# Short-term Responses of Terrestrial Ants Populations to Forest Thinning in the Santa Cruz Mountains

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## ABSTRACT

As wildfires increase in frequency and intensity in California, forest thinning has emerged as a pivotal silvicultural strategy to mitigate fire risks and enhance ecosystem resilience. This study examined the ecological effects of forest thinning on terrestrial ant populations within Santa Cruz, California. Employing ants as bioindicators, we set up pitfall-traps to sample them over four sampling periods in two years of time. We then assessed changes in their abundance, species richness, and community composition across nine sites using a randomized block design. Our results reveal that post-thinning, the total abundance of ants significantly declined, with the most substantial decrease observed in the high canopy retention treatment. Similarly, species richness consistently diminished across all thinning intensities. Notably, statistical analysis highlighted a significant relationship between environmental factors and ant abundance pre-thinning, with temperature positively correlated and humidity negatively correlated. However, these effects lessened post-thinning, indicating that thinning alters microclimatic conditions influencing ant populations. Seasonal analysis further demonstrated significant variations, with ant abundance significantly reduced in winter compared to spring. Despite extensive thinning, the ants community composition showed moderate but not statistically significant shifts. These results underline the intricate dynamics between forest management practices and ant population responses, suggesting that both anthropogenic and natural factors should be carefully considered to sustain biodiversity and ecosystem health. Future research should continue to explore the interactive effects of seasonality and environmental management practices to refine our strategies for biodiversity conservation in forested ecosystems.

## KEYWORDS

forest ecology, ant biology, population ecology, ecological management, seasonal variations

# INTRODUCTION

Wildfires have long played a crucial role in shaping California's ecosystems, contributing to the formation of the state's diverse landscapes. However, the past few decades have witnessed a dramatic increase in both the frequency and severity of these wildfires, escalating risks to the environment, public health, and the economy (Cova et al. 2023). Factors contributing to this increase include climate change, human expansion into fire-prone areas, and historical forest management practices (Qiu et al. 2022). In response to this growing threat, forest thinning has been widely implemented as a silvicultural strategy to reduce fire risk (Liu et al. 2019, Yu et al. 2022). This technique involves selectively removing potentially hazardous vegetation—including dense tree cover, shrubs, bushes, and grasses—and establishing strategic vertical fuel breaks that effectively limit the spread of the most destructive crown fires. Thinning also aims to restore natural forest conditions, which can withstand fires better than unmanaged forests (Graham et al. 2004, Greenberg et al. 2010). However, previous research efforts on forest thinning's ecological effects have been limited, given the relatively recent application of thinning for ecological restoration (Dwyer and Mason 2018).

Understanding the extensive ecological impacts of forest thinning is crucial for developing informed and effective forest management strategies that align with conservation and sustainability goals. By creating openings in the canopy at various scales, thinning enhances light availability and increases spatial pattern variability in the forest understory (Flathers et al. 2016).These changes, in turn, elevate ground temperatures and alter the microclimate, with effects that vary according to the intensity of thinning. The resulting environmental modifications provoke complex cascading effects on the composition, structure, and reproductive dynamics of understory vegetation (Sanderson et al. 1995). Moreover, the accumulation of biomass on the forest floor alters the biophysical properties of soil, influencing nutrient cycling, resource heterogeneity, and microbial and fungal activities (Liu et al. 2019, Moreno et al. 2022, Pearce and Venier 2006). Furthermore, the altered forest canopy plays a crucial role—it buffers precipitation and regulates local temperature by creating a vertical light gradient (Bruijnzeel and Vertessy 2004, Prescott 2002, De Lombaerde et al. 2022, Pfeifer et al. 2018, De Frenne et al. 2019), ultimately affecting forest hydrology through changes in rainfall distribution, soil water absorption, and evapotranspiration processes (Aronson et al. 2014). Even though the general impacts of thinning are increasingly recognized, the specific effects on the diverse and dynamic wildlife populations within forest ecosystems have yet to be fully examined.

To understand these ecological consequences from natural environmental changes or anthropogenic management practices, scientists frequently utilize bioindicators, which are certain functional groups that reflect the state and dynamics of the environment (Campbell et al. 2018). Among the various bioindicators, arthropods, especially ants, stand out due to their sensitivity to environmental changes (Gerlach et al.2013, Borges et al. 2021). Ants are particularly valuable as bioindicators because of their abundance, widespread distribution, relative ease of collection, and sensitivity to ecological dynamics (King et al. 1998). They also play crucial roles in the food web and contribute significantly to ecosystem processes such as carbon and water flux, decomposition, and nutrient cycling (Bharti 2016, Lawes et al. 2017, Ribas et al. 2011). The population dynamics of ants are expected to be sensitive to forest thinning and its associated ecological changes. Climatic factors such as temperature, humidity, and precipitation significantly influence insect diversity within forest ecosystems by affecting resource availability and ecological conditions essential for various ant species. Additionally, seasonality — the recurrent temporal patterns of resource availability and climate fluctuations within a year — may also impact ant populations, along with their biotic interactions and community composition (Queiroz et al. 2023). Variations in the diversity and population size of ants can, in turn, have profound effects on ecosystem structure and functions, given their roles as herbivores, generalist predators, and facilitators of litter movement (Kendrick et al. 2015).

Despite the majority of studies focusing on coleoptera as a bioindicator, the response of ant communities to forest thinning remains less explored. The influence of varying thinning intensities on ants population also has not been thoroughly investigated. This knowledge would equip conservation scientists, landowners, and policymakers with critical insights necessary for implementing forest management that is both effective and sustainable. Such strategies are designed to reconcile the objectives of forest restoration with the need to mitigate ecological impacts on interconnected species. Furthermore, studying ants offers a window into broader ecological dynamics, shedding light on species interactions and the consequences of habitat modification on food web structures (Greenberg et al. 2010).This study posed several research questions centered on the effects of forest thinning and seasonal changes on ant populations: What is the effect of environmental variables (temperature and relative humidity) on total abundance of ants population? How do thinning across various treatments and seasonality affect the total abundance of ant population? How do thinning across various treatments and seasonality affect the species richness of ant population? Lastly, how do thinning across various treatments and seasonality affect community composition of ant population? I expected environmental variables would significantly affect ant populations and all of the three ant population parameters would be significantly different between thinning treatments and seasons.

## METHODS

### Study area

This study is conducted as part of a collaborative project involving Professor Kipling Will's lab and Professor Scott Stephen's lab, both within the Department of Environmental Science, Policy, and Management (ESPM) at UC Berkeley, along with the Amah Mutsun Land Trust. The research is located in the Ben Lomond Mountains within the San Vicente Redwoods Preserve in the Santa Cruz Mountains, California. This area, ranging in elevation from 2,640 to 2,680 feet, is characterized by a warm-summer Mediterranean climate. The predominant soil types are sandy loam and fine sandy loam, which are deep, moderately acidic, and well-drained (United States Department of Agriculture, 2009). The whole Ben Lomond Mountains experienced different levels of buring from the CZU Lightning Complex Fire of August 2020, which is regarded as the most severe wildfire Santa Cruz County has seen in over a century, as described by the Santa Cruz Civil Grand Jury. This catastrophic event burned for over a month, consuming more than 86,000 acres and severely impacting forests and surrounding communities. The specific region for this study was selected due to its minimal or low burn severity from the CZU fire, as determined by **Normalized Burn Ratio** (NBR) analysis conducted using *GoogleEarth Engine* and *ArcGIS Pro* (Figure 1). The NBR is an index designed to highlight burnt areas and assess burn severity. This site selection was critical, as areas with higher burn severity had insufficient vegetation remaining for effective thinning and biodiversity studies. The region is predominantly a mixed evergree forest, featuring large heritage oaks, such as Coast live oak, Canyon live oak, and Shreve oak, with a significant madrone component.

