UNIVERSITY OF CALIFORNIA SAN DIEGO

Macronutrient preferences and stable-isotope variation of the Argentine ant across multiple habitats

A Thesis submitted in partial satisfaction of the requirements
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in

Biology

by

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The Thesis of Grace Jurgela is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

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DEDICATION

To my parents, brother, friends, and everyone else that supported my journey along the way. Thank you.

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ACKNOWLEDGEMENTS

I would like to thank Dr. David Holway for his guidance and support throughout the time I've spent in his lab. I would also like to thank Dr. Jon Shurin, Dr. Carolyn Kurle, and Dr. James Nieh for their support as well. This project would not have been possible without the help and support of my fellow graduate peers and undergraduate volunteers. Many thanks to Kayleigh Cassidy, Eleanor Fausett, Sky Kezmoh, Elizabeth Spencer, Vaneh Baghdassarian, William Cummins, Chaewon Ham, and Mads Kelly. Extra special thanks to Eddie Correra and Alex Jurgela for their prolonged hours in the lab and field respectively. A final special thank you to Christopher Winters, without whom I would not be where I am today.

This thesis contains unpublished material that is being prepared for submission for publication of the material. The thesis author was a coauthor for this material with Holway, David. The thesis author was the primary author of this thesis.

ABSTRACT OF THE THESIS

Macronutrient preferences and stable-isotope variation of the Argentine ant across multiple habitats

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Grace Jurgela

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Professor David Holway, Chair

The compensation hypothesis predicts that the value of a nutrient increases with its scarcity in the environment. Organisms will thus seek out limiting nutrients in order to maximize their growth. In this study, we evaluated this hypothesis by examining Argentine ant (*Linepithema humile*) foraging preferences in three different habitats (intertidal beach, riparian woodland, and scrub) in southern California. We used standardized baiting (protein, carbohydrate) transects and stable isotope analysis to determine if short-term behavioral responses at baits reflect longer-term patterns of resource assimilation. Habitats were replicated in eight blocks of each of the three habitats. Ants showed strong preferences for carbohydrate

baits in all three habitats, but the δ15N values significantly differed as a function of habitat. The δ15N values of the Argentine ant were highest in beach habitats, reflecting assimilation of marine-derived resources, intermediate in riparian woodlands, and lowest in scrub. Carbohydrate preferences exhibited by the Argentine ant across the environmental gradient reflect the well-known preferences for sugar exhibited by this species and more generally reflect how short-term behavioral responses may not always reflect longer patterns of resource assimilation.

Introduction

Introduced species attribute much of their success to lack of factors that limit their populations. Macronutrient limitations can exert pressure on introduced species and limit growth through bottom-up control (Tsang et al. 2020). To circumvent this and maximize their success, invading organisms are predicted to follow the principles of the Compensation Hypothesis (Kaspari & Yanoviak 2001). Utilizing the idea of Liebig's law of the minimum, this nutrient limitation hypothesis predicts that organisms will favor foraging on the most limiting nutrient in their environment in order to maximize growth or performance (Liebig 1855; Kaspari & Yanoviak 2001; Davidson 2005). Ability to adapt foraging techniques to exploit nutrients that vary in abundance by habitat type is a reason why invaders are able to see widespread success.

The diverse foraging strategies of the Argentine ant (*Linepithema humile*) are a major reason why this species is such a successful invader (Markin 1970; Grover et al. 2007; Lach et al. 2010). This generalist species is a scavenging predator but shows strong preferences for carbohydrates that it acquires from honey dew, floral nectar, and extrafloral nectar (Way 1963; Markin 1970, Ludka et al. 2015, Hanna et al. 2015). Adapting behaviors to exploit the most limiting nutrients may contribute to invasion success (Ricciardi et al. 2013). Carbon and nitrogen are essential macronutrients for ants, as nitrogen-rich protein is necessary for larval growth while carbon-rich carbohydrates sustain worker metabolism. Macronutrient imbalances can affect colony demographics (Markin 1970; Grover et al. 2007). This study considered Argentine ant foraging behavior across intertidal, coastal sage scrub, and riparian ecosystems across a 30-km stretch of coastal San Diego County to determine if Argentine ants altered their foraging behavior based on macronutrient availability in different habitat types.

