0
29	512654.6, 3603855.6	0.1	3	2	66.67	2	0
30	512684.7, 3603614.9	4.6	9	9	100	8	2
31	513368.3, 3604539.2	1.6	9	9	100	9	1
32	514816.9, 3608824.9	1.1	6	6	100	3	0
33	512519.1, 3609086.8	4.6	9	9	100	6	5
34	509838.9, 3605546.1	0 (linear)	4	4	100	4	0
35	510218.2, 3605178.9	1 (linear)	4	4	100	4	0
36	510227.7, 3604849.1	2 (linear)	12	7	58.33	5	8

37	511903.5, 3605008.8	3 (linear)	4	2	50	1	0
38	514397.3, 3609972.3	4 (linear)	2	1	50	2	1
39	514208.4, 3609720.1	5 (linear)	2	2	100	2	0
43	512226.0, 3604660.4	9 (linear)	4	2	50	2	3
45	509705.2, 3605168.9	11 (linear)	2	2	100	2	0
46	509616.9, 3604836.3	13.2	18	18	100	8	2
47	509305.2, 3604820.2	1.3	9	9	100	9	5
48	509715.0, 3605054.2	0.2	3	3	100	3	0
		Average: 13.76	Total: 624	Total: 360	Average: 73.27	Total: 229	Total: 75

Appendix 2: Pairwise Mantel results at the point level with two response variables and two life stages

	Variable	Correlation Coefficient	P
Larva Presence/Absence			
	Crown density of points	0.194	**0.002**
	Average Tecate cypress DBH (diameter at breast height)	0.194	**0.002**
	Average Tecate cypress height	0.162	**0.002**
	Distance between points	-0.063	**0.038**
	Tecate cypress density	0.072	**0.050**
	Slope of point	0.050	0.181
	Leaf Litter, Rock, and Bare Ground	-0.062	0.256
	Density of woody plants, excluding Tecate cypress	-0.028	0.414
	Woody richness, excluding Tecate cypress	-0.023	0.558
	Stand of stand	0.015	0.750
	Herbaceous richness	0.011	0.804
	Herbaceous density	-0.011	0.828
	Density of grasses	0.0002	0.996

	Variable	Correlation coefficient	P
Larva Abundance			
	Woody richness, excluding Tecate cypress	0.189	0.063
	Density of woody plants, excluding Tecate cypress	-0.122	0.194
	Slope of plot	-0.118	0.228
	Herbaceous richness	-0.111	0.291
	Herbaceous density	-0.145	0.297
	Average Tecate cypress DBH (diameter at breast height)	-0.081	0.414
	Distance between points	-0.107	0.429
	Density of leaf litter, rock, and bare ground	-0.133	0.430
	Size of stand (nearest to points)	-0.107	0.459
	Crown density of points	-0.041	0.565
	Density of grasses	0.062	0.723
	Tecate cypress density	0.029	0.758

	Variables	Rho	P
Adult Presence/Absence			
	Tecate cypress density	0.118	**0.001**
	Average Tecate cypress DBH (diameter at breast height)	0.134	**0.001**
	Slope of plot	0.054	**0.021**
	Herbaceous density	-0.060	**0.030**
	Distance between points	-0.042	**0.032**
	Density of woody plants, excluding Tecate cypress	0.034	0.058
	Herbaceous richness	-0.016	0.532
	Woody richness, excluding Tecate cypress	0.011	0.657
	Size of stand (nearest to point)	0.008	0.775
	Density of grasses	0.008	0.825
	Density of leaf litter, rock, and bare ground	0.003	0.924

	Variables	Rho	P
Adult Abundance			
	Density of woody plants, excluding Tecate cypress	-0.08704123	0.056
	Crown density of points	0.06044370	0.186
	Density of leaf litter, rock, and bare ground	-0.1032342	0.197
	Size of stand (nearest to point)	0.067530191	0.243
	Tecate cypress density	0.05181012	0.292
	Density of grasses	0.0756494954	0.357
	Herbaceous density	0.04157301	0.588
	Woody richness, excluding Tecate cypress	0.02281725	0.642
	Average Tecate cypress DBH (diameter at breast height)	0.03540878	0.651
	Herbaceous richness	-0.02679210	0.716
	Slope of points	-0.01803671	0.797
	Average Tecate cypress height	-0.005209954	0.937

Appendix 3. Pairwise Mantel results at the stand level with two response variables and two life stages

	Variables	Rho	P
Larva Fraction Seen			
	Average Tecate cypress DBH (diameter at breast height)	0.178	**0.027**
	Density of woody plants, excluding Tecate cypress	0.091	0.153
	Tecate cypress density	0.087	0.231
	Density of grasses	-0.056	0.528
	Density of leaf litter, rock, and bare ground	-0.056	0.552
	Herbaceous density	0.035	0.653
	Herbaceous richness	-0.028	0.741
	Slope of stands	0.013	0.872
	Distance between stands	-0.009	0.890
	Size of stand	0.014	0.905
	Woody richness	0.008	0.939

	Variables	Rho	P
Larva Abundance			
	Density of leaf litter, rock, and bare ground	-0.200	**0.045**
	Size of stand	0.151	0.077
	Average Tecate cypress DBH (diameter at breast height)	0.130	0.109
	Herbaceous richness	-0.115	0.147
	Distance between stands	-0.069	0.265
	Density of grasses	-0.099	0.271
	Herbaceous density	-0.062	0.446
	Woody richness	0.068	0.473
	Tecate cypress density	0.024	0.786
	Density of woody plants, excluding Tecate cypress	-0.015	0.841
	Slope of stand	-0.008	0.901

	Variables	Rho	P
Adult Fraction Seen			
	Tecate cypress density	0.229	**0.004**
	Herbaceous density	-0.104	0.139
	Woody richness	-0.121	0.152
	Herbaceous richness	-0.111	0.161
	Slope of stand	0.086	0.213
	Distance between stands	-0.070	0.26
	Density of leaf litter, rock, and bare ground	-0.099	0.298
	Average Tecate cypress DBH (diameter at breast height)	0.058	0.541
	Density of grasses	0.042	0.618
	Size of stand	0.048	0.645
	Density of woody plants, excluding Tecate cypress	-0.017	0.804

	Variables	Rho	P
Adult abundance			
	Size of stand	0.208	**0.023**
	Woody richness, excluding Tecate cypress	-0.156	**0.046**
	Density of woody plants, excluding Tecate cypress	-0.113	0.068
	Density of leaf litter, rock, and bare ground	-0.116	0.214
	Distance between stands	-0.076	0.214
	Herbaceous density	-0.085	0.245
	Herbaceous richness	-0.086	0.311
	Tecate cypress density	-0.071	0.364
	Density of grasses	0.059	0.517
	Average Tecate cypress DBH (diameter at breast height)	-0.043	0.621
	Slope of stand	-0.027	0.723