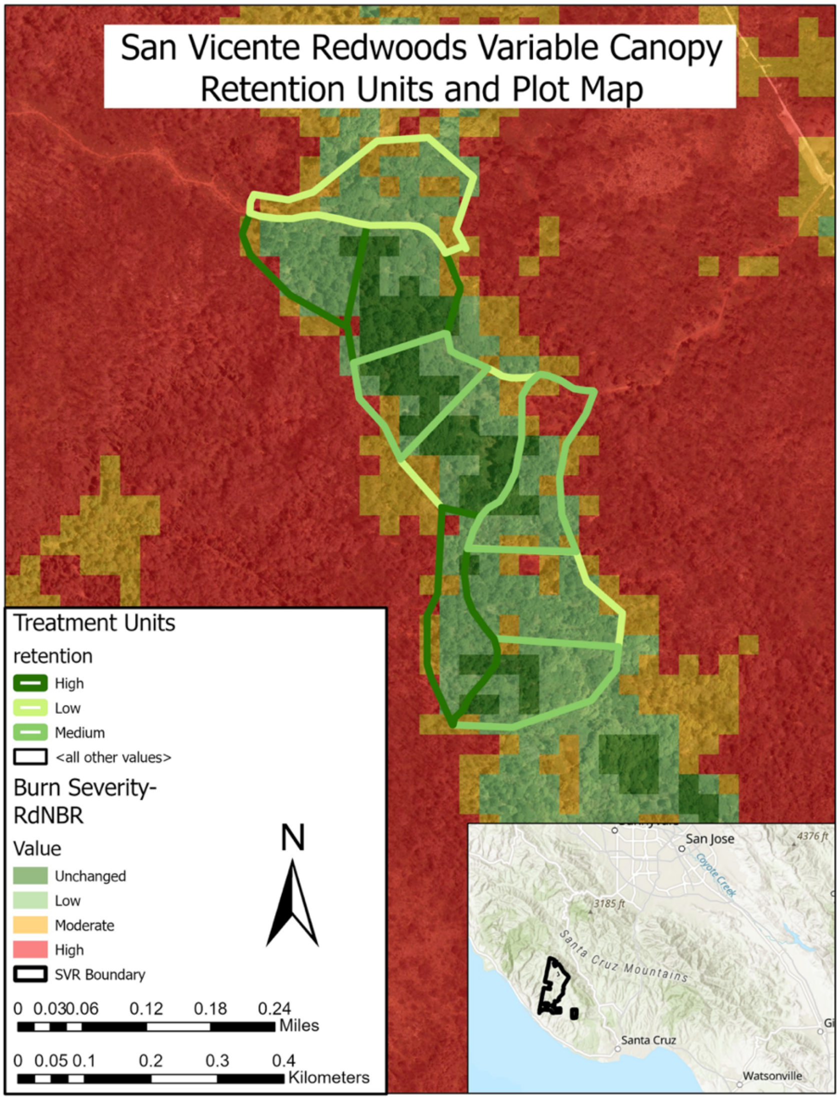


**Figure 1. Burn severity map of San Vicente Redwoods from the CZU fire in 2020**. The entire region was classified into four levels of burn severity based onthe Normalized Burn Ratio (NBR), from“Unchanged” as the lowest to “ High” as the highest. Our specific study area had dominantly unchanged to low burn severity. Map was made using ArcGIS Pro. Credit: Stephens Lab, UC Berkeley ESPM.

## Study organism

The primary study organisms in this research are terrestrial ants. Ants are classified within the order Hymenoptera and are renowned for their advanced eusocial behavior (Borowiec et al.2020). They represent one of the most ubiquitous and ecologically dominant groups, and they are among the most diverse faunal groups on Earth (Andersen 2021). It is estimated that there are over 15,700 described ant species, excluding numerous potentially undiscovered species (Schultheiss et al.

2022). According to a comprehensive review by Ward 2005, there are 281 species across 44 genera present in California.

## Study design

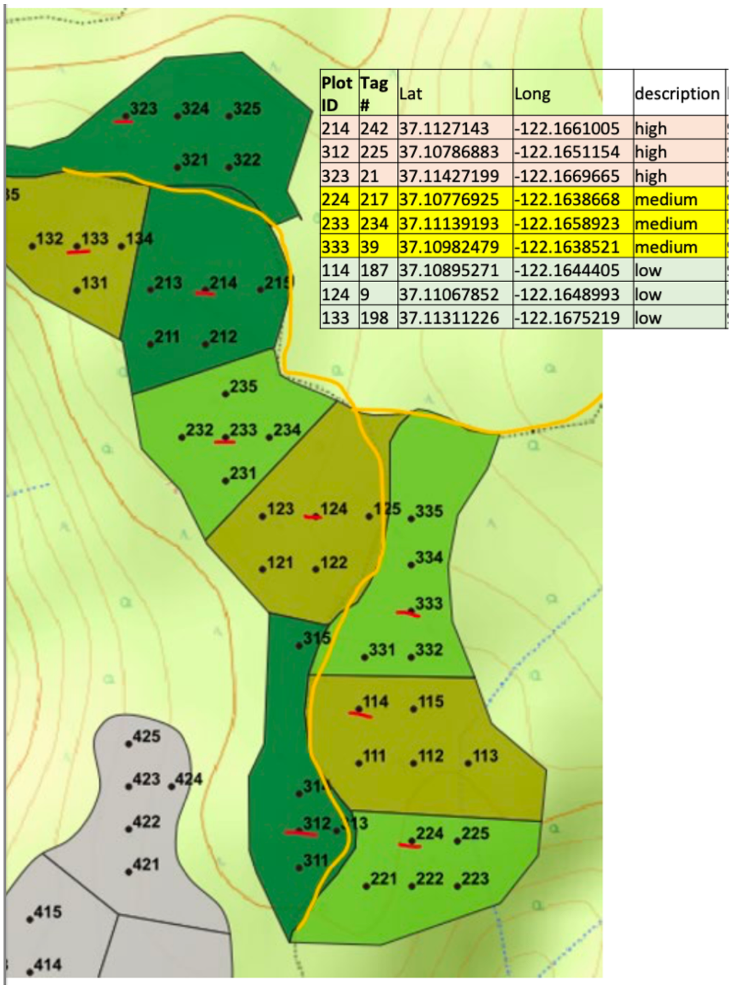
To evaluate the effects of varying forest thinning intensities on the abundance and species richness of terrestrial ants, we implemented a randomized complete block design. The study area was divided into nine similarly-sized sampling sites, each serving as an experimental unit and assigned a unique label. Each unit received one of three treatment intensities: high canopy retention (80%), medium canopy retention (50%), and low canopy retention (20%), with three units allocated to each intensity level. For clarity, these intensities will be referred to as "High," "Mid," and "Low" throughout this paper. The treatments varied in the percentage of forest canopy retained after thinning; for instance, the "High" treatment preserved 80% of the original forest canopy. This deliberate distribution aimed to highlight the contrasts between adjacent blocks. Figure 2 shows the field photos of our nine sampling sites with their labels, and Figure 3 details the specific treatment layout and assignments for these sites.

(214) (312) (323)

(224) (233) (335)

(115) (124) (133)

**Figure 2. Photos of the 9 experiment units of our study with corresponding site label below.** Photos were taken in Fall 2022 after various thinning treatments have been implemented. Credit: Will Lab, UC Berkeley ESPM.



| Plot ID | Tag # | Lat | Long | description |
|---|---|---|---|---|
| 214 | 242 | 37.1127143 | -122.1661005 | high |
| 312 | 225 | 37.10786883 | -122.1651154 | high |
| 323 | 21 | 37.11427199 | -122.1669665 | high |
| 224 | 217 | 37.10776925 | -122.1638668 | medium |
| 233 | 234 | 37.11139193 | -122.1658923 | medium |
| 333 | 39 | 37.10982479 | -122.1638521 | medium |
| 114 | 187 | 37.10895271 | -122.1644405 | low |
| 124 | 9 | 37.11067852 | -122.1648993 | low |
| 133 | 198 | 37.11311226 | -122.1675219 | low |

**Figure 3. Map showing distribution of specifc thinning intensity treatment to the nine total experiment units.** The table aside presents Plot ID (the unique 3-digit label), Latitude and Longitude, and description of canopy retention level corresponding to each of the 9 experiment unit. Credit: Will Lab, UC Berkeley ESPM.

## Terrestrial ants sampling

To effectively conduct ant sampling, we installed eight pitfall traps in each of the nine experimental units, resulting in a total of 72 traps. Starting from a central stake, we positioned the traps along two azimuths 90 degrees apart, with four traps along each direction, beginning 3 meters from the center (as illustrated in Figure 4). The traps consisted of standard 16 oz. (473 ml) polyethylene terephthalate (PET) cups, commonly known as “red party cups,” with a cup opening of 95 mm in diameter and a height of 121 mm. To protect the traps from rain, we covered the cups with 205 x 205 mm polycarbonate (Lexan) sheets, secured by plastic stakes (Figure 5). Each cup was placed into a PVC pipe tube, which was vertically buried to a length of 150 mm and had a nominal diameter of 4 inches (102 mm). These tubes served as fixed sampling points throughout the duration of the study.