These habitats were selected due to a hypothesized macronutrient availability gradient, allowing for potential diversity in feeding behaviors. Due to the high abundance of detritus and marine wrack in intertidal systems, there is potential for high nitrogen abundance in this system (Winters et al., *In review*). The lack of primary producers, and thus nectar and honeydew producing insects, presumably leaves this system carbohydrate deficient. Inversely, the abundance of honeydew producing insects in highly productive riparian systems may leave this habitat with a carbohydrate abundance. Coastal sage scrub was implemented as a control in this study, as there was no evidence to believe that there is an extreme deficiency or abundance of either nitrogen or carbon availability in this system. If this macronutrient gradient exists within these systems, the Argentine ant may alter its feeding preferences to reflect the C:N ratio of available resources in each habitat.

In this study, investigations were conducted through the combined use of behavioral assays (baiting experiments) and stable isotope analysis to determine long- term nutrient assimilation. We predict that when the Argentine ant is given the choice between protein and carbohydrate, it will preferentially recruit to the most limiting of these two macronutrients (Compensation Hypothesis). Longer term imbalances in macronutrient availability, however, should be reflected in the δ15N values for this species. Given that most sources of carbohydrates come from low trophic levels (primary producers and herbivores), the δ15N values should be lowest in habitats with the most consistent carbohydrate availability (Tillberg et al, 2007, Menke et al. 2010, Wilder et al. 2012). We thus predict that ants in beach habitats will have elevated δ15N while ants in the nitrogen deficient riparian habitats will have lowered δ15N. Finally, we predict that the trend preferences observed in the behavioral assays will be reflective of the limiting nutrient determined via stable isotope analysis.

Methods

To determine how the macronutrient preferences of the Argentine ant change across different habitat types, we measured recruitment to protein and carbohydrate baits at 24 sites in coastal San Diego County (Table 1A). Sites were divided into eight (spatial) blocks with each block including a beach site, a riparian site, and a scrub site. At each site we placed 30 baits in a transect in which we alternated carbohydrate (n = 15) and protein (n = 15) baits. Individual baits were separated by at least 10 m. Baits were placed level and on the ground in open areas (i.e., minimal leaf litter) for 60 min. Baiting at intertidal sites occurred above the median high tide line (as in Winters et al., *in review*). All baiting occurred in October 2023 between 3 - 6 pm and within temperatures of 10 to 30° C (as determined optimal in Markin 1970).

Each bait was placed in an uncapped 50-ml centrifuge tube. Carbohydrate baits consisted of two cotton balls saturated in a 20% weight-on-weight sucrose solution. The cotton balls were inserted into the bottom of each tube with the use of forceps. Protein baits consisted of a 20% weight-on-weight protein powder (Garden of Life (unflavored raw organic protein)) solution. For each type of bait the exposed area over which ants recruited was approximately the same. After 60 min in the field, we capped the tube of each bait. 707 of 720 total baits were recovered and placed in a freezer at 0^{o}C until processing, which involved counting all of the ants in each tube.

To determine if habitat-specific macronutrient preferences reflect longer-term differences in protein and carbohydrate availability, we used stable isotope analysis. Samples were collected in October 2023 at each of the 24 sites used in the baiting experiment (Table 1A). At each site we collected foraging Argentine ant workers (n = > 40) as well as perennial plants (lemonadeberry (*Rhus integrifolia*) and California buckwheat (*Eriogonum fasciculatum*)) at riparian and scrub

sites, and giant kelp (*Macrocystis pyrifera*) and surf grass (*Phyllospadix* sp. (*Zosteraceae*)) at intertidal sites. At riparian and scrub sites, plant samples were collected from new growth of 1-4 individual plants of each species. Intertidal samples were collected from freshly washed up primary producers. These were rinsed with distilled water in the lab to remove sand. Samples were kept in a cooler in the field until they were moved to a 0ºC degree freezer within 3 h of collection. For preparation, we removed the gasters of the ants. All samples were desiccated in a drying oven at 55-60º C at least 48 hours. Samples were then homogenized with mortar and pestle and a homogenized mass of 0.8 - 1.1 mg (ants) or 2.0 - 3.0 mg (autotrophs) was placed in individual 5 x 9 mm tin capsules and sent to the University of California Davis Stable Isotope Facility for stable isotope analysis.