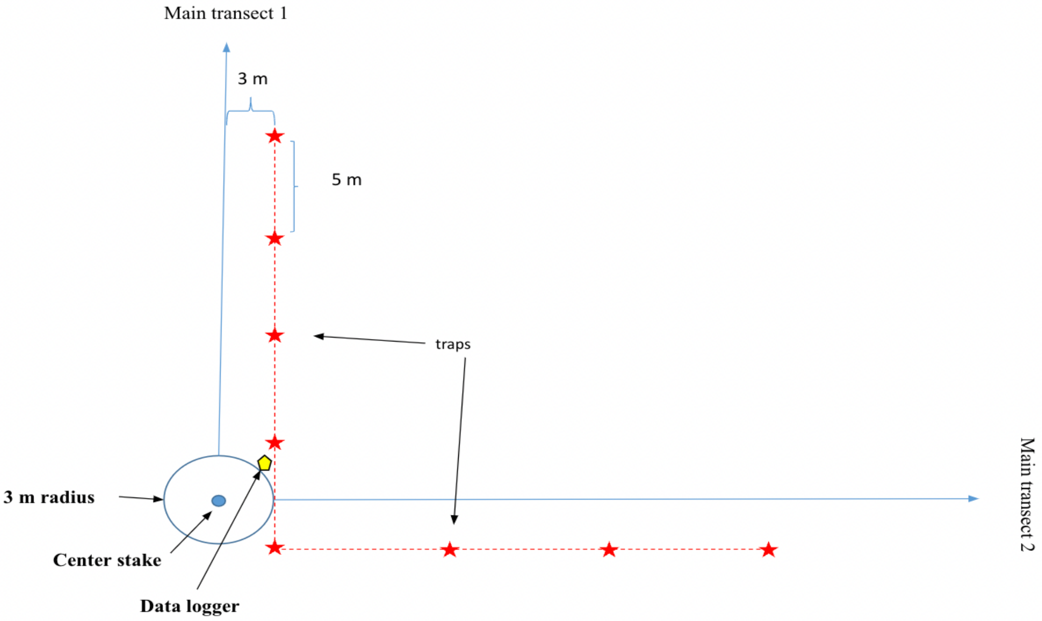


**Figure 4. Illustration of the 8 pitfall traps set-up at each of the experiment unit.** Traps are each separated by 5 meters, and a logger collecting environmental data is placed at each unit. Credit: Will Lab, UC Berkeley ESPM

**Figure 5. Pitfall trap set-up process photo.** It involes digging deep hole underground (5A) and covering trap with plastic rain shield stabalized by one plastic stake at each corner stabilizing it (5B).

## Environmental data collection

To gather environmental data at each sampling site, we installed a TinyTag Explorer® data logger near the central stake (Figure 6). The logger was set to record temperature and relative humidity at three-minute intervals during active sampling periods. Data retrieval was conducted using TinyTag Explorer software, from which we calculated the average temperature and humidity values for each site during each sampling period.

**Figure 6. TinyTag Explorer logger set up at each sampling site**. Credit: Will Lab, UC Berkeley ESPM

Based on estimates of seasonal ground arthropod activity in the region (Weary et al. 2019) as well as local expertise from my mentor, Kipling Will, we determined that two four-week sampling periods per year would suffice to obtain representative samples. The first sampling interval runs from mid-November to mid-December, followed by a second period in May. Each of these four-week periods is divided into two two-week segments. This segmentation is crucial as extending trap deployment beyond two weeks leads to significant sample degradation and increased disturbances to the traps. A typical sampling cycle is structured as follows: traps and data loggers are set up on the first day; on day 14, samples are collected and propylene glycol—a killing agent and preservative that is safe for mammals—is refreshed; on day 28, final samples are gathered, pipes are sealed, and data loggers are retrieved. Our initial sampling phases were conducted in November 2021 and May 2022, before the implementation of canopy thinning treatments in the summer to fall of 2022. These sessions provided baseline data on the ant populations prior to any treatment interventions. Subsequent sampling sessions were conducted in November 2022 and Spring 2023, following the thinning treatments. During active sampling, each trap cup is filled with approximately 150 ml of 100% propylene glycol. When not in active use, the PVC pipes are capped to prevent unintended captures. Collected samples are transferred into tagged whirl-packs containing ethanol and stored under refrigeration. In the laboratory, we sorted, mounted, identified ants to the species level using identification keys under microscope, and quantified all species.

## Analysis

### *Effect of environmental variables*

The total abundance of ants was assessed by summing the counts of individual ants collected from each sampling site during specific sampling periods throughout the year. Species richness was determined by counting the distinct species identified at each site during each sampling period. To explore the effects of environmental factors on ant populations, I applied a Generalized Additive Model (GAM) using the **gam** function from the **mgcv** package in RStudio. Unlike linear regression, GAM allows for the smooth modeling of nonlinear relationships between predictors and the response variable. This method is particularly well-suited for ecological data, where relationships between continuous variables such as temperature are often nonlinear and complex (Hastie and Tibshirani, 1990). The **mgcv** package implements GAMs with penalized regression splines, which automatically control the degree of smoothness to prevent overfitting.

### *Effect of thinning, treatment, and seasonality on total abundance and species richness*

To evaluate the effects of varying thinning intensities and seasonal changes on ant populations, I utilized Generalized Linear Mixed-effects Model (GLMM) through the **glmmTMB** function in the **glmmTMB** package in RStudio. The response variable was either abundance or species richness, based on the specific research question. The fixed effects included thinning status (either "pre" - before thinning or "post" - after thinning), treatment intensity ("high", "mid", and "low"), and season ("winter" or "spring"), with the sampling site designated as a random effect. A Poisson distribution was employed to model ant population counts. For the assessment of fixed effects' relative importance, the **glmm.hp** package was used to calculate their marginal $R^2$, indicating the proportion of variance explained by each predictor (Lai et al. 2022).

### *Effect of thinning, treatment, and seasonality community composition*

To analyze the community composition of ant populations, I conducted Non-metric Multidimensional Scaling (NMDS) based on a Bray-Curtis distance matrix, using the **metaMDS** function in the **vegan** package. Subsequently, an Analysis of Similarity (ANOSIM) was performed with the **anosim** function, employing 9,999 random permutations to assess the significance of differences in population composition.

## RESULTS

### Ants inventory and effects of environmental variables

We identified 11 distinct ant species across seven genera in our study area. Notably, *Formica Integroides* was overwhelmingly the most numerous, surpassing the combined counts of all other species. Due to their exceptionally high numbers, we limited the count to 25 individuals per trap, although most traps contained more than this figure. Therefore, for *Formica integroides*, we analyzed their relative abundance based on the percentage of traps per sampling site that contained at least 25 individuals, rather than the total count. We visualized their relative abundance as a qualitative heatmap (Figure 7) instead of conducting quantitative statistical tests. For this reason, we also excluded them from population composition analysis, as their exceedingly large number compared to all other ants would exert a disproportionally high bias. *Formica integroides* are still included for species richness analysis, as they represented one unique species. On the other hands, we calculated the abundance of other ant species—collectively referred to as 'other ants' in this study, which primarily included *Stenamma sequoiarum, Temnothorax nevadensis, and Aphaenogaster occidentalis*—by actual numbers. Additional species identified were *Formica accreta* and two unidentified *Formica* species, along with fewer occurrences of *Prenolepis imparis, Liometopum luctuosum, Camponotus vicinus,* and *Camponotus laevigatus.* Pictures of all ant species are shown in Appendix.

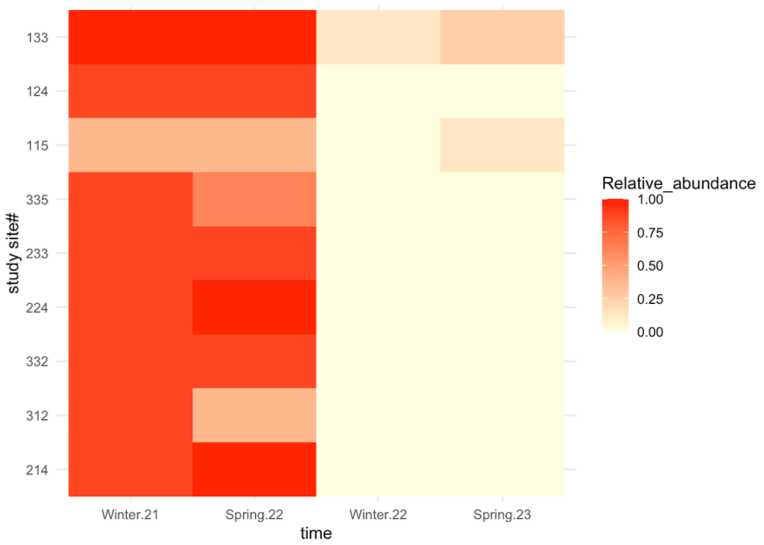


**Figure 7. Heatmap of *Formica Integroides* relative abundance.** The map shows the proportion of traps (from 0 to 1) with at least 25 *Formica Integroides* across all sampling sites through the four sampling seasons.

Across all study sites, we observed a general decrease in average temperature and an increase in relative humidity during both spring and winter seasons. Despite these changes, no significant differences in average temperature or relative humidity were detected among the 'high,' 'mid,' and 'low' treatment sites. A Generalized Additive Model analysis demonstrated a statistically significant influence of both average temperature (p-value = 0.00046, $R^2 = 0.702$) and relative humidity (p-value = 0.00344, $R^2 = 0.488$) on the total abundance of other ants before thinning. The abundance of these ants increased non-linearly with temperature and decreased linearly with humidity. After thinning, these relationships persisted, though the influence of environmental factors was notably diminished, indicated by lower $R^2$ values for temperature (p-value = 0.0603, $R^2 = 0.367$) and humidity (p-value = 0.0064, $R^2 = 0.342$). Furthermore, I conducted linear regression analysis of the relationship between the relative abundance of *Formica integroides* and the total abundance of other ants, which showed a slight, albeit non-significant, negative correlation (t = -0.376, p-value = 0.7181). This finding ensures that Formica Integroides does not significantly confound the observed effects of environmental factors. Plots of my GAM are shown in Figure 8.

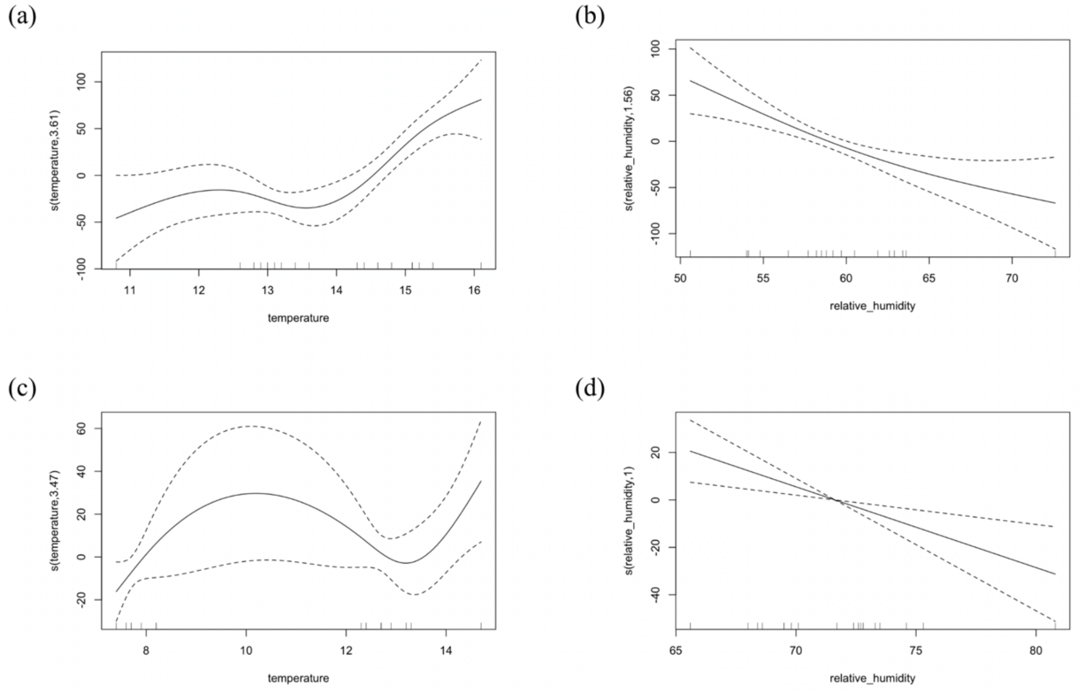


**Figure 8. Plots of all my GAMs analysis.** The central, full line represents the estimated main smooth effect of the predictor variable on the response variable: (a) temperature pre-thinning, (b) relative humidity pre-thining, (c) temperature post-thinning, and (d) relative humidity post-thinning. This line shows how other ants abundance changes as the predictor variable changes, and is accompanied by two other dash lines which represent the upper and lower bounds of 95% confidence interval for the smooth.

## Total abundance of other ants

Results from my generalized linear mixed model revealed a statistically significant decrease in the total abundance of other ants post-thinning compared to pre-thinning across all treatments (p-value < 0.0001). However, the magnitude of this reduction varied substantially among the treatments (Figure 9). The greatest decline in ant abundance was noted in the high treatment group, followed by the mid treatment group, with the smallest reduction observed in the low treatment group. Statistically significant differences in ant abundance between pre- and post-thinning conditions were evident in both the high (z = -2.405, p-value = 0.0069) and mid (z = -2.701, p-value = 0.016) treatments when compared to the low treatment. Nevertheless, no significant difference was found between the high and mid treatment groups. The *glmm.hp ()* function analysis indicated that thinning ($R^2 = 47.05$) and treatment ($R^2 = 52.95$) were similarly strong predictors of ant abundance. Additionally, the model results indicated slight variability in ant abundance (variance = 0.1565) across specific sampling sites, serving as random effects that were not explained by the thinning and treatment conditions. My generalized linear mixed model on seasonality revealed a statistically significant reduction in the total abundance of other ants during winter compared to spring (p-value < 0.0001). Additionally, the extent of the decline in ant abundance from pre- to post-thinning varied significantly between the seasons (Figure 10). The decrease was significantly less pronounced in winter than in spring, as indicated by an estimate of 0.874, a z-value of 7.826, and a p-value of 5.02e-15. A higher $R^2$ value associated with season (63.72) compared to thinning (36.27) suggests that seasonality had a stronger influence on the abundance of other ants than thinning practices did.

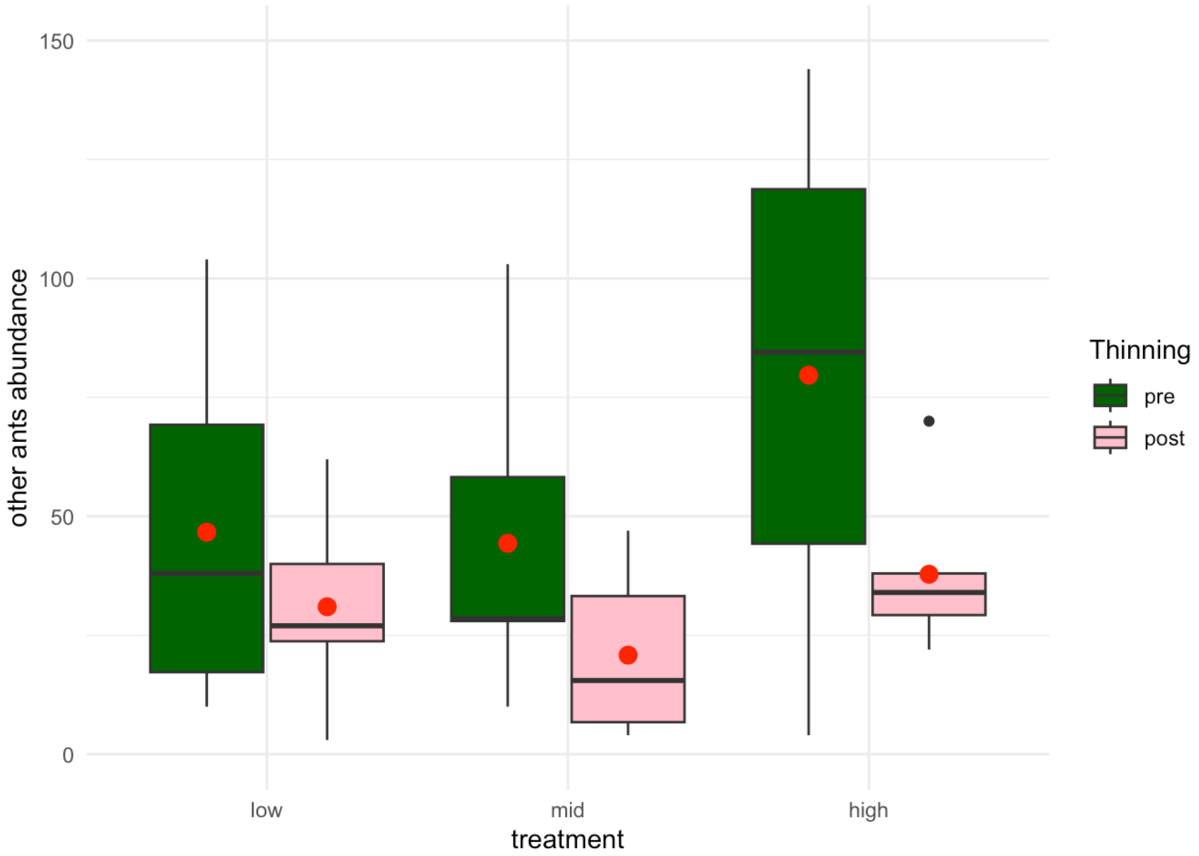


**Figure 9. Boxplot depicting the abundance of other-ants across different thinning treatments (low, mid, high) before and after thinning.** The boxplots are color-coded to distinguish between pre-thinning (green) and post-thinning (pink) conditions. Each box represents the interquartile range (IQR) of the abundance data, with the median indicated by a horizontal line within the box and the mean by a red dot. Outliers are represented as black dots. Boxplot created using *ggplot* in Rstudio.