All data analysis was conducted in R (R Core Team 2021). We used mixed effects models to test if macronutrient preferences and δ15N values depended on habitat type. In these analyses, spatial blocks (n = 8) of beach, scrub, and riparian habitat were treated as a random effect. For ant recruitment, we considered the proportion of tubes of each bait type with ants at each site as the response variable. In separate analyses, we assessed three levels of ant activity: the proportion of tubes with ants, the proportion of tubes with ants in which more than 10 ants were present, and the proportion of tubes with ants in which more than 50 ants were present. These latter two response variables can be interpreted as different levels of recruitment that reflect increasing ant preferences. For the analysis of stable isotope data, we first consider how naturally occurring δ15N values varied as a function of habitat type. Second, we used perennial plant material collected at riparian and scrub sites to account for site-level variation in δ15N values (Roeder and Kaspari 2017). To obtain baseline corrected δ15N values, we subtracted the mean δ15N value of the plant material (the average of the mean lemonade berry and mean buckwheat

samples) from each site from the respective δ15N value of the ants. California buckwheat was not collected at Penasquitos Creek; for this site we used the mean buckwheat δ15N value for all other sites. Although baseline corrections have limitations (Kjeldgaard et al. 2021), δ15N plant values are based on samples replicated within and among species to ensure representative estimates of δ15N plant values for each site. The δ15N values for the Argentine ant at beach sites, however, could not be corrected.

Results

Sites were selected based on the presence of the Argentine ant, and this species was found at over 93% of baits that had ant activity (370/395). About 7% of baits (25/395) contained ants aside from the Argentine ant and about 6% contained other arthropod bycatch (22/395). Baits attracted the Argentine ant at all sites, but this species was present at more baits at riparian and scrub sites compared to beach sites (Figure 1A; linear mixed effects model (effect of habitat type): $t = 4.288$, df = 38, $P = 0.000119$). For subsequent analyses on recruitment, we only considered baits at which ants were present. For baits with ants at which 10 or more workers were present, recruitment was independent of bait type (linear mixed effects model (effect of macronutrient): $t = -1.145$, df = 38, $P = 0.259$) but varied across habitat with recruitment at riparian and scrub sites higher than that at beach sites (Figure 1B; linear mixed effects model (effect of habitat type): $t = 4.430$, df = 38, $P < 0.00001$). For baits with ants at which 50 or more workers were present, however, we observed a slightly different pattern. Recruitment again varied across habitat with recruitment at riparian and scrub sites higher than that at beach sites (Figure 1B; linear mixed effects model (effect of habitat type): $t = 3.228$, df = 38, $P = 0.00257$). This higher level of recruitment also revealed that more carbohydrate baits had high levels of recruitment compared to protein baits (linear mixed effects model (effect of macronutrient): $t = -2.267$, df = 38, $P = 0.02916$) across all habitat types.

Naturally occurring variation in stable isotope values for the Argentine ant revealed substantial variation (c. 7 ‰) in the δ15N values across the three habitats (Figure 2A). Ants from intertidal beach environments had the highest values δ15N values, whereas ants from scrub environments had the lowest δ15N values. A comparison of corrected δ15N values revealed that

these values were significantly higher at riparian sites than at scrub sites (Figure 2B; linear mixed effects model: t = -4.608, df = 7, P = 0.00246).