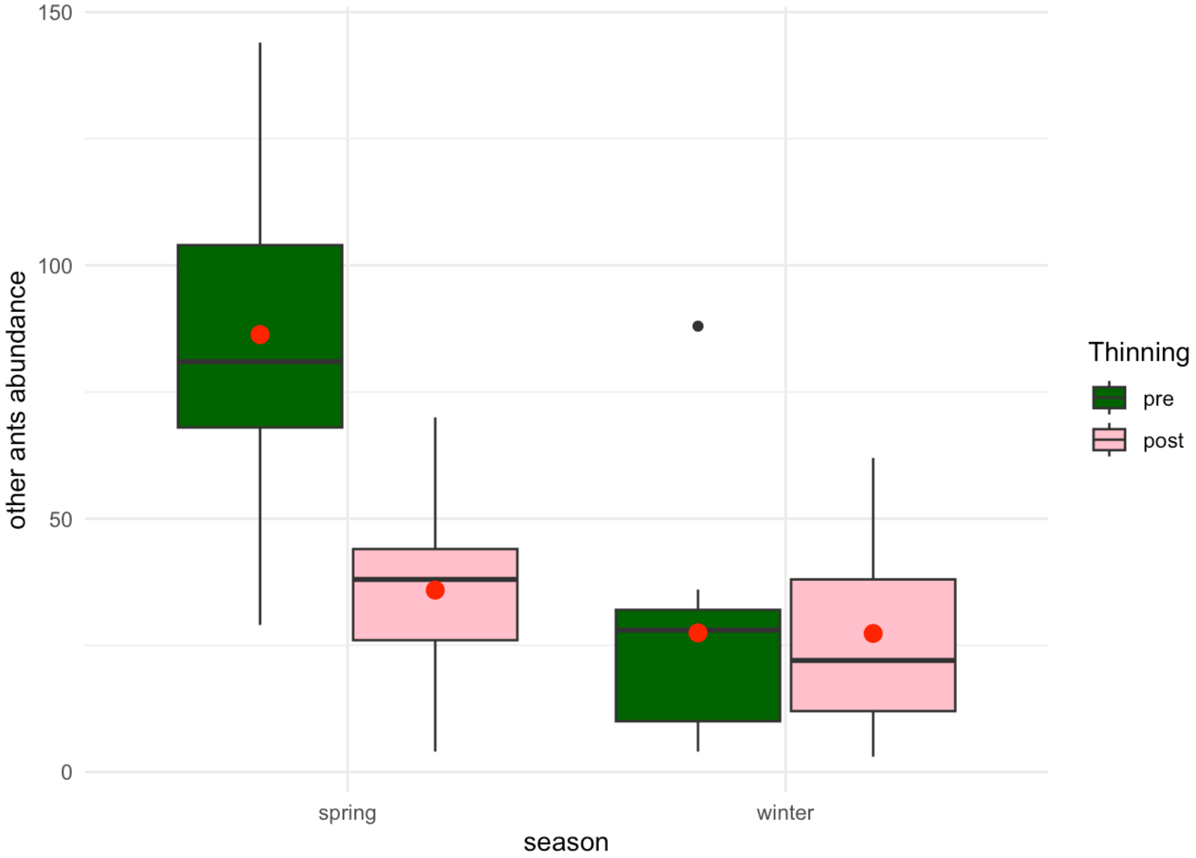


**Figure 10. Boxplot depicting the abundance of other-ants across different seasons (spring and winter) before and after thinning.**

## Species richness of ants

I observed a statistically significant decrease in the richness of all ant species post-thinning compared to pre-thinning across all treatments (p-value < 7.42e-12). Unlike the trends observed with total abundance, the magnitude of this reduction did not vary significantly among the treatments, with p-values remaining high (p-value = 0.713 for high vs low treatment, p-value = 0.781 for mid vs low treatment, p-value = 0.861 for high vs mid treatment). This uniformity in species richness reduction across treatments was corroborated by results from the glmm.hp() function analysis, indicating that thinning alone almost completely accounted for the differences in ant species richness ($R^2 = 99.78$), while the relative importance of the treatment was minimal ($R^2 = 0.22$). Furthermore, the GLMM analysis revealed no random effects attributable to specific sampling sites (variance = 0), suggesting that all observed differences in ant species richness were adequately explained by the fixed effects of thinning and treatment. The analysis of seasonality using my generalized linear mixed model demonstrated a statistically significant decrease in the richness of ant species during winter as compared to spring, with a compelling statistical significance (p-value < 2e-16). The reduction in ant species richness from pre- to post-thinning exhibited no significant seasonal variation (z = -1.079, p-value = 0.2804). Both season and thinning emerged as similarly potent predictors of ant species richness, with $R^2$ values of 47.94 and 52.06, respectively. These factors significantly outperformed treatment in predicting ant species richness. Boxplots showing my results are shown below as Figure 11 and Figure 12.

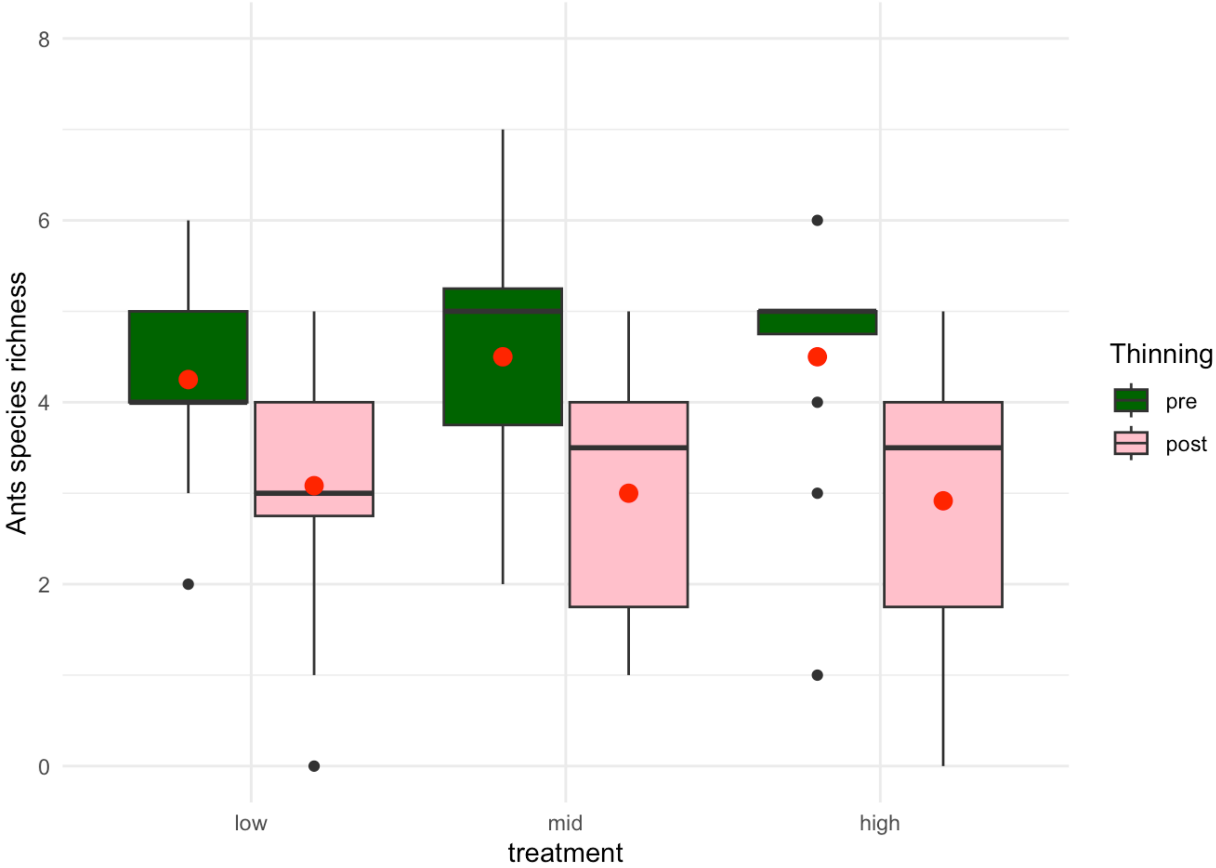


**Figure 11. Boxplot depicting the species richness of ants across different thinning treatments (low, mid, high) before and after thinning.**