Discussion

The proportion of baits that observed Argentine ant recruitment were found to have similar activity at both bait types at scrub and riparian sites (Figure 1B). Intertidal beach sites saw significantly less activity than the other habitats. At beach sites, carbohydrate baits saw more recruitment than protein baits (Figure 1). This finding is consistent with the compensation hypothesis; however, reduced overall activity at beach sites must be taken into consideration (Figure 1A). This trend was similar for baits at beach sites that experienced heavy recruitment, as seen in Figure 1C. However, at scrub and riparian habitats, we observed higher recruitment activity at carbohydrate baits compared to protein baits in both habitats. The δ15N signatures of ants at scrub habitats were found to be lower than those at riparian habitats (Figure 2). This finding was somewhat unexpected, as it suggests the ants in scrub regions may be assimilating more carbohydrates than they do in riparian habitats. As a result, our findings are not consistent with the belief that riparian Argentine ants are as nitrogen limited as previously thought. The role of the scrub and riparian habitats within the hypothesized macronutrient gradient of carbon to nitrogen availability is refuted, as the findings do not show evidence for nitrogen limitation in riparian habitats (Figure 2).

Preference for carbohydrate baits at beach habitats are consistent with findings in other carbohydrate limited habitats (Kaspari et al. 2012). Brown food web dominated habitats host an abundance of microbial activity which are responsible for carbohydrate limitation (Kaspari et al. 2012). For green food web dominated systems, studies have also supported the compensation hypothesis through observed preference for protein baits at nitrogen deficient systems, such as monoculture plantations (Tsang et al, 2020), and carbohydrate abundant rainforest canopies

(Kaspari & Yanoviak 2001). However, this is not something that was observed in this study, as no preference for protein baits over carbohydrates were observed. Our findings were more consistent with other studies that have found widespread preference for carbohydrate baits through conduction of cafeteria experiments seasonally and spatially (Bezdekova et al 2024).

Stable isotope observations in other studies have been consistent with the compensation hypothesis (Tsang et al, 2020). Findings in these studies demonstrate attraction to the limiting nutrient, where ants that were attracted to protein baits were observed to have lower δ15N (Tsang et al, 2020). Our findings are in conflict with these results, as the Argentine ants in scrub habitats with lowest δ15N did not have significant preference for recruiting to protein (Figure 2; Figure 1B). In fact, this trend was found to be opposite if proportion of tubes with heavy recruitment was considered, where there was a preference for low δ15N ants to exploit carbohydrate baits (Figure 1C). A potential reason for this may be due to the reduction of exoskeletal development in an environment where aggressive interactions are reduced (Peeters et al, 2017). If Argentine ants in scrub environments are experiencing fewer interactions with prey and competitors, this may be reflected in minimized energy investment in the exoskeleton. This may in turn be reflected in reductions in assimilated carbon and nitrogen levels, as exoskeleton development requires substantial amounts of protein. (Vincent & Wegst, 2004). However, it is unclear why this trend would not extend to Argentine ants in riparian zones.

The results of the stable isotope analysis are not what was expected from the short-term behavioral assays conducted by baiting. Since the results of the baiting experiment showed that Argentine ant activity at scrub sites behaved similarly to riparian zones (Figure 1), it would have

been expected for the ants from these habitats to have similar δ15N values. This is not supported by ants from scrub habitats having the lowest assimilation of δ15N in their tissue (Figure 2). It would be expected that scrub ants would have been attracted to the protein baits based on these results similarly to Tsang et al (2020), but this was not what was observed. This study did not find conclusive evidence for the compensation hypothesis, as nitrogen deficient ants were not found to strategically forage their limiting nutrient as expected (Mayntz et al. 2005). The baiting results provide evidence that scrub habitats may not be as nitrogen limited as expected from the stable isotope results, while also showing that riparian habitats are not nitrogen limited as was initially hypothesized.

The findings of this study are an example of behavioral assays not being representative of long term trends in nutritional ecology. Many studies utilize short term assays to estimate long term trends (Bezdeckova et al. 2024; Law & Parr 2020), or stable isotope analysis exclusively (Davidson 2005). Combining these methods can give a more well-rounded understanding of processes at work (Kaspari & Yanoviak 2012; Tsang et al. 2024). Fleshing these experiments with additional methods such as stable isotope analysis for a longer term understanding of nutritional assimilation is necessary to reach conclusions in nutritional ecology. Further studies on this topic should consider if the trends observed are replicable through time and in drier years. Future studies should consider integrating behavioral assays with stable isotope analysis.