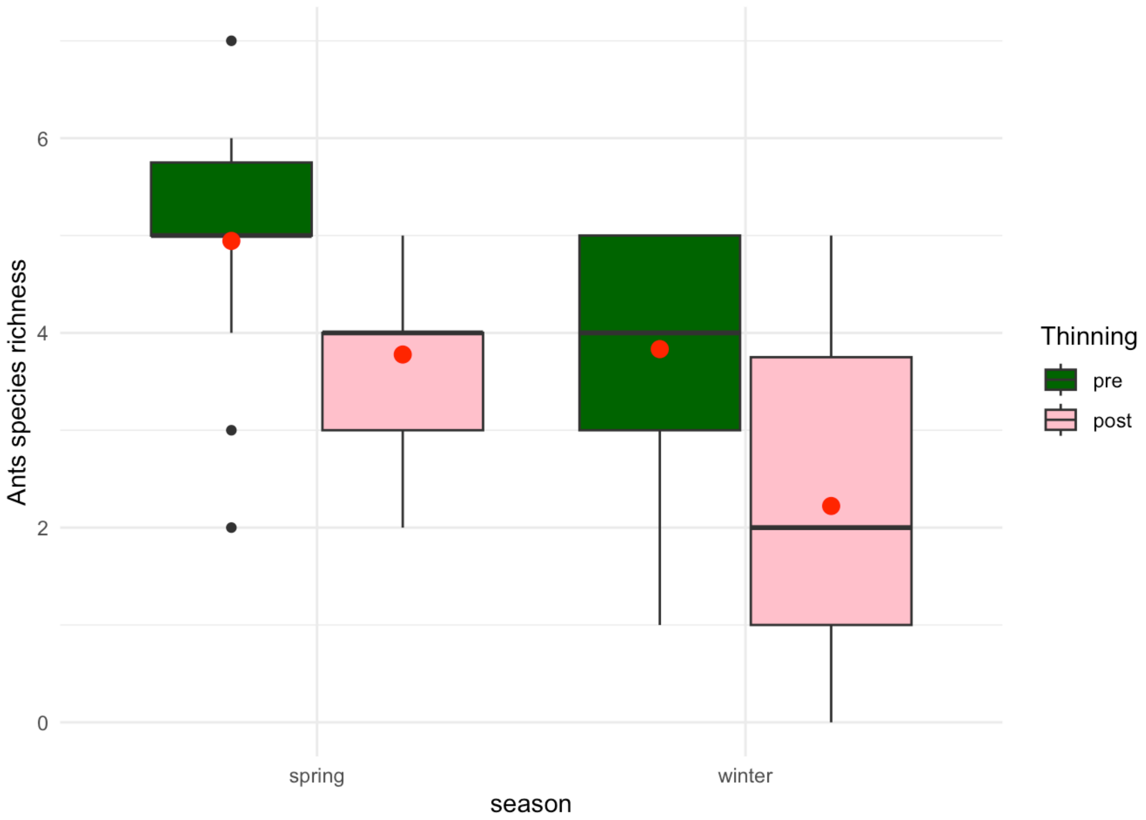


**Figure 12. Boxplot depicting the species richness of ants across different seasons (spring and winter) before and after thinning.**

## Community composition of other-ant populations

NMDS ordination plots, illustrating the community composition of ant populations and the impact of various fixed effects, were generated using the **ggplot** function in RStudio and are presented below as Figure 13 and Figure 14. The ordination achieved a low stress value of 0.081, indicating an excellent representation of the dissimilarities in species composition among the samples. Dimension 1 effectively discriminated between pre- and post-thinning conditions, while Dimension 2 allowed for the differentiation between treatments and seasonal variations. An Analysis of Similarity (ANOSIM) test indicated that the differences in ant community composition between pre-thinning and post-thinning were moderate but not statistically significant (p-value = 0.083), and the variations among treatments were minimal (p-value = 0.874). However, the composition of ant populations exhibited significant seasonal differences, with distinct community structures in spring and winter (p-value < 0.00001).

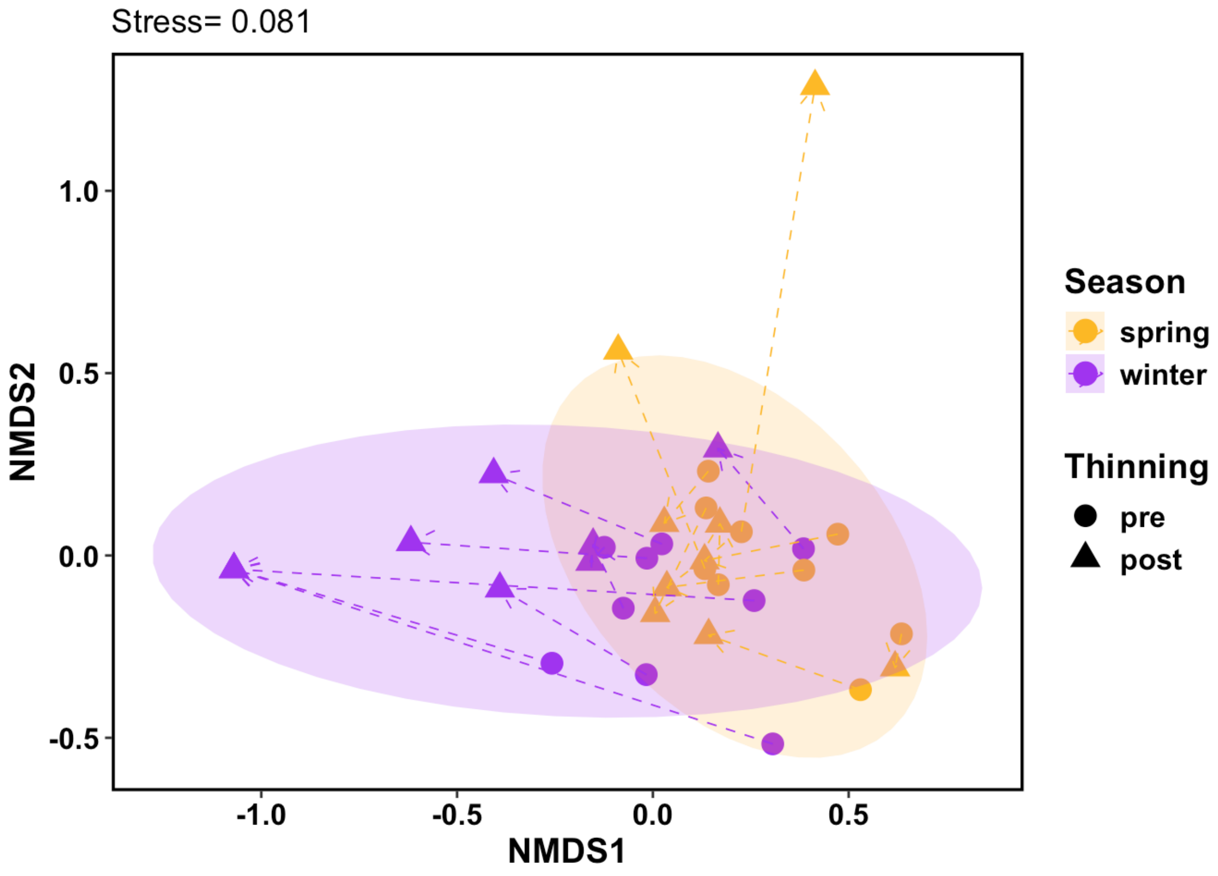


**Figure 13. Non-metric Multidimensional Scaling (NMDS) analysis illustrating the community composition differences of ant populations before and after thinning treatments, across two seasons.** Each point represents the ant community at a specific sampling site, with colors indicating the season (golden for spring, purple for winter) and shapes denoting the thinning treatment (circles for pre-thinning, triangles for post-thinning). The closer are two points on the plot, the more similar they are ub terms of ants population community composition. A 95% confidence interval ellipse encapsulate the centroid of the data points for each season is included, illustrating where the data points are most likely to fall in relation to different groups. Stress value of 0.081 indicates a good representation of the dissimilarities in two dimensions. Arrows represent the movement from pre- to post-thinning conditions, suggesting shifts in ant community compositions.