Acknowledgements

I would like to thank Dr. David Holway for his guidance and support throughout the time I've spent in his lab. I would also like to thank Dr. Jon Shurin, Dr. Carolyn Kurle, and Dr. James Nieh for their support as well. This project would not have been possible without the help and support of my fellow graduate students and undergraduate volunteers. Many thanks to Kayleigh Cassidy, Eleanor Fausett, Sky Kezmoh, Elizabeth Spencer, Vaneh Baghdassarian, William Cummins, Chaewon Ham, and Mads Kelly. Extra special thanks to Eddie Correra and Alex Jurgela for their prolonged hours in the lab and field respectively. A final special thank you to Christopher Winters, without whom I would not be where I am today.

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Tables

Table 1A: Table of site locations and coordinates at which baiting and collection for stable isotope analysis occurred

Beach Sites	**Beach Coordinates**	**Scrub Sites**	**Scrub Coordinates**	**Riparian Sites**	**Riparian Coordinates**
Tourmaline Beach	32.805759386690074, -117.2618749300406	Kate Sessions	32.813295115891577, -117.23747282108098	Tecolote Creek	32.810404, -117.196121
Windansea Beach	32.831796726518 3, -117.28105017656917	La Jolla Natural Park	32.843404897697255, -117.26147294479583	San Clemente Creek	32.842128, -117.213693
Scripps Pier	32.866259170909764, -117.2541718765167	Skeleton Canyon	32.867924875850 74, -117.24734516538533	Rose Creek	32.860695, -117.210517
Black's Beach	32.880983307677718, -117.25200300739687	UCSD Ecological Park	32.887211482706691, -117.23744480219551	Penasquitos Creek	32.905528, -117.220087
Del Mar State Beach	32.962468925700153, -117.26989405440646	Crest Canyon	32.953010800571924, -117.25309487688978	Carmel Creek	32.940213, -117.214059
Fletcher's Cove	32.991506463346616, -117.27131655858278	San Dieguito Park	32.999001498026 83, -117.234740776 4287	San Dieguito River	33.007063, -117.193888
Swami's Beach	33.034051073566, -117.29549912957974	Manchester Preserve	33.030470035471 89, -117.25146466343867	Escondido Creek	33.021714, -117.246428
Moonlight Beach	33.048360532553 48, -117.29929247404984	Oak Crest Park	33.044941770391 03, -117.26579534133154	Encinitas Creek	33.064351, -117.258535

Figures

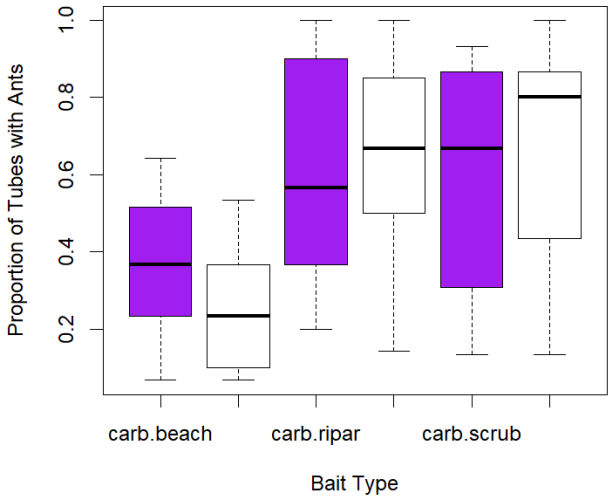

Figure 1A: Proportion of tubes that had ant activity at all. Purple bars represent carbohydrate based baits while white represent protein baits. Beach activity was lower than that at the other sites overall, with activity at protein baits being lower than carbohydrate. Utilizing a mixed effects model, it was found that there was a strong effect of habitat ($P < 0.0001$), but no significant effect of bait type on activity after variance for triad was taken into consideration.