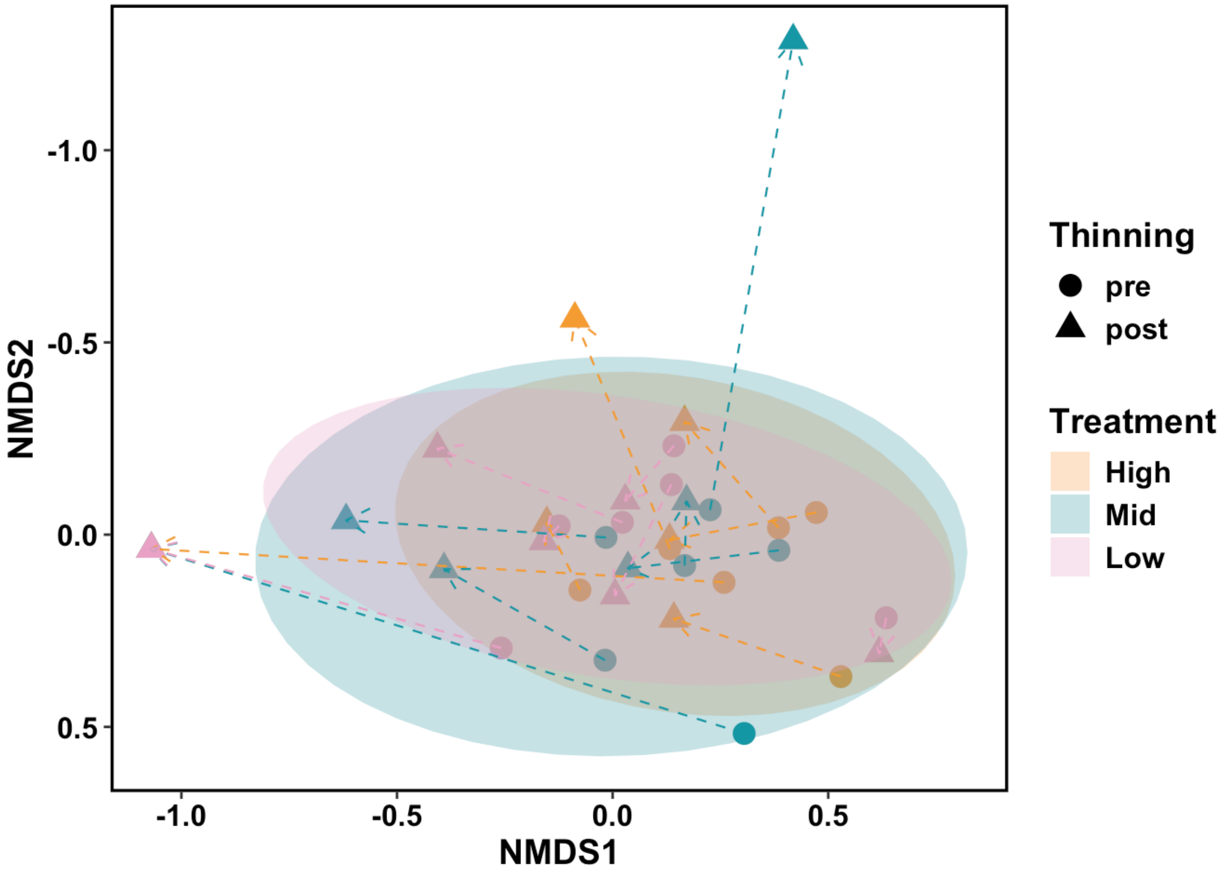


**Figure 14. Non-metric Multidimensional Scaling (NMDS) analysis illustrating the community composition differences of ant populations before and after thinning treatments, across the three treatments.** This NMDS plot is essentially identical to the previous one since it is based on the same ant population data. However, this version differentiates by color to indicate treatment levels: golden for "high", green for "mid", and pink for "low". It also includes a 95% confidence interval ellipse around the centroid of the data points for each treatment group. Arrows on the plot illustrate the shift from pre- to post-thinning conditions, indicating changes in ant community compositions.

## DISCUSSION

### Effects of environmental variables

My results demonstrate that both temperature and relative humidity significantly impacted the total abundance of other-ants in my study. Specifically, ant abundance increased with higher average temperatures and decreased with higher relative humidity. This observed positive correlation with temperature aligns with my initial expectations, reflecting the thermophilic nature of ants—organisms that thrive in relatively high temperatures (Parr and Bishop 2022). Multiple studies supported this relationship, including one by Kendrick et al. 2015, which reported a rapid increase in ant abundance and species richness as the forest floor warmed. It is important to highlight that while ants prefer higher temperatures, they do so up to a specific threshold, at which point their abundance and fitness are maximized. Exceeding this temperature threshold can impair cellular functions and significantly reduce ecological performance. Ants are highly responsive to thermal changes, affecting their metabolic rate, development stages, nest site selection, and overall ecological efficiency (Shik et al. 2019). As temperatures rise, habitats previously too cold for ants become warmer, enabling more ants to establish stable populations (Bishop et al. 2019). Collectively, these findings reinforce the critical role temperature plays in supporting the abundance of ant populations, thus contributing to the extensive body of evidence on this topic.

On the other hand, the observed negative correlation between relative humidity and ant abundance in my study does not represent a consistent pattern across the literature. For instance, Levings 1983 reported an opposite trend, with higher ant abundance during the wet seasons compared to dry ones on Barro Colorado Island, Panama. Similarly, studies in Brazil have shown higher ant population abundance during the rainy season across various forest types (Coelho and Ribeiro 2006), with one study noting ant abundance was approximately twice as high in the rainy season compared to the dry season (Silva et al. 2014). Furthermore, a meta-analysis by Queiroz et al. 2023 identified a general trend of significant reduction in ant abundance during the dry season. These contrasting observations can largely be attributed to the tropical climate of the previous study locations, where relative humidity varies dramatically between the wet and dry seasons. In contrast, our study site in Santa Cruz experiences a coastal Mediterranean climate characterized by warm, dry summers and cool, moist winters, leading to less pronounced seasonal variations in relative humidity. As such, the influence of relative humidity on ant abundance appears to be highly variable and climate-dependent. Supporting this, studies from secondary tropical dry forests in Brazil and Mexico have identified a positive association between ant abundance and the dry season (Marques et al. 2017), although other research using pitfall traps in Mexico found no clear seasonal differences in ant abundance. Additionally, a study in South Italy, which has a climate similar to our study site, reported higher ant population abundance and species richness in winter than in summer (Muscolo et al. 2021), diverging from our findings. These disparate results highlight the complex and uncertain relationship between relative humidity and ant population abundance, suggesting the influence of additional environmental factors.

While both temperature and relative humidity were significantly correlated with the total abundance of other ants before thinning, only relative humidity remined so after thinning, and their relative effects both diminished. This reduction is primarily attributable to thinning operations altering a range of environmental variables within the forest, many of which are closely linked to ant population dynamics. For instance, factors such as arthropod species richness, the prevalence of dominant tree species, and overall tree species richness have all been documented to influence ant abundance significantly (Grevé et al. 2018). Consequently, considering temperature or relative humidity in isolation results in a less pronounced correlation with ant abundance. Additionally, the observed but not statistically significant negative effect of the relative abundance of *Formica integroides* on the total abundance of other ants suggests a lack of both interference and exploitative competition among ant species within the study area. This finding indicates that competition for resources—whether direct, as in the restriction of access to food and territory, or indirect—is not a predominant interaction among the ant species sampled.

### Community composition of other ants populations

The composition of other ant population exhibited significant seasonal variations, with marked differences between the winter and spring sampling periods. This finding aligns with previous research, including studies conducted in Brazil by Miranda et al. 2022 and Marques et al. 2017, which reported significant seasonal variations in ant species composition. The primary driver behind these variations is the change in resource availability and habitat heterogeneity between seasons. Seasonal fluctuations in productivity, litter depth, resource distribution, and the phenological patterns of plants substantially influence ant assemblages. These seasonal changes affect various aspects of ant communities, including activity intensity and spatial distribution. Moreover, different ant species show varying degrees of tolerance and specialization to changing climatic conditions, which contributes to temporal variations in population composition, as noted by Leal et al. 2003. The moderately but not statistically significant difference in other ants population composition before and after thinning contrasted sharply with my expectations, as thinning typically results in substantial environmental modifications within the forest, which are anticipated to influence ant composition. Supporting this expectation, Basu 1997 observed a clear divergence in ant community composition between primary and logged forests in India, conditions that closely mirror the pre- and post-thinning scenarios in my study. This discrepancy suggests that the impact of thinning on ant populations may vary based on additional ecological or regional factors not captured in this analysis. Moreover, the scale of time could play a crucial role; while immediate effects might not be evident, long-term trends and shifts in community composition could emerge as ecosystems adjust to the altered conditions. Monitoring these changes over extended periods may reveal more pronounced trends and provide deeper insights into the temporal dynamics of ant populations following forest management interventions.