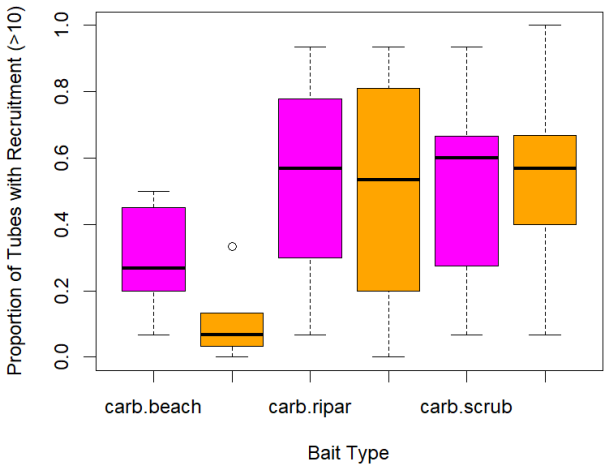

Figure 1B: Proportion of tubes that had recruitment defined as >10 ants per bait. Pink represents carbohydrate based baits while orange represents protein based baits. Recruitment was lowest at protein baits at beach sites, which supports the hypothesis. However, overall low activity at beach baits may suggest another factor may be at play. Mixed effect model demonstrated that there was a strong effect of habitat type (P = 9.937e-6), but there was no significant effect of bait type on recruitment.

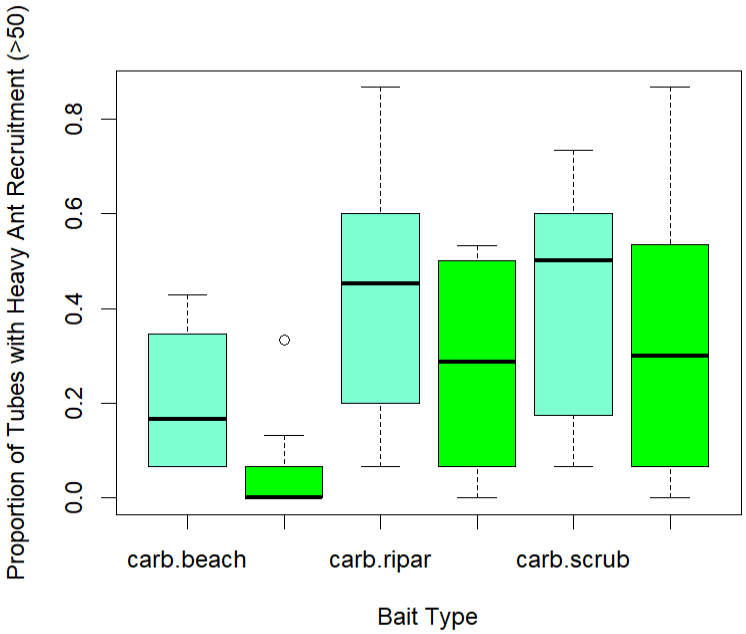

Figure 1C: Boxplot demonstrating proportion of baits that saw heavy recruitment (defined as >50 ants per tube). Teal bars are representative of carbohydrate baits and green bars are representative of protein baits. Heavy recruitment was lowest at protein baits at beach sites. Similarly to analysis done for recruitment (>10), this may be due to another factor at play, such as lower overall abundance of ants at this habitat type. There was also a significant effect when environment was tested as a fixed effect using a mixed effects model ($P = 0.0008792$). Heavy recruitment was also found to be significantly higher at carbohydrate baits for all sites ($P = 0.0216997$).