The consistent population composition of other ants across various treatments observed in this study aligns with findings by Quevedo et al. 2014 in Spain, where they reported virtually no effect of specific forestry management strategies on terrestrial ant population composition. This included control strategies (analogous to high retention in this study), selective thinning (similar to mid retention), and clear-cutting (akin to low retention). One possible explanation for the apparent lack of a clear pattern in our findings could be that the differences in environmental conditions across the canopy retention gradient were not as pronounced as initially anticipated, at least in the short term. As mentioned earlier, it is plausible that longer-term monitoring of ant populations might reveal changes in population dynamics under each thinning treatment. Such extended observation periods could provide deeper insights into the subtle ecological impacts of forestry management practices, potentially uncovering delayed or cumulative effects that short-term studies cannot detect.

### Other-ants total abundance

My results indicate a strong correlation between thinning practices and the total abundance of ants, demonstrating a statistically significant reduction following thinning compared to pre-thinning. This overall negative impact aligns with expectations, as ecosystem disturbances such as thinning typically reduce population biomass in the short term. However, the effects of thinning on ant populations are not uniformly negative. For instance, studies like Quevedo et al. 2014 reported no effect of selective logging on ant abundance, whereas Vasconcelos et al. 2000 observed a positive impact on ant populations in forested environments. These findings underscore the complex and variable nature of thinning effects, which likely result from differing forest types, climatic and weather conditions, soil types, and other environmental factors specific to each study area. Such variability suggests that the ecological consequences of thinning are highly context-dependent, suggesting a detailed understanding of local conditions when planning and implementing forest management practices.

My findings reveal a significant interaction effect between thinning and treatment on the resulting changes in ant population abundance. Specifically, the variance in ant abundance between pre- and post-thinning was most substantial under the "high" treatment, which maintains 80% of the canopy, and is considerably less under the "low" treatment, where only 20% of the canopy is retained. This pattern confirms that modifications in canopy cover due to thinning significantly affect microclimatic conditions and resource availability, thereby exerting selective pressure on ant communities Neves et al. 2013. Additionally, the results align with the hypothesis that greatly reduced canopy cover in the "low" treatment enhances sunlight penetration to the forest floor, increasing ground temperatures and potentially benefiting ant populations Grevé et al. 2018. Such an increase in temperature might counterbalance the adverse effects of thinning, leading to only minimal reductions in ant abundance. Contrary to this expectation, a study by Muscolo et al. 2021 found that a medium level of canopy retention led to significantly greater differences in ant abundance compared to both the high and low levels. This discrepancy could be explained by the regrowth of understory vegetation, which might stabilize soil moisture across all treatments and minimize variations in ground temperature. Consequently, the anticipated temperature differences across varying levels of canopy retention might not have been significant enough to impact the overall abundance of ants significantly. This inconsistency suggests that other ecological factors, such as the selection of dominant tree species, could influence ant populations. Since our thinning treatments were randomly applied within the study site, they may have resulted in an uneven distribution of major tree species across different treatments, potentially obscuring the isolated effect of canopy retention on ant dynamics.

On the other hand, seasonality significantly influenced ant population dynamics, with a notably higher abundance observed during spring compared to winter. This pattern aligns with the impact of environmental variables discussed earlier. Spring's warmer temperatures and lower relative humidity, which prevail during our sampling periods, create conditions that are conducive to higher ant activity and abundance. Furthermore, the differential impact of thinning on ant populations abundance between the seasons suggests that ant responses to habitat manipulation are modulated by seasonal dynamics. The lesser decline in ant abundance during winter may be attributed to the reduced activity and lower baseline abundance during colder months, which could make the immediate effects of thinning less apparent. The higher $R^2$ value for seasonality compared to thinning substantiates the dominance of natural seasonal cycles over anthropogenic disturbance in regulating ants abundance in the short term of this study. This finding suggests that while management practices such as thinning do alter habitat structure and resource availability, the intrinsic seasonal rhythms play a more critical role in shaping ecological communities.

**Ants population species richness**

Similar to total abundance, ant species richness significantly declined following thinning, highlighting the detrimental impact of this intervention on ant populations. This observation is supported by Basu 1997, who found that primary, closed canopy forests hosted a higher species richness compared to forests with newly logged, open canopies in India. Despite this general decline, my study revealed no significant interaction between thinning and treatment types; the reduction in ant species richness was uniform across all three treatments. The glmm.hp analysis underscores this effect, showing that thinning alone accounts for nearly all observed changes in species richness ($R^2 = 99.78$), with treatment differences having minimal impact ($R^2 = 0.22$).This uniform reduction contrasts with the variable interaction effects observed in ant abundance, likely due to the inherently low species diversity at the sampling sites. In environments with limited species pools, dramatic changes in species richness are less likely following treatment because the presence of a species—regardless of individual count—counts equally towards richness. Given the low diversity at my sampling sites, where *Formica integroides* dominates alongside only four other significantly present species, no noticeable change in species richness was observed regardless of the thinning treatment. This pattern echoes the findings of Dáttilo and Dyer 2014, who noted that canopy openness did not significantly affect ant species richness. The limited species pool essentially caps the potential for observing varied responses in species richness across different thinning treatments.

The analysis of seasonal effects confirmed a significant decrease in ant species richness during winter compared to spring, underscoring the influence of seasonal dynamics on biodiversity. Despite the overall decline, the reduction in species richness from pre- to post-thinning showed no significant seasonal variation, suggesting that the initially limited species diversity at my sampling sites might mask any potential seasonal effects. Nevertheless, both season and thinning proved to be significant predictors of species richness, with comparable $R^2$ values. This finding indicates that although thinning substantially impacts ant species dynamics, seasonal conditions are equally pivotal. These findings highlight the complex interplay between anthropogenic management practices and natural seasonal cycles in determining biodiversity outcomes.

## Limitations

### Methodological limitations

A primary limitation of my analysis is the arbitrary use of 25 as a threshold for measuring *Formica integroides* abundance. In the absence of existing research to guide an appropriate cap, we set a limit of 25 individuals per pitfall trap per sampling period. This decision means that abundance was measured binarily, which could significantly influence the observed population dynamics of *Formica integroides.* Future research should focus on establishing a scientifically justified threshold that accurately reflects ecological reality and affects how results are interpreted.

### Environmental survey constraints

Additionally, due to constraints of time and resources, our survey of environmental conditions at the sampling sites was not as comprehensive as necessary, both before and after the thinning process. This limitation restricts our understanding of how various environmental factors might influence ant populations. Expanding future surveys to include a broader range of environmental variables, such as dominant tree species, would enable more nuanced insights into how these factors individually and collectively impact ant population dynamics.

### Data collection and analysis

Moreover, while ongoing efforts to collect ant samples continue, the analysis currently includes only data from the first year post-thinning. Identifying ants to the species level is a time-consuming and challenging process, compounded by the large number of specimens collected. Extending the analysis to include long-term data would provide a clearer picture of population trends and their interactions with environmental changes over time. Employing statistical tools like time series analysis could offer further insights into how ant populations recover following forest thinning and help detect spatial and temporal patterns across the ant communities.

### Future research directions and broader implications

Future studies should aim to refine data collection methods to reduce the labor intensity of ant identification and increase the comprehensiveness of environmental assessments. Developing and validating a more accurate threshold for *Formica integroides* and other species would enhance the reliability of population studies. Additionally, incorporating advanced statistical analyses and longer monitoring periods will enrich our understanding of the ecological impacts of forest management practices on ant populations. Overall, what we found emphasizes the need for forest management and conservation strategies to consider the temporal aspects of animal ecology. Understanding the seasonal patterns of target species can lead to more effective timing and implementation of management actions, potentially mitigating adverse impacts while enhancing habitat conservation outcomes.

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# APPENDIX

**Figure A1.** Images of all ant species from this study. All images source: AntWiki.

*Formica integroides*

*Formica accreta*

*Stenamma sequoiarum*

*Temnothorax-nevadensis*

*Aphaenogaster occidentalis*

*Prenolepis imparis*

*Camponotus laevigatus*

*Liometopum luctuosum*

*Camponotus vicinus*