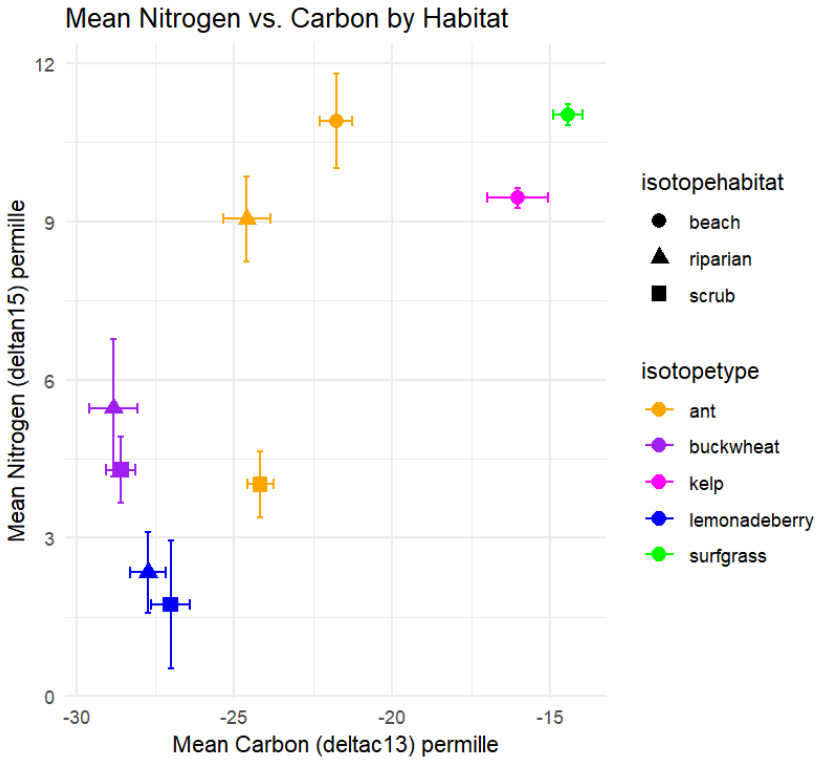

Figure 2A: Mean δ15N and δ13C values for each isotope sample type plotted in a bivariate plot with standard error bars. δ15N values were found to be statistically significant from each other for the fixed effects of sample type and habitat type ($P < 0.05$). Beach ants were found to have a higher δ15N than both riparian and scrub ants, consistent with predictions based on high nitrogen availability in this habitat. Riparian ants were higher in δ15N than hypothesized and scrub ants were lower in δ15N than hypothesized.

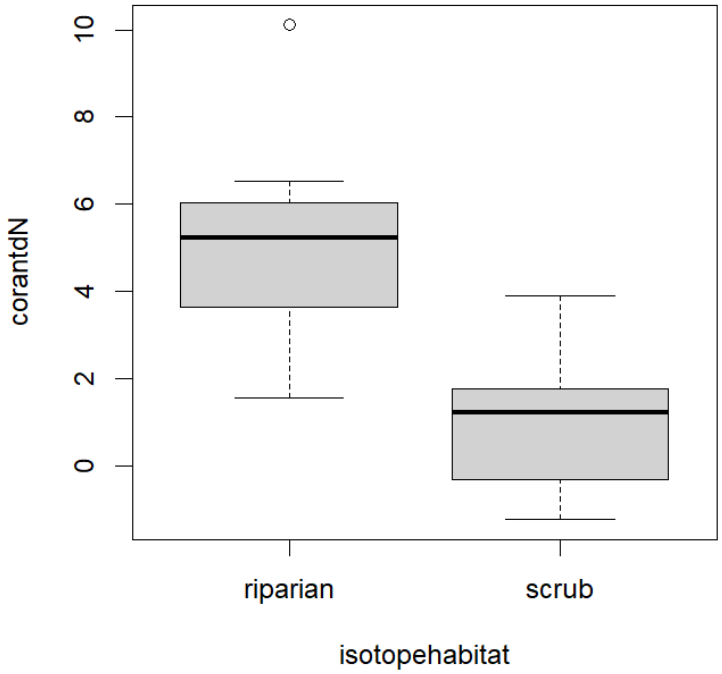

Figure 2B: Corrected δ15N (post adjustment for spatial variance calculated through subtraction of mean buckwheat and lemonade berry by site from respective ant δ15N) by habitat